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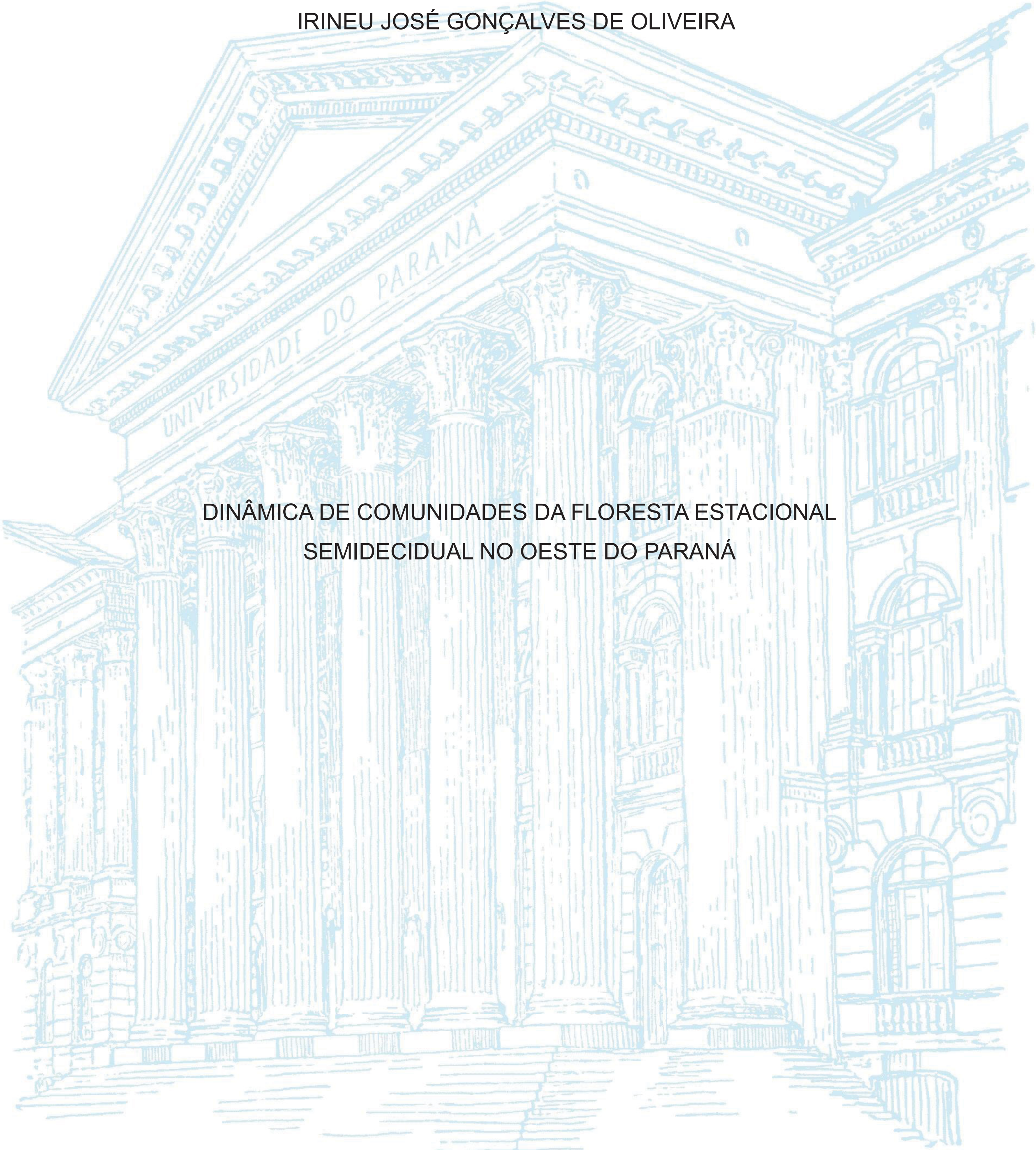
IRINEU JOSÉ GONÇALVES DE OLIVEIRA



DINÂMICA DE COMUNIDADES DA FLORESTA ESTACIONAL SEMIDECIDUAL NO OESTE DO PARANÁ

CURITIBA
2024

IRINEU JOSÉ GONÇALVES DE OLIVEIRA

DINÂMICA DE COMUNIDADES DA FLORESTA ESTACIONAL SEMIDECIDUAL NO OESTE DO PARANÁ

Dissertação apresentada como requisito parcial à obtenção do grau de Mestre em Botânica, no Curso de Pós-Graduação em Botânica, Setor de Ciências Biológicas, da Universidade Federal do Paraná.

Orientador: Prof. Dr. Victor Pereira Zwiener

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TERMO DE APROVAÇÃO

Os membros da Banca Examinadora designada pelo Colegiado do Programa de Pós-Graduação BOTÂNICA da Universidade Federal do Paraná foram convocados para realizar a arguição da Dissertação de Mestrado de **IRINEU JOSÉ GONÇALVES DE OLIVEIRA** intitulada: **Dinâmica de comunidades da floresta estacional Semidecidual no Oeste do Paraná**, sob orientação do Prof. Dr. VICTOR PEREIRA ZWIENER, que após terem inquirido o aluno e realizada a avaliação do trabalho, são de parecer pela sua APROVAÇÃO no rito de defesa.

A outorga do título de mestre está sujeita à homologação pelo colegiado, ao atendimento de todas as indicações e correções solicitadas pela banca e ao pleno atendimento das demandas regimentais do Programa de Pós-Graduação.

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RESUMO

As florestas tropicais abrigam uma parcela significativa da biodiversidade global e desempenham um papel crítico na regulação do clima e no sequestro de carbono. Infelizmente, atividades antropogênicas impactaram irreversivelmente essas áreas. Enquanto no Brasil a devastação das áreas de floresta se iniciou em 1500, com a chegada dos colonizadores europeus, no estado do Paraná essa destruição é mais recente, iniciada apenas na década de 1920. A maior parte das florestas do estado foi derrubada e transformada em áreas agricultáveis. O Parque Nacional do Iguaçu (PNI) foi um dos poucos remanescentes dessa onda de destruição no estado. Nosso estudo buscou analisar as florestas do PNI, ao longo de onze anos de monitoramento para entender as dinâmicas demográficas e a variação espaço temporal da diversidade beta das comunidades de espécies arbóreas. A coleta de dados foi realizada quatro vezes entre 2011 e 2022 em 21 parcelas permanentes instaladas no PNI. Foram avaliadas riqueza, abundância, área basal total, índices de diversidade e equidade, e variáveis demográficas (mortalidade, recrutamento e crescimento). Também avaliamos a variação da beta diversidade entre os locais e os anos para inferir os mecanismos de mudança na biodiversidade. Observamos uma redução na riqueza, abundância individual, diversidade e equidade, um aumento na mortalidade e uma diminuição no recrutamento ao longo dos anos. O crescimento diminuiu nos primeiros anos (2011 a 2013) e se estabilizou posteriormente. A substituição foi o componente que mais explicou a diversidade beta espacial encontrada. A diversidade beta temporal revelou que as dissimilaridades entre os anos, inicialmente dominadas por ganhos nas ocorrências/abundâncias de espécies, gradualmente foram substituídas por perdas ao longo do tempo. As perdas superaram os ganhos no último período (2015–2022). Também observamos heterogeneização biótica no último período. A mortalidade de árvores desempenhou um papel crucial nas mudanças da comunidade, e essas reduções populacionais têm tendencia a aumentar em razão da maior incidência de eventos climáticos extremos devido às mudanças climáticas. Nossos resultados alertam para uma possível perda de biodiversidade em um dos remanescentes mais importantes da Mata Atlântica.

Palavras-chaves**:** Mata Atlântica; variáveis demográficas; florestas maduras; dinâmica de comunidades; beta-diversidade.

ABSTRACT

Tropical forests harbor a significant portion of global biodiversity and play a critical role in climate regulation and carbon sequestration. Unfortunately, anthropogenic activities have irreversibly impacted these areas. While forest devastation in Brazil began in 1500 with the arrival of European colonizers, in the state of Paraná, this destruction is more recent, starting only in the 1920s. Most of the state's forests were cut down and converted into agricultural areas. Iguaçu National Park (INP) was one of the few remnants of this wave of destruction in the state. Our study aimed to analyze the forests of INP over eleven years of monitoring to understand the demographic dynamics and spatio-temporal variation of beta diversity in tree species communities. Data collection was carried out four times between 2011 and 2022 in 21 permanent plots installed in the INP. We assessed richness, abundance, total basal area, diversity and evenness indices, and demographic variables (mortality, recruitment, and growth). We also evaluated the variation in beta diversity between locations and years to infer the mechanisms of biodiversity change. We observed a reduction in richness, individual abundance, diversity, and evenness, an increase in mortality, and a decrease in recruitment over the years. Growth declined in the early years (2011 to 2013) and stabilized thereafter. Replacement was the component that most explained the spatial beta diversity found. Temporal beta diversity revealed that dissimilarities between years, initially dominated by gains in species occurrences/abundances, were gradually replaced by losses over time. Losses outweighed gains in the last period (2015–2022). We also observed biotic heterogenization in the last period. Tree mortality plays a crucial role in community dynamics, and these population reductions are likely to increase due to the higher incidence of extreme climatic events driven by climate change. Our results warn of a possible loss of biodiversity in one of the most important remnants of the Atlantic Forest.

Keywords: Atlantic Forest, Beta-diversity, Demographic variables, Old-growth Forest, Community dynamics.

SUMÁRIO

1 INTRODUÇÃO E OBJETIVO GERAL

A Mata Atlântica, considerada um hotspot da biodiversidade (Bellard *et al.*, 2014; Myers *et al.*, 2000) em razão da sua pungente diversidade e alto grau de endemismo, sofreu danos irreversíveis em razão das atividades humanas. Esse bioma já perdeu grande parte da sua cobertura vegetal original (Rezende *et al.*, 2018) em virtude da expansão agrícola, industrialização e urbanização (Ribeiro *et al.*, 2011). O grau de destruição variou conforme a região, sendo a Floresta Estacional Semidecidual (FES) — caracterizada por indivíduos que perdem as folhas na estação seca (IBGE, 2012) — uma das mais impactadas, atualmente com apenas de 7% de vegetação remanescente (Ribeiro *et al.*, 2009).

Grande parte do desmatamento da Mata Atlântica brasileira remonta a chegada dos colonizadores europeus no país em 1500 (Ribeiro *et al.*, 2011). No estado do Paraná, entretanto, o desmatamento se iniciou de forma mais tardia, apenas na década de 1920, em razão da expansão cafeeira para oeste (Gubert-Filho, 2010). A sua degradação foi relativamente rápida, visto que essas florestas estavam localizadas em terrenos planos e solos férteis (Santos *et al.*, 2006) e as regiões desmatadas foram convertidas em áreas agrícolas. Apesar dos esforços conservacionistas discutidos ao longo desse período, tanto por políticos quanto por naturalistas, a busca pelo crescimento econômico prevaleceu sobre qualquer tentativa de conservação da vegetação (Gubert-Filho, 2010). Entre as poucas áreas remanescentes dessa onda de destruição encontra-se o Parque Nacional do Iguaçu, considerado um patrimônio natural da humanidade (UNESCO World Heritage Centre, n.d.).

Localizado no oeste paranaense, o Parque Nacional do Iguaçu apresenta área total de 185.262,50 ha, com perímetro de 420 km² e é considerado um dos maiores remanescentes da Mata Atlântica (Ribeiro *et al.*, 2009). O parque apresenta uma gradiente de altitude que vai de 100 a 750 m sobre o nível do mar, aumentando conforme se distancia do Rio Iguaçu (Souza *et al.*, 2017). Nas regiões mais altas, a vegetação típica de FES dá lugar a um ecótono com a Floresta Ombrófila Mista (Souza *et al.*, 2019) — subformação caracterizada pela presença de *Araucaria angustilofia* (Bertol.) Kuntze (IBGE, 2012) e que ocorre nas regiões entre 800 e 1200m de altitude (Roderjan *et al.*, 2002). A presença dessa espécie nas regiões mais altas é um exemplo dos processos organização das comunidades ecológicas que regem composição da biodiversidade.

Os processos de organização das comunidades retratam a ideia de que filtros como a dispersão, o ambiente abiótico e as interações bióticas restringem e ditam a estrutura e composição das comunidades (Götzenberger *et al.*, 2012). Tais processos ocorrem em diferentes escalas espaciais, e diferentes princípios se aplicam a diferentes escalas (Leibold *et al.*, 2004). Na escala regional, fatores como o clima, o pool de espécies, especiação, extinção, migração e distúrbios naturais são relativamente mais importantes. Na escala da paisagem, a vegetação é principalmente influenciada pelo histórico de uso da terra, a cobertura vegetal, a conectividade, a quantidade de borda e interior de florestas, as dinâmicas populacionais de herbívoros, polinizadores e dispersores de sementes (Arroyo-Rodríguez *et al.*, 2017). Já na escala local, as características do solo, o regime de distúrbios, o tamanho e forma do fragmento, o microclima (luz, temperatura e umidade) e as interações bióticas (competição, predação e patógenos) são os principais processos que influenciam a vegetação (Arroyo-

Rodríguez *et al.*, 2017; Schupp; Fuentes, 1995). Na ausência de perturbações ambientais, a substituição dessas espécies ocorre de forma autônoma, podendo ser predita através do pool regional de espécies com potencial invasor de fragmentos vizinhos (O'Sullivan; Terry; Rossberg, 2021). Distúrbios naturais, como a queda de árvores, influenciam a composição de espécies dependendo da intensidade e da localização do distúrbio (Sheil; Burslem, 2003). Já as perturbações antrópicas, em especial as mudanças climáticas, são responsáveis por substituições globais ao longo do tempo em diversos ambientes (Dornelas et al., 2014). Essas substituições ao longo do espaço e do tempo podem, em parte, serem observadas através da diversidade beta (Baselga, 2010; Legendre, 2014, 2019; Socolar *et al.*, 2016).

Os ambientes naturais expostos a danos podem experimentar processos de aumento ou diminuição da diversidade beta, dependendo dos fatores envolvidos (Arroyo-Rodríguez *et al.*, 2017; Lôbo *et al.*, 2011; Socolar *et al.*, 2016) e da escala em que é analisada (Barton *et al.*, 2013). A homogeneização biótica (diminuição da diversidade beta com o tempo) ocorre com a substituição de espécies endêmicas e especialistas por espécies pioneiras, geralmente mais generalistas e de ampla distribuição geográfica (Lôbo *et al.*, 2011) podendo levar a uma perda de funções e serviços ecológicos (Filgueiras *et al.*, 2021; Tabarelli; Peres; Melo, 2012). O aumento da diversidade beta, também pode ser causada por impactos, como a perda de conectividade entre fragmentos, que impede a troca de espécies, reduz as populações e consequentemente aumenta a diferenciação entre os fragmentos, principalmente na escala local (Arroyo-Rodríguez *et al.*, 2013). O entendimento desses processos é crucial para o entendimento sobre a biogeografia, a ecologia e conservação dos ambientes (Baselga, 2010; Socolar *et al.*, 2016).

Entender como os parâmetros populacionais (recrutamento, crescimento e mortalidade) respondem aos fatores bióticos e abióticos que regem a composição, tamanho e idade das comunidades também é uma tarefa importante (McDowell *et al.*, 2020; van der Sande *et al.*, 2017). Além da composição de espécies, esses fatores controlam o tamanho e a idade das comunidades (McDowell *et al.*, 2020). Ainda que o padrão de resposta das comunidades frente as mudanças climáticas em relação a esses parâmetros seja variado (McDowell *et al.*, 2020; Rozendaal *et al.*, 2020; Torres *et al.*, 2023), a mortalidade mostra fortes indícios de aumentar (McDowell *et al.*, 2018). A melhor forma de entender esses parâmetros é através de estudos de longa duração (Hughes *et al.*, 2017). Infelizmente, muitos desses estudos acabam fracassando, seja por razões financeiras ou pela falta de foco em relação ao objeto estudado (Lindenmayer; Likens, 2009; Lovett *et al.*, 2007). Apesar desses desafios, a importância desses estudos é inegável. Eles são cruciais para a gestão de ecossistemas e de recursos naturais, bem como na definição de metas realísticas para a conservação (Lindenmayer; Likens, 2009). Estudos de cronossequência — nos quais se comparam áreas de diferentes idades, assumindo que as diferenças e os padrões observados estão relacionadas aos diferentes estágios sucessionais de cada uma — possuem vantagens, tais como a maior facilidade e velocidade para serem realizados (Pickett, 1989). Porém, esses estudos podem não captar todas os possíveis efeitos e variações observados em estudos de longa duração (Pickett, 1989). Tendo isso em mente, nosso estudo teve como objetivo analisar as comunidades do Parque Nacional do Iguaçu em relação as taxas demográficas (mortalidade, recrutamento e crescimento) além de avaliar as mudanças na diversidade beta, tanto espacial quanto temporal, através do monitoramento de parcelas permanentes instaladas no parque e acompanhadas ao longo de 11 anos.

2 CAPÍTULO I*

SPATIO-TEMPORAL VARIATION OF TREE ABUNDANCE AND RICHNESS REVEALS BIODIVERSITY LOSS IN A TROPICAL MEGADIVERSE HOTSPOT

*Capitulo formatado de acordo com as regras da revista “*Austral ecology”.*

Spatio-temporal variation of tree abundance and richness reveals biodiversity loss in a tropical megadiverse hotspot.

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Data availability

The data that support the findings of this study are available from the corresponding author, upon request.

Competing interests

The authors declare that they have no known competing financial interests or personal relationships that could have appeared to influence the work reported in this paper.

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Abstract

Tropical forests harbor a significant share of global biodiversity and play a critical role in climate regulation and carbon sequestration. Unfortunately, anthropogenic activities have irreversibly impacted these areas. To predict biodiversity responses to global changes and optimize conservation efforts, it is essential to comprehend the dynamics of old-growth forest communities. In this study, we analyze the old-growth forests of the Iguacu National Park along eleven years of monitoring to understand the demographic dynamics and spatio-temporal beta diversity variation of tree species assemblages. Data collection was conducted four times between 2011 and 2022 on 21 permanent plots installed in the Iguaçu National Park. Richness, abundance, total basal area, diversity and evenness indices, and demographic variables (mortality, recruitment, and growth) were evaluated. We also assessed beta diversity variation across sites and years to infer the mechanisms of biodiversity change. We observed a reduction in richness, individual abundance, diversity, and evenness, an increase in mortality, and a decrease in recruitment over the years. Growth decreased in the first years (2011 to 2013) and stabilized onwards. Replacement was the component that most explained spatial beta diversity. Temporal beta diversity revealed that dissimilarities between years, initially dominated by gains in species occurrences/abundances, gradually shifted toward losses over time. Ultimately, losses outweighed gains in the last period (2015–2022). We also found evidence of biotic homogenization in the last period. Tree mortality plays a crucial role in community changes, and such population reductions are expected to increase with a higher incidence of extreme weather events under climate change. Our results warn of a potential biodiversity loss in one of the most important remnants of the Atlantic Forest.

Keywords: Atlantic Forest, Beta diversity, Demographic variables, Old-growth Forest, Community dynamics.

1. Introduction

Tropical forests are home to a vast array of biodiversity (Pennington et al., 2015; Pillay et al., 2022) and play a crucial role in climate regulation and the global carbon cycle (Lawrence and Vandecar, 2015; Taubert et al., 2018). Anthropogenic activities, including land-use changes, climate change, pollution, invasion by exotic species, and habitat loss, have inflicted irreparable damage on such biodiverse ecosystems (Barnosky et al., 2011; Newbold et al., 2015; Tittensor et al., 2014). Of particular concern are old-growth tropical forests, which are irreplaceable for conserving tropical species and functions (Luyssaert et al., 2008; M. R. Rosa et al., 2021; Scarano and Ceotto, 2015). However, such preserved forests are increasingly rare and threatened by anthropogenic impacts (Rezende et al., 2018; Ribeiro et al., 2009; Zwiener et al., 2018). Understanding how the structure and diversity of old-growth forests vary through space and time is essential to predict how these forests respond to human impacts and ultimately affect ecosystem services and biodiversity conservation.

Biodiversity changes can be assessed through beta diversity, which is defined in the broad sense as a measure of variation in species composition across habitats (Anderson et al., 2011; Whittaker, 1972). This variation may result from different ecological processes, such as environmental filtering, dispersal limitation, biotic interactions, and historical and stochastic factors (Arroyo-Rodríguez et al., 2017; Götzenberger et al., 2012; Zwiener et al., 2020). When analyzing spatial community data from an environmental gradient, beta diversity reflects two different phenomena: species replacement (or turnover) and richness differences (Baselga, 2010; Legendre, 2014; Podani and Schmera, 2011; Schmera et al., 2020). Species replacement (hereafter replacement) implies the simultaneous gain or loss of species along a gradient and can be associated with changes in composition. Richness difference reflects the environmental diversity available in different locations and can be related to changes in richness between those communities (Legendre, 2014; Schmera et al., 2020). When considering the community variation between periods (temporal beta-diversity), we must analyze this variation as gains or losses of species or individuals, which can tell us the direction of change in beta diversity in communities between time intervals (Legendre, 2019; Legendre and Condit, 2019).

In this sense, understanding community dynamics in old-growth tropical forests also involves analyzing key population parameters such as growth, recruitment, and mortality, which respond to diverse biotic and abiotic factors (Capers et al., 2005; McDowell et al., 2020; van der Sande et al., 2017). Such demographic processes shape communities' age, size, and composition and are changing uncertainly in recent years because of anthropogenic impacts (McDowell et al., 2020). While mortality is deemed to increase in human-induced climate change scenarios, the effect of these changes in recruitment and growth can vary (McDowell et al., 2020). The most common causes of tree death are stochastic events, hydraulic failure, and carbon starvation (McDowell et al., 2018; Rozendaal et al., 2020). Both hydraulic failure and carbon starvation are related to water stress (Sevanto et al., 2014), and severe droughts are known to suppress photosynthesis (Doughty et al., 2015), which may explain the increased mortality related to drought in tropical forests (Doughty et al., 2015; Feldpausch et al., 2016; Phillips et al., 2010; Zuleta et al., 2017). Droughts can also cause wilting and reduced survival in young plants, affecting recruitment rates (Engelbrecht and Kursar, 2003), and are also related to reduced secondary growth (Ruiz-Benito et al., 2014). Strong winds can also influence those population parameters, increasing mortality (Bauman et al., 2022) and stimulating growth (Gardiner et al., 2016). Other impacts, such as CO2 and temperature increase, wildfires, and insect outbreaks are known to affect those population parameters

(McDowell et al., 2020) as well as soil composition and nutrient availability (Quesada et al., 2012; Torres et al., 2023; Yuan et al., 2019). Long-term monitoring is essential to understand the effects of demographic processes on community dynamics. Unfortunately, the high costs and funding scarcity have constrained such studies in recent years (Hughes et al., 2017; Lovett et al., 2007; C. Rosa et al., 2021).

The Brazilian Atlantic Forest has suffered large impacts on its vegetation cover, as centuries of anthropogenic activities have reduced this biome to a mere 28% of its original extent (Rezende et al., 2018) and left most of its species threatened with extinction (de Lima et al., 2024). Furthermore, most of the remaining fragments are less than 50 hectares in size, inserted in an agricultural matrix, or located in remote areas, such as mountainous regions (Borda-Niño et al., 2020; Ribeiro et al., 2009). Over the past 30 years, the Atlantic Forest's coverage has remained stable, with the rates of deforestation and restoration balancing each other out (M. R. Rosa et al., 2021). However, the primary loss has been in the old-growth forest, significantly reducing crucial ecological interactions unique to these habitats (M. R. Rosa et al., 2021; Valiente-Banuet et al., 2015). While some studies have assessed demographic rates and community dynamics in the Brazilian Atlantic Forest (e.g. Dalmaso et al., 2020; Higuchi et al., 2008; Mews et al., 2011; Oliveira Filho et al., 2007; Peixoto et al., 2012; Salami et al., 2017; Silva and Araújo, 2009; Torres et al., 2023) most of these studies were conducted in small forest fragments, with less frequency (only two periods of time). Here, we analyze the forest dynamics along 11 years of monitoring in the Iguaçu National Park (INP) in southern Brazil, one of the largest remnants of the old-growth Atlantic Forest. Our main goal is to evaluate demographic rates and spatial-temporal beta diversity of tree species assemblages to infer potential pathways and determinants of community dynamics. More specifically, we address the following questions: i) What is the contribution of growth, recruitment, and mortality to the demographic dynamics of tree assemblages? ii) Which components of spatial beta diversity (replacement and richness/abundance differences) and temporal beta diversity (species/individuals gain or loss) explains most of the variation across communities and years? iii) Did the INP suffer from biotic homogenization or heterogenization across the years? Given the increasing influence of climate change, we expect an increase in mortality rates, a reduction in recruitment, and a decrease in growth. We also expect the replacement component to explain most of the spatial beta diversity, an increase in the species loss component of temporal beta diversity, and an increase in homogenization between plots.

2. **Methods**

2.1.Study region and sites

The study was conducted in the Iguaçu National Park, one of the largest protected remnants of the Atlantic Forest (Ribeiro et al., 2009). With 1850 km² of primarily old-growth forest and well-preserved habitats, the INP is considered a World Heritage Site by UNESCO, and together with connected forest remnants from Argentina and Paraguay, represents one of the last refuges of the Atlantic Forest biodiversity hotspot (UNESCO World Heritage Centre, n.d.). The park is located in southwestern Brazil (Fig. 1). The history of deforestation in this region is relatively recent. Until the 1920s, it was mostly untouched by anthropogenic activity (Gubert Filho, 2010). Because of its relatively flat land and fertile soils (Santos et al., 2006)), a wave of deforestation occurred in this region from 1965 to 1990, primarily due to the conversion of land into agriculture, and, as a result, it has become one of the most deforested regions in the Atlantic Forest domain (Gubert Filho, 2010) with the INP being one of the few relatively untouched remnants. The region's climate is characterized by hot and humid summers and drier winters with mild temperatures without a defined dry season (Beck et al., 2018).

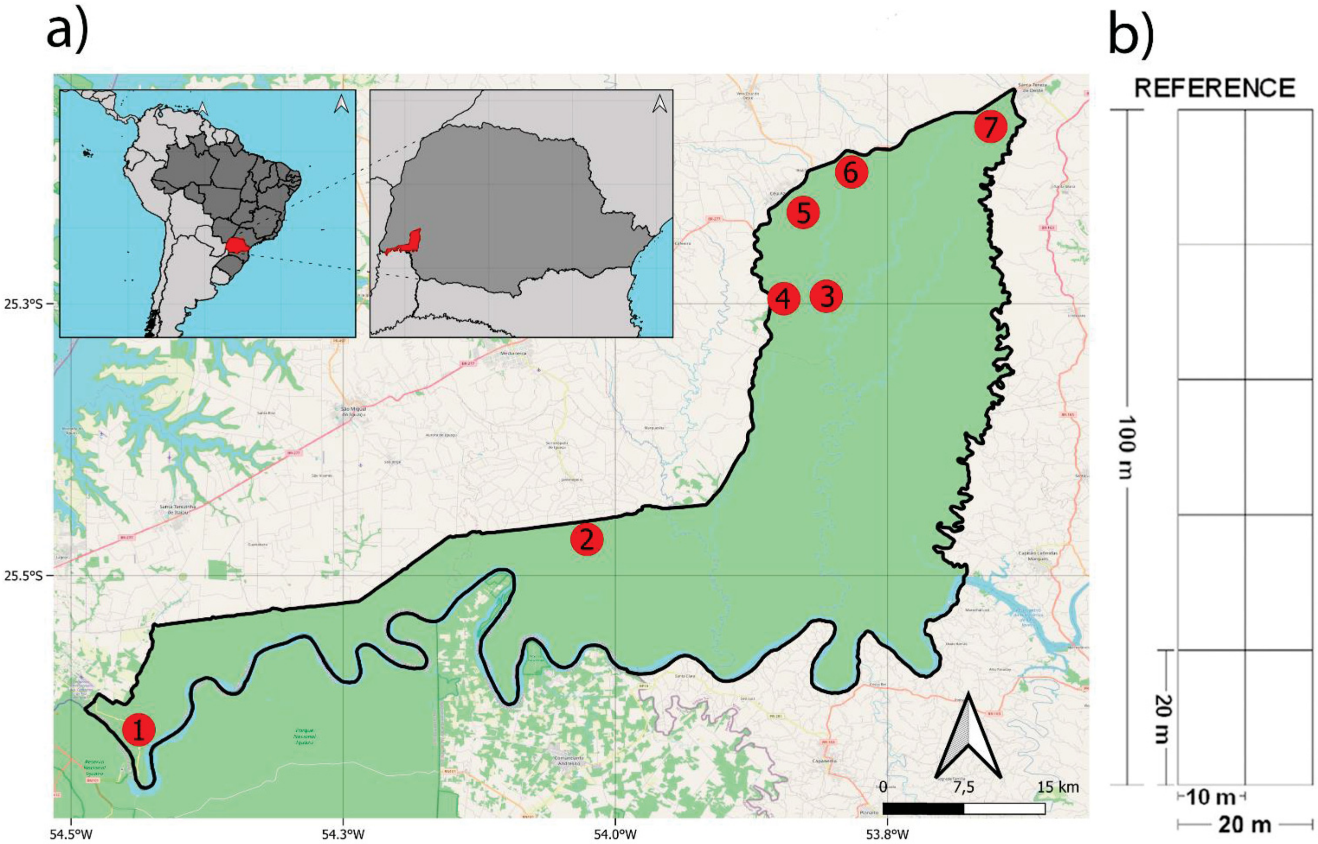


Figure 1. Geographical location of sampling units in the Iguaçu National Park. Red dots represent the plot groups. The black line represents the INP borders. Map data copyright: (OpenStreetMap contributors, 2017).

Seven locations were selected to consider the environmental and floristic variation across the INP, ranging from 100 to 800 meters above sea level (Fig. 1a). These locations were spread across the INP, separated by a distance ranging from 5 to 100 km. Three permanent plots of 100x20 meters (Fig. 1b) were established in each of the seven locations. These plots were arranged at varying distances from each other, aligned parallel to the riverbed and along the drainage slopes. The samplings were conducted in 2011, 2013, 2015, and 2022 (see Souza et al., (2019) for more details). All trees with a diameter at breast height of 5 cm or greater were included in the sampling process. Each individual was identified, measured, and marked with metallic tags containing a unique number. Additional details were also recorded, such as the point of morphological inversion, stratification (canopy, immediately below the canopy, or understory), exposure to light, and the presence of epiphytes. The total sampled area was 4.2 hectares.

2.2. Community structure and population metrics

To assess the general structure of ecological communities over the years, we calculated the species richness, individual abundance, total basal area (m^2/year), Shannon index (H'), and equability (Pielou index; J').

The demographic variables, which express the rates of mortality, recruitment, and growth, were calculated for the three sampling periods: 2011 to 2013 (hereafter T1), 2013 to 2015 (hereafter T2), and 2015 to 2022 (hereafter T3). To calculate mortality and recruitment rates, we used the *forestdin* function from Higuchi (2018) in R (R Core Team, 2023) using inventory data from each year. Growth rates were calculated as annual basal area growth (m^2) per year for trees that were present in both censuses in every period. Equations for calculating these demographic variables are based on the literature (Oliveira Filho et al., 2007; Salami et al., 2017; Sheil et al., 1995, 2000) and can be found in the supplementary material (Appendix S1).

2.3.Analyses

To test if the differences in demographic rates (mortality, recruitment, and growth) were significantly different ($p<0.05$) among periods, we built three Generalized Estimated Equations (GEE) models, one for each demographic variable. GEE models are an extension of generalized linear models for longitudinal data (Liang and Zeger, 1986). They are a better alternative to other longitudinal tests, such as repeated measures ANOVA and MANOVA, which require fixed repeated time intervals (de Melo et al., 2022). All models used Gaussian distribution with identity link since it presented the lowest QIC values (Pan, 2001). Models were built using the *geepack* package in R (Halekoh et al., 2006). We used a generalized linear model (GLM) to test whether plot groups differed for every demographic variable in each period. GLM models were built using gamma distribution with identity link since presented the lowest AIC values (Burnham and Anderson, 2004).

For spatial beta diversity, we followed Legendre, (2014). The calculations were made using the function *beta.div.comp* from the *adespatial* package (Dray et al., 2023). We used the Podani family decompositions (Legendre, 2014; Podani et al., 2013; Podani and Schmera, 2011) for occurrence and abundance data, using Jaccard dissimilarity and its quantitative form (Ruzicka dissimilarity; Legendre and De Cáceres, 2013). Beta diversity was decomposed in Replacement (Repl), Richness Difference (RichDiff; when dealing with occurrence data), and Abundance Difference (AbDiff; when dealing with abundance data). The maximum beta diversity possible for these dissimilarities is 0.5 (Legendre, 2014).

To analyze the community variation between years, we calculated the temporal beta diversity index (TBI) for all periods for both abundance and occurrence data, as described by Legendre, (2019). In short, this index compares compositional data between years. The data is then randomly permuted, and the index and two p-values (parametric and permuted) are calculated, giving the overall direction of change. Since both p-values did not differ in interpretability (both agreed when there were significant differences), we show only the permuted value in this paper. The null hypothesis for the p-values states that the species assemblage observed in site *i* (i.e. site under study), is not exceptionally different between t1 and t2 compared to other assemblages that could have been observed at the same two times at this site. The index can be decomposed into two components: B (gain) and C (loss). Since we used both occurrence and abundance data, the loss and gain are relative to the number of species occurrences and individuals, respectively. The sum of both components equals the dissimilarity between years and ranges between 0 and 1. A B-C plot (Legendre, 2019) was used to display the relative importance of loss and gain processes through the study sites. To test whether there has been a biotic homogenization or heterogenization since 2011, we compared dissimilarities (Jaccard for occurrences and Ruzicka for abundances) using a paired Wilcoxon test.

3. Results

3.1.General Structure

We observed a decrease in richness, abundance, basal area, alpha diversity (Shannon index), and evenness (Pielou index) in 2022. For all these metrics, the values found in 2022 in the INP are the lowest ever recorded (Table 1).

	2011	**2013**	**2015**	**2022**
Richness	163	164	166	161
Abundance	4085	4237	4339	3857
Total basal areal (m^2)	132.48	137.58	137.52	131.05
Diversity (H’)	4.008	3.998	3.951	3.876
Evenness (J')	0.787	0.78	0.773	0.763

Table 1. Richness, abundance, basal area, diversity (Shannon index; H’), and evenness (Pielou index; J’) in all samplings in the Iguaçu National Park.

3.2. Demographic variables

We recorded an increase in mortality rates along the survey periods (Fig. 2a), with a net loss of 482 individuals in the last period (T3). Among these, 94 trees were observed as standing dead, and ten individuals of palm heart (*Euterpe edulis* Mart.) were found to have been illegally cut down. We observed that mortality rates were indeed different for every period (Fig 2a.; GEE: T1/T2, $z = -4.94$, $p<0.001$; T1/T3, $z = -9.05$, $p <0.001$; T2/T3: $z = -3.30$, $p = 0.001$). We found no differences between plot groups in any period for mortality(Fig. 2b).

For recruitment, we found significant differences between T1/T3 (GEE: $z = 2.43$, $p<0.001$) and T2/T3 (GEE: $z = 3.27$, $p<0.001$; Fig. 2a). No significant differences were found for T1/T2 (Fig. 2a). We observed differences between plot groups for recruitment only in T1 (GLM: $x^2(6) = 20.09$, $p = 0.002$; Fig 2b).

For growth, we observed a significant reduction between T1/T2 (GEE: $z = 2.760$, $p = 0.012$) and T1/T3 (GEE: $z = 3.300$, $p = 0.003$; Fig 2a) but no differences between T2/T3. Between plot groups, we observed differences in T3 (GLM: $x^2(6) = 30.7$ $p <0.001$; Fig. 2b).

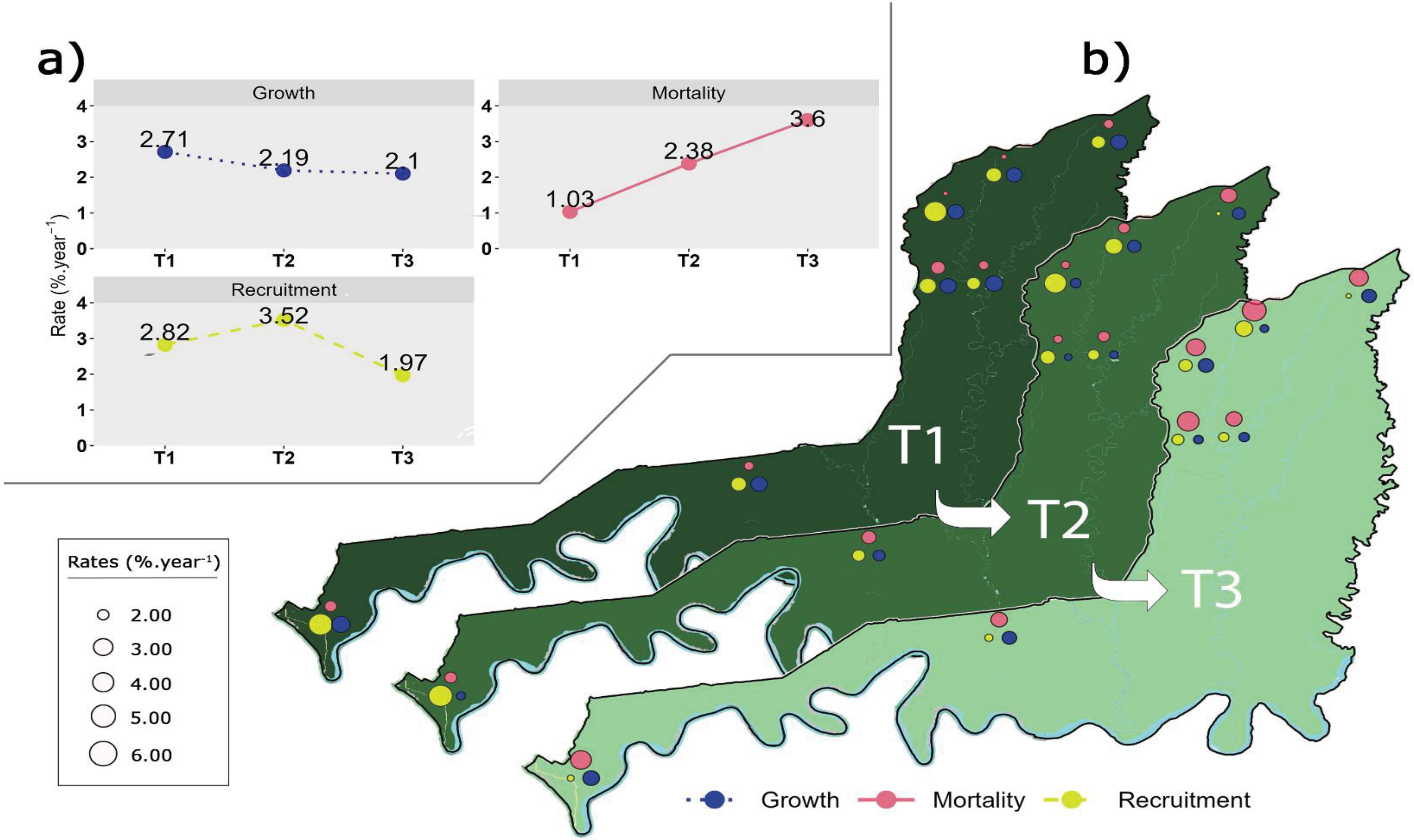


Figure 2. (a) Annual rates of change for demographic variables for each period; (b) Annual rates of change in demographic variables for each plot group. The size of the points is proportional to the rates. Map data copyright: (OpenStreetMap contributors, 2017).

3.3. Spatial beta diversity

For all years, replacement was the component that explained most of the total beta diversity for both occurrence data (Fig. 3a) and abundance data (Fig. 3b). For both types of data, beta diversity and its components remained relatively stable.

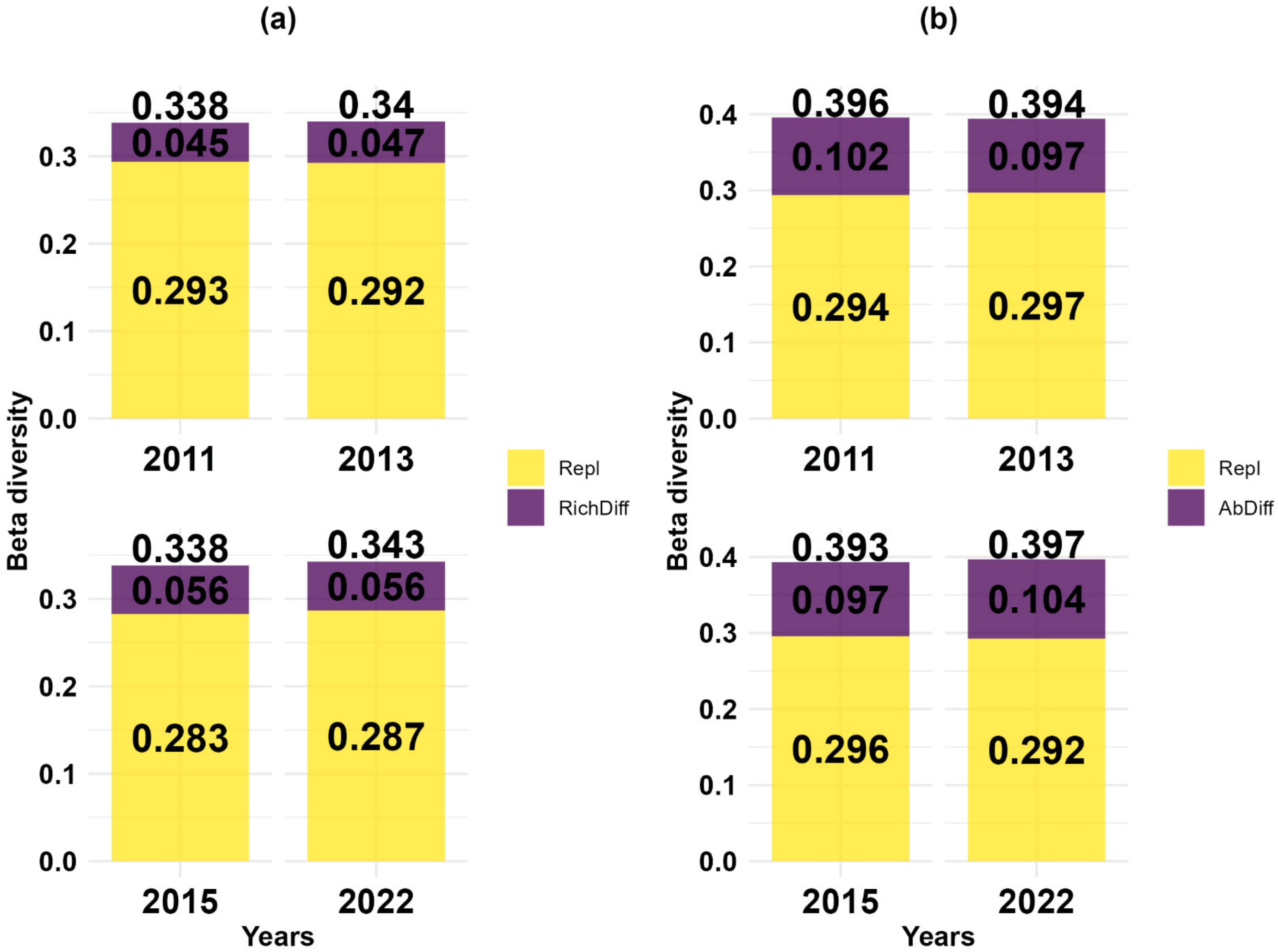


Figure 3. Occurrence (a) and Abundance (b) components of beta diversity. The values at the top of the bars represent total beta diversity.

3.4.Temporal beta diversity

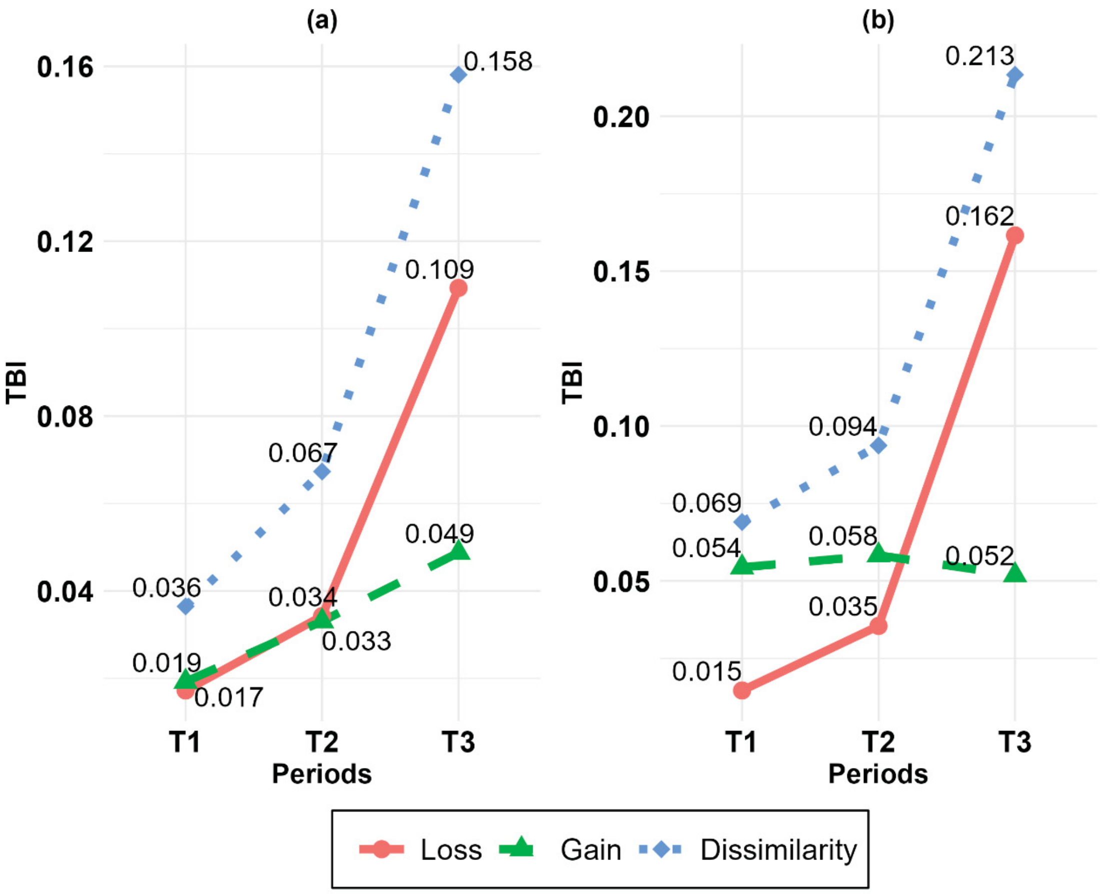
In T1, variation in occurrence remained similar in both the gain and loss of species (Fig 4a). Eight plots indicated gains, six losses, and seven remained neutral (Fig 5a). No significant differences were observed in the occurrence data during this period. For abundance, the dissimilarity consists mainly of gain rather than loss (Fig 4b). This positive shift in abundance encompassed 19 out of 21 plots, with two plots indicating a loss and one showing no changes (Appendix S2). The t-test revealed that gains and losses were significantly different (t = 5.01, p = 0.001), with gain dominance.

In T2, changes in occurrences also remained similar regarding species gain and loss (Fig 4a). Nine plots showed gains, nine showed losses, and three remained neutral (Fig 5b). No significant differences were observed in the occurrence data during this period. For abundance data, while gain still dominated the disparity, there was a decrease in the ratio between gain and loss compared to the first sampling period (Fig 4b). Positive change was observed in 13 out of the 21 plots, while seven plots were dominated by loss, and one plot remained unchanged for abundance (Appendix S2). There were no significant differences between gain and loss for abundance data in this period.

The most substantial change was observed in the T3, with loss surpassing gain and constituting most of the dissimilarity in occurrence and abundance data (Fig 4a,b). For occurrence data, two plots showed gains; one remained neutral, and the rest was dominated by losses (Fig 5c). For abundance, only one plot showed gains in abundance (Appendix S2). The t-test revealed significant differences in gains and losses, with loss dominance (occurrence: t = -4.56, p = 0.001; abundance t = -6.65, p = 0.001).

In T1, biotic homogenization was found for occurrence (w = 7179, p = 0.009), and abundance (w = 13587, p = 0.004) data. In T2 there have been no significant differences in dissimilarities. In T3 we observed biotic heterogenization for both occurrence (w = 7614, p <0.001) and abundance (w = 7615, p < 0.001) data.

Figure 4. Changes in temporal beta diversity components across all sampling periods. The sum of components Loss and Gains equals Dissimilarity. (a) Occurrence data; (b) Abundance data.



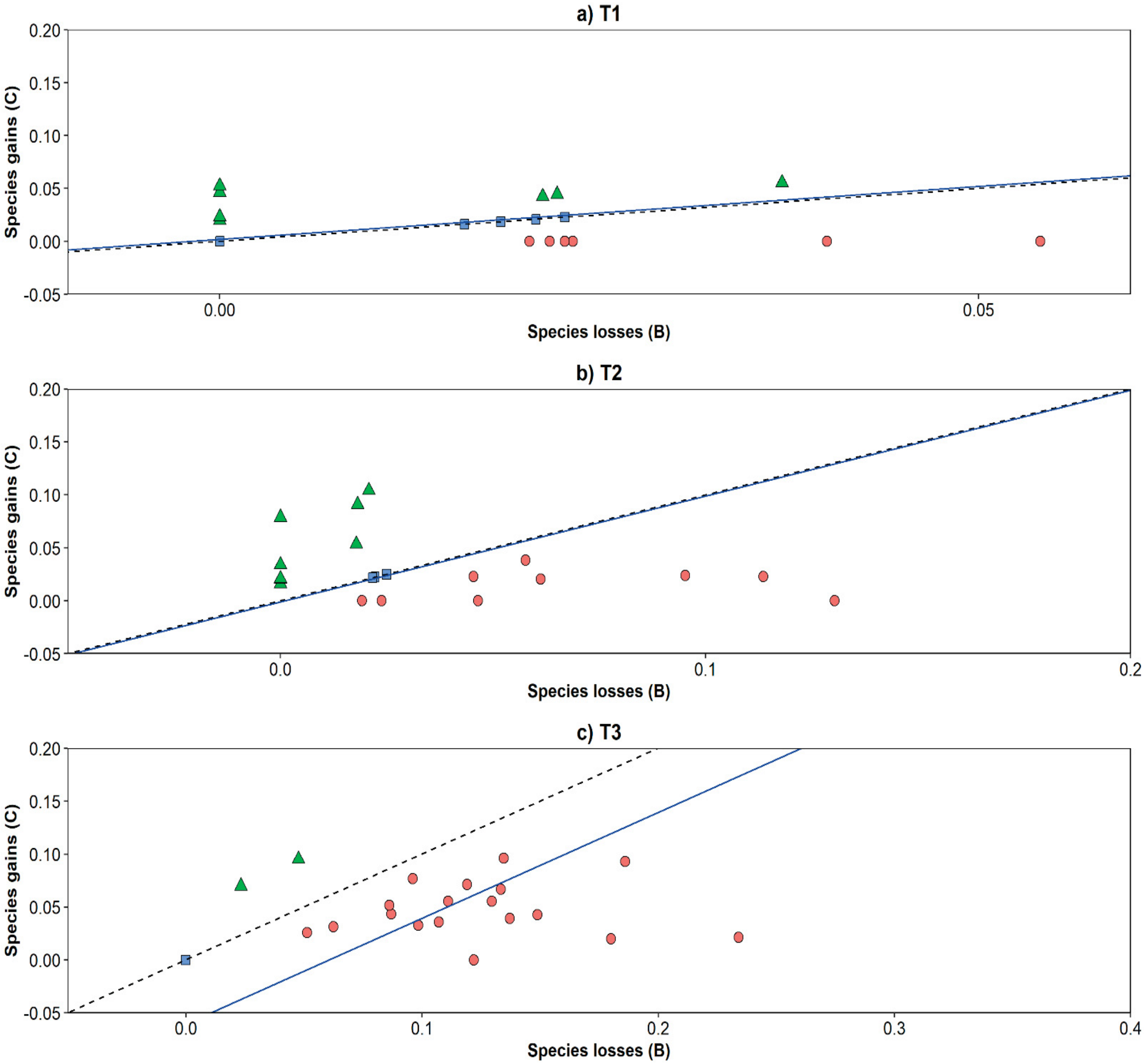


Figure 5. B-C plots for occurrence data for all periods. The black dashed line (slope 1) is where gain equals losses. The blue solid line crosses the centroid of the points and is parallel (slope = 1) to the green line. Its position above the green line indicates gain dominating losses, while the contrary is also valid. Triangles (green) indicate plots that gained individuals, circles (red) indicate plots that lost individuals, and squares (blue) indicate plots with no change in individuals.

4. Discussion

The reduction of biodiversity in impacted habitats characterizes the Anthropocene (Malhi et al., 2014). Such changes in preserved old-growth tropical forests highlight the extent of the impacts and warn of the potential loss of species and human well-being (Cardinale et al., 2012; Gibson et al., 2011; Hong et al., 2022; Mackey et al., 2020). Our results show a significant increase in tree mortality over 11 years of monitoring, which led to an overall reduction of species diversity, basal area, and affected temporal-beta diversity. Communities are ecological units that are dynamic in essence (Vellend, 2010). Understanding the processes that support population and community dynamics is fundamental to sound management and conservation decisions.

4.1.General community structure

Community structure and compositional changes over time, and space may reveal patterns and processes affecting biodiversity and ecosystem services (Arroyo-Rodríguez et al., 2017; Cardinale et al., 2012; Socolar et al., 2016). We observed a decrease in species richness, number of individuals, total basal area, and diversity and evenness indices, which indicate a potential local decline in plant biodiversity. Despite evidence of relative stability of global local plant biodiversity over time (Vellend et al., 2013), our results show a trend of biodiversity loss evidenced by long-term forest demographic dynamics (Barlow et al., 2016; Díaz et al., 2019; McDowell et al., 2020).

4.2. Demographic dynamics

Tree mortality represents one of the main dimensions of demographic variation of tree species assemblages (McDowell et al., 2020; McMahon et al., 2019). We show an increase in mortality rates in the last years that affected the entire INP. The rise in mortality aligns with expectations under climate change scenarios and follows trends observed in old-growth tropical forests in recent years (Bauman et al., 2022; Díaz et al., 2019; McDowell et al., 2018, 2020). Drought emerges as a major contributor to increased mortality in tropical forests (Feldpausch et al., 2016; Phillips et al., 2010; Zuleta et al., 2017). Notably, in 2020, southern Brazil experienced one of the most severe droughts on record (Grimm et al., 2020), which may account for the observed mortality increase. Another factor contributing to the mortality increase is wind disturbance events (Bauman et al., 2022; Liebsch et al., 2021). Strong winds can snap tree trunks or even uproot entire trees (Gardiner et al., 2016). The INP region was also impacted by a "bomb cyclone" in 2020 (Gobato and Heidari, 2020), which likely affected the mortality rates found, as evidenced by fallen trees and snapped trunks observed during fieldwork. Other studies conducted in the Atlantic Forest that underwent disturbances, such as drought (Mews et al., 2011), floods (Appolinário et al., 2005), and wind disturbances (Liebsch et al., 2021) also observed high mortality rates. This could indicate climate change-induced changes in the INP, which are related to the recent extreme events and other factors since an increase in mortality has also been recorded in T2 compared to T1 (Fig. 2a). Because small shifts in mortality rates can result in large shifts in population turnover in relatively short periods (McMahon et al., 2019), if the rates continue high, we may have a compositional shift in the INP communities in a few years.

Anthropogenic impacts such as habitat reduction, fragmentation, and climate change also have the potential to induce community shifts by influencing seed production, viability, germination, emergence, and survival (Lloret et al., 2009). In young plants, extreme droughts can cause wilting and may reduce survival, which impacts recruitment rates (Engelbrecht and Kursar, 2003). Other indirect factors, such as changes in frugivore abundance and composition, may affect plant movement (Mokany et al., 2014) by reducing seed dispersal and the probability of seeds reaching suitable habitats for germination (Beckman and Rogers, 2013). These phenomena may have contributed to the observed reductions in recruitment found in the INP in recent years (T3; Fig. 2).

Different species have different growth responses to changes in climate (Klos et al., 2009) and different impacts may cause varied responses by plants concerning growth (McDowell et al., 2020). While drought may cause a reduction in growth (Ruiz-Benito et al., 2014), strong winds may stimulate it through thigmomorphogenesis (mechanical-induced changes in growth and development; (Braam and Chehab, 2017; Gardiner et al., 2016). Responses to competition are also important regarding growth since forest structure and dynamics are primarily influenced by it (Rozendaal et al., 2020). Under stress, some tree species trade off defense and maintenance for growth, which seems to provide a competitive advantage over other individuals (Doughty et al., 2015) Interestingly, we observed a significant reduction in growth between T1 and T2, but it stabilized between T2 and T3, which suggests that the factors leading to decreased recruitment and increased mortality in recent years impacted growth in such ways that some factors positively affected growth, while others had negative effects, resulting in variable responses and an apparent stable pattern.

4.3. Beta diversity

We observed relative stability in total spatial beta diversity and their components for occurrence and abundance data in all years. Most of the total beta diversity found is related to the replacement component, which indicates a high species composition variation (Schmera et al., 2020). For other studies conducted in the Brazilian Atlantic Forest, replacement also explained most of the beta diversity (Bergamin et al., 2017; Dalmaso et al., 2020).

When analyzing the temporal beta diversity variation, we saw an increase in dissimilarity along the periods for both occurrence and abundance data (Fig 4a,b). Over the years, gains gave way to losses as the main component of temporal dissimilarity. This loss dominance was also found in a few studies (Abdul Aziz et al., 2024; Brice et al., 2019; Legendre and Condit, 2019), all of which linked it with different anthropogenic disturbances.

In T1, we observed biotic homogenization for both types of data. Plots in T1 are becoming more homogeneous in species occurrences (some are gaining species, while some are losing since gain and loss components are similar; Fig. 4a) while the number of individuals in each species is becoming more similar (most related to a gain in individuals rather than loss, since gain dominated loss for abundance data in T1; Fig. 4b). At least for abundance, where the gain is significantly higher than the loss, a process of additive homogenization (Socolar et al., 2016) occurs, with the increase of the same species in different plots. Since in T2 we found no evidence for continuing this phenomenon (as we found no significant differences for dissimilarities in this period), this homogenization may be due to a natural variation composition between plots, which stabilized in the following years.

In T3, however, we see evidence for biotic heterogenization for both occurrence and abundance data. Since loss dominated gains for both indices in this period, this could imply a process of subtractive heterogenization, where beta-diversity increases after a disturbance because many species become rarer, but few become extinct (Arroyo-Rodríguez et al., 2017; Socolar et al., 2016). This increase in beta diversity may result from different pathways followed by ecological communities after disturbances regimes, combined with dispersal limitation and environmental heterogeneity (Arroyo-Rodríguez et al., 2017; Kramer et al., 2023). If the loss trend continues, it may lead to a biotic homogenization (decrease in beta-diversity) of the INP communities, which happens when rare and specialist species are gradually replaced by generalists adapted to human-modified landscapes (Lôbo et al., 2011; McKinney and Lockwood, 1999; Olden and Rooney, 2006) and represent possible next step after a disturbance induced beta diversity increase (Socolar et al., 2016).

Our findings show that the Iguaçu National Park, one of the largest and most important protected areas in the Atlantic Forest (Ribeiro et al., 2011), has suffered biodiversity loss in recent years. Climate change and extreme weather events, in which the Atlantic Forest is particularly vulnerable (Bellard et al., 2014), may play an important role in the community and demographic dynamics (Díaz et al., 2019; Liebsch et al., 2021; McMahon et al., 2019; Scarano and Ceotto, 2015; Walck et al., 2011). However, such factors remain to be explored. Unfortunately, international goals to keep climate change to a minimum will probably not be met (Díaz et al., 2019), and global warming is due to increase in the near future (IPCC, 2023). Of primary relevance is understanding how natural or anthropogenic changes affect patterns of community structure, demographic dynamics, species richness, beta diversity, and ecosystem functions to support the management and conservation of biodiversity and human well-being (Cardinale et al., 2012; Gibson et al., 2011). In this sense, long-term monitoring represents an important tool to shed light on the effects of anthropogenic impacts on biodiversity and ecosystem functioning (Hughes et al., 2017; Pickett, 1989).

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Appendix

Appendix S1 - The dynamic variables were calculated for the considered periods in the main paper (T1, T2, and T3). These variables express the count of individuals and the basal area (measured through the diameter of each tree). The average annual mortality rates (M), recruitment (R) and growth (GR) were computed using the following expressions:

$$M = \{1-[(N_0-m)/N_0]^{(1/t)}\} \times 100 \quad (1)$$

$$R = \{1-[1-(r/N_t)]^{(1/t)}\} \times 100 \quad (2)$$

$$GR-\{1-[1-(Ab_g/Ab_t)]^{(1/t)}\} \times 100 \quad (3)$$

Where:

t = time elapsed between samplings

N_0= Initial count of individuals

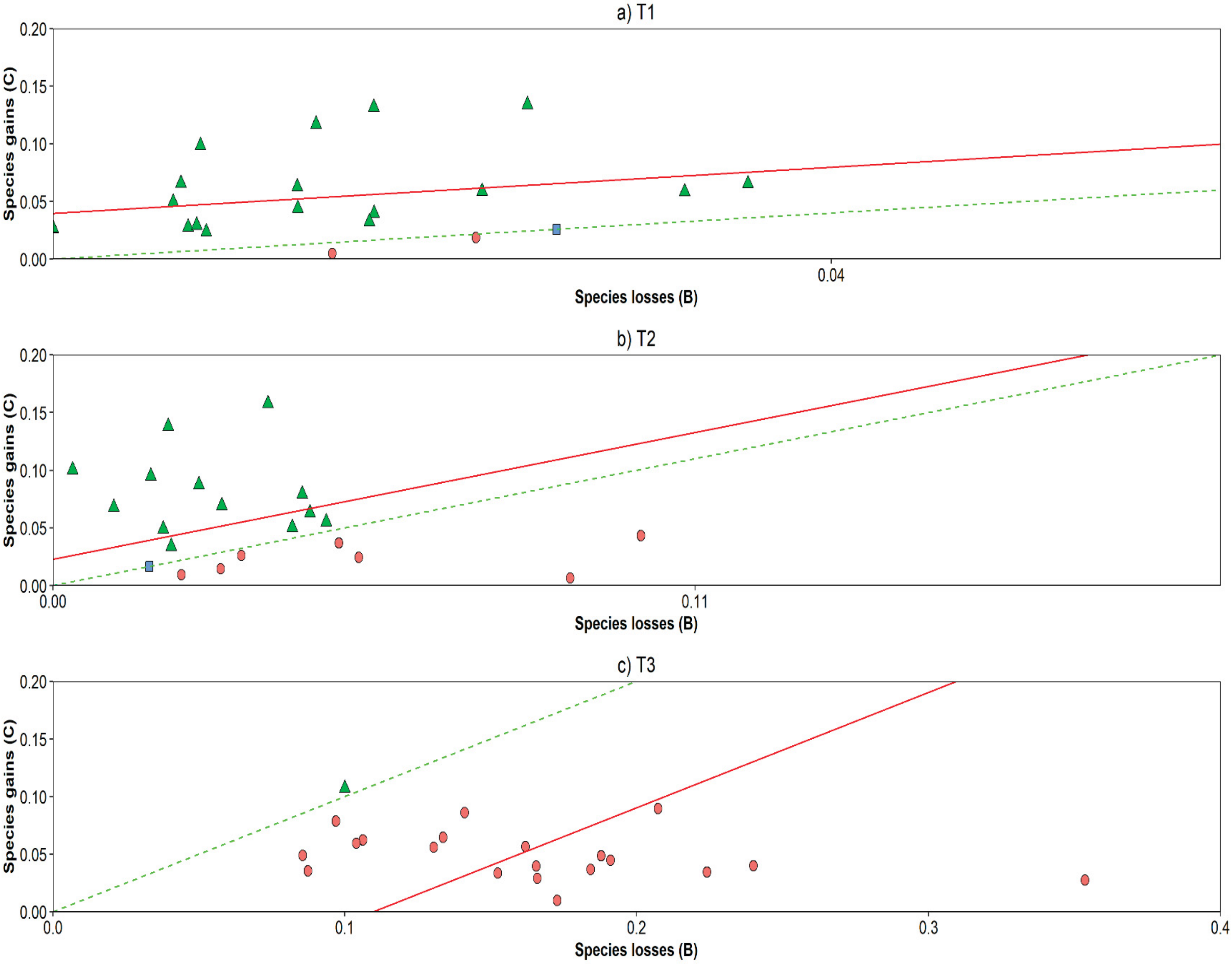
N = Final count of individuals

m = number of deaths

r = number of recruitments

Ab_g = Basal area of individuals

Ab_0 = Initial basal area
Ab_t = Final basal area



Appendix S2. B-C plots for abundance data for all periods. The black dashed line (slope 1) is where gain equals losses. The blue solid line crosses the centroid of the points and is parallel (slope = 1) to the green line. Its position above the green line indicates gain dominating losses, while the contrary is also valid. Triangles (green) indicate plots that gained individuals, circles (red) indicate plots that lost individuals, and squares (blue) indicate plots with no change in individuals.

3 CONCLUSÃO

Nosso estudo no Parque Nacional do Iguaçu revelou uma diminuição na biodiversidade de árvores, com a redução do número total de indivíduos, da diversidade de Shannon e da equabilidade de Pielou e na área basal, além de um aumento na mortalidade e uma queda no recrutamento de novos indivíduos. O crescimento, por outro lado, ficou relativamente estável. Notamos que a substituição foi o componente que mais explicou a beta diversidade espacial, indicando que a variação na composição de espécies do parque ao longo do gradiente ambiental é grande. Em relação a beta diversidade temporal, foi observado um aumento do componente de perda de ocorrências/abundâncias em relação ao componente de ganho ao longo dos anos. Também observamos uma heterogeneização biótica subtrativa no último período, que ocorre quando algumas espécies desaparecem de alguns locais (ex. parcelas) mas não são extintas regionalmente (ex. parque inteiro). Essas mudanças podem indicar um impacto crescente das mudanças climáticas no parque, embora mais pesquisas sejam necessárias para confirmar isso. Este estudo também destaca a importância de pesquisas de longa duração para o manejo e conservação de áreas protegidas, pois alguns dos aspectos observados só foram possíveis devido ao extenso período de monitoramento.

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APÊNDICES

ANEXO 1 – NORMAS DE FORMATAÇÃO DA REVISTA *Austral Ecology*

Free Format submission

Before you submit, you will need:

- Your manuscript can be a single file including text, figures, and tables, or separate files – whichever you prefer.
    - All required sections relevant to the chosen manuscript type should be contained in your manuscript (eg: abstract, introduction, methods, results, and conclusions etc).
    - Figures and tables should have legends.
    - References may be submitted in any style or format, as long as it is consistent throughout the manuscript, but it is recommended that the journal's style is followed.
    - It is strongly recommended that you follow the guidelines of *Austral Ecology* manuscripts when submitting your first draft. Please do pay close attention to having your references correctly formatted. If references are poorly formatted it can be perceived as a poor reflection on your eye to detail; and a disservice to the reviewers that will be spending a substantive amount of time giving you constructive feedback.
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    - data availability statement
    - funding statement
    - conflict of interest disclosure
    - permission to reproduce material from other sources
    - Your co-author details, including affiliation and email address. *(Why is this important? We need to keep all co-authors informed of the outcome of the peer review process.)*

If the manuscript, figures or tables are difficult for you to read, they will also be difficult for the editors and reviewers. If your manuscript is difficult to read, the editorial office may send it back to you for revision.

General Style Points

- Manuscripts should be double-spaced.
- The journal uses UK spelling.
- Before you submit, please make sure that your paper has been edited by a competent English speaker that has a good grasp of scientific English and its nuances. Papers with poor grammar are more likely to be rejected – so to reduce the burden on our reviewers. This enables reviewers to focus on the research primarily presented and not be detracted into fixing grammar and style issues. If you are worried about this, please contact the Editor-in-Chief before submission.

- All measurements must be given in SI units
- Abbreviations should be used sparingly. Initially use the word in full, followed by the abbreviation in parentheses. Thereafter use the abbreviation.
- At the first mention of a chemical substance, give the generic name only.
- Trade names should not be used.
- Continuous line numbering must be enabled in the main document.