EFFECT OF THE REMOVAL OF REGENERATING INDIVIDUALS ON THE SEEDLING BANK DYNAMICS IN PLANT COMMUNITIES

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ABSTRACT – The use of forest seedling banks is recommended for producing seedlings of species essential for specific forest typologies for which propagation poses challenges. However, given the lack of understanding of how human intervention, such as the removal of regenerating individuals from the forest, influences the composition and structure of the plant community, there is a pressing need for further research. Our primary objective here was to identify the effects of seedling removal on natural regeneration in forest communities and to characterize seedling bank dynamics three years after anthropogenic intervention. A randomized block design was used for the experiment, consisting of five removal intensities (0, 25, 50, 75, and 100% removal), with evaluations conducted every three months for three years. All individuals of the shrub-arboreal component between 5–55 cm heights were measured. Collected data were analyzed to determine the impacts of the removal of individuals and the influence of environmental elements on the seedling community. We found that the shrub-arboreal component of the forest community exhibited marked resilience three years following the removal of regenerating individuals. Removal of up to 50% of regenerating individuals does not appear to interfere with plant community dynamics, suggesting species with a high density of individuals in the seedling bank are resilient to the impacts of human intervention. Although climatic seasonality also affects seedling bank dynamics in plant communities, this effect depends on the level of human intervention in an area and, therefore, has been omitted from the analysis.

Keywords: Natural regeneration ; Forest resilience; Seedling removal.

EFEITO DA REMOÇÃO DE INDIVÍDUOS REGENERANTES NA DINÂMICA DO BANCO DE PLÂNTULAS EM COMUNIDADES DE VEGETAIS

RESUMO – O uso do banco de plântulas da floresta é indicado para produção de mudas de espécies importantes, porém de difícil propagação, para determinada tipologia florestal. No entanto, intervenções como a retirada de indivíduos regenerantes da floresta podem influenciara composição e a estrutura da comunidade de plantas, devendo ter seus impactos previamente estudados. Dessa forma, o presente estudo objetivou identificar os impactos da remoção de plântulas sob a regeneração natural de uma comunidade florestal, bem como caracterizar a dinâmica do banco de plântulas três anos após intervenção antrópica. O experimento foi conduzido no delineamento blocos ao acaso, sendo os tratamentos compostos por cinco intensidades de remoção de indivíduos do banco de plântulas (0, 25, 50, 75 e 100% de remoção) e realizadas avaliações a cada 3 meses, por um período de 3 anos. Foram mensurados todos os indivíduos do componente arbustivo-arbóreo com altura entre 5 e 55 cm. Os dados obtidos foram analisados quanto ao impacto causado pela remoção dos indivíduos e a influência dos elementos ambientais sobre a comunidade de plântulas. Após três *anos de observações constatou-se que a vegetação do componente arbóreo-arbustivo apresentou capacidade de resiliência posterior a remoção dos indivíduos regenerantes. De maneira geral, a remoção de até 50% dos indivíduos não interfere na dinâmica da comunidade vegetal, podendo assim ser utilizada para espécies que apresentam elevada densidade de indivíduos no banco de plântulas. A sazonalidade climática direciona a dinâmica do banco de plântulas em comunidades vegetais, no entanto esta influência é dependente do nível de intervenção antrópica a qual a área foi submetida.*

Palavras-Chave: Regeneração natural; Resiliência florestal; Remoção de plântulas.

1. INTRODUCTION

Increasing anthropogenic activity has triggered significant changes in environmental conditions globally, threatening the survival of many native species (Kerr and Currie, 1995). Forest and soil degradation are limiting barriers to the sustainable development of terrestrial ecosystems (Liu et al., 2012) and are among the primary causes of biodiversity loss worldwide (Catterall et al., 2012).

Planting native forest species has yielded satisfactory results in restoring biodiversity (Chazdon, 2008; Brancalion et al., 2019). The primary goal of reforesting efforts using native tree species is to slow or reverse biodiversity loss by counteracting obstacles to natural regeneration (Catterall et al., 2008). As Rodrigues et al. (2009) note, successful restoration of tropical ecosystems requires the use of plant species that are pre-adapted to the regional environmental conditions.

However, seedlings of native forest species are often difficult to obtain, especially those that commonly occur in the final successional stages (Turchetto et al., 2016), mainly due to difficulties in obtaining seeds and a lack of technology for producing many native forest species. Such deficiencies often lead to low-diversity restoration of uniform plantations, which can compromise the future sustainability of restored forests, as is often the case for areas within fragmented landscapes (Viani and Rodrigues, 2008).

Previous research has led to recommendations that seedlings produced by naturally regenerating individuals in tropical forests be removed and replanted in nurseries to generate additional seedling stock (Viani and Rodrigues, 2008; Viani et al., 2012; Turchetto et al., 2016), allowing seedlings to become established before being transferred to natural sites. An important advantage of this approach is that large quantities of seedlings of species from forest types that are difficult to propagate can be readily produced (Turchetto et al., 2016).

In Brazil, however, seedling removal is not addressed in current environmental legislation due to a scarcity of research on its impacts on forest communities. Because of this deficiency, at present, this approach can only be used as a mitigation measure for the production of seedlings in cases where formal authorization has been granted for forest containment or replacement. In addition, different regeneration strategies depend on the type of anthropic disturbance (Denslow, 1980). Moreover, strategies in subtropical ecosystems largely depend on seasonal climate, which influences plant community composition and structure (Brokaw and Scheiner, 1989). Thus, research on the effects of modification or management of natural seedling banks must be conducted to prevent irreversible damage to the diversity, productivity, and connectivity of populations, communities, and the ecosystem as a whole (Viani and Rodrigues, 2008).

In the present study, our primary goal was to identify the impacts of seedling removal on the natural regeneration of a forest community and characterize the seasonal dynamics of the seedling bank three years after anthropic intervention. We sought to address the following two questions: a) Do high intensities of seedling removal compromise the dynamics of natural regeneration? and b) Is removal intensity linked to species density?

2. MATERIAL AND METHODS

2.1. Study area

The study was conducted in a remnant of the Subtropical Seasonal Forest (29°27'14.71" S and

53°18'17.86" W) in the extreme south of the Atlantic Forest Biome, in the central region of the state of Rio Grande do Sul, Brazil. The soil in the area is classified as Regolithic Neosol (EMBRAPA, 2013) and the climate is subtropical, with an average annual rainfall of 1560 mm (Alvares et al., 2013) and well-defined seasons (Figure 1). The forest fragment we focused on is characterized as a secondary forest in an advanced stage of succession, with the last human intervention occurring more than 50 years ago; little sign of this intervention can be seen today.

2.2. Experimental design and data collection

A randomized block design was used for the experiment, with treatments consisting of five intensities of removal of individuals from the seedling bank (0, 25, 50, 75, and 100% removal). Treatments were distributed in 15 blocks subdivided into five plots of 1 m × 2.5 m, for a total of 75 plots. Additional details about the experimental design are presented in Turchetto et al. (2018).

Seedlings were considered to be individuals of the shrub-arboreal component ranging in height from 5–55 cm. The initial evaluation (conducted in October 2013) identified these plants based on the APG IV classification system (The Angiosperm Phylogeny, 2016). All individuals meeting this criteria were marked with metallic plates in the initial evaluation, facilitating the removal of individuals via random draw. Determination of basic phytosociological parameters (density, frequency, dominance, and importance) allowed for the identification of species with the highest densities in the seedling bank (Turchetto et al., 2017).

Following the initial evaluation, individuals were removed from each plot in accordance with the assigned removal intensities (0, 25, 50, 75, and 100% removal) in November 2013. Individuals were carefully dug up from the soil using a gardening shovel to minimize possible damage to the remaining seedlings. In all subsequent evaluations (i.e., from 3 to 36 months after removal), information pertaining to the number of individuals and species present in each plot was recorded, and assessments were performed every three months.

2.3. Data analysis

To assess the impacts of seedling removal on natural regeneration, an analysis of variance (ANOVA)

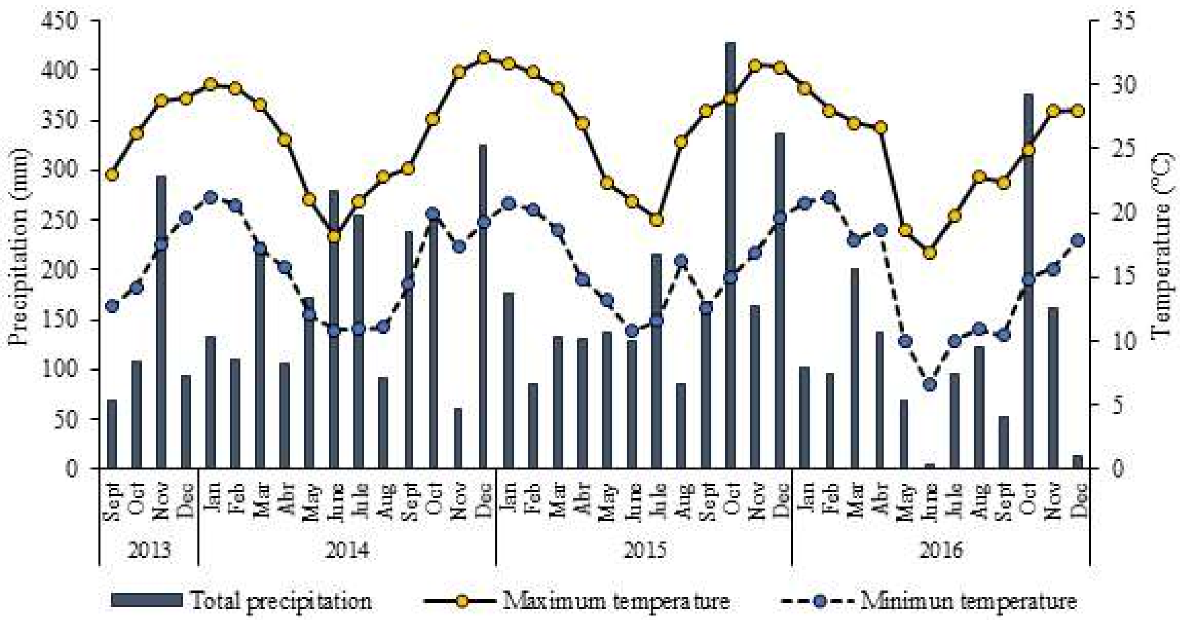

Figure 1 – Meteorological data for the study region (total precipitation, average maximum and minimum temperatures). Source - Meteorological Station of the Department of Plant Science of the Federal University of Santa Maria (2018).

Figura 1 – Dados meteorológicos da região de estudo (precipitação total, temperatura máxima média e temperatura mínima média). Fonte - Estação Meteorológica do Departamento de Fitotecnia da Universidade Federal de Santa Maria (2018).

was performed using generalized mixed linear models (GLM), with negative binomial distribution controlling for overdispersion and the likelihood-ratio test evaluated using the R packages 'MASS' (Venables and Ripley, 2002) and 'car', respectively. Pairwise comparisons of the estimated marginal means were then undertaken using the 'emmeans' package in R (Lenth et al., 2023).

The numbers of individuals and species between the initial evaluation (time zero) and subsequent evaluation periods were compared within each treatment using Dunnett's test to evaluate the resilience of the seedling community.

All analyses and graphics were performed in R Studio 4.0.0 (R Core Team 2020) at a 5% probability. Model fit was checked by comparing the fitted plot with a residual value plot, distribution in a QQ plot, and a histogram.

3. RESULTS

At 36 months, removal intensities below 50% of regenerating individuals presented the best results in terms of the numbers of individuals and regenerating species (Figure 2), whereas removal intensities equal to or greater than 75% had a negative effect on the density and richness of species present during natural regeneration.

When the number of individuals observed in the initial evaluation (time 0) was compared to the subsequent assessment, no significant differences were found for removal intensities of 0% (p= 0.562), 25% (p = 0.811), and 50% (p = 0.6955). However, at 36 months, seedling densities in plots with removal intensities of 75% (p = 0.048) and 100% (p=0.0020) were significantly lower than initial levels (Figure 3).

Differences in the number of species observed between evaluation periods were similar to those observed for the number of individuals. Community richness was not restored under removal intensities of 75% (p = 0.007) and 100% (p < 0.0001) (Figure 4), whereas under removal intensities of 25% and 50%, variation was similar to that observed in control plots (0% removal). These fluctuations corresponded to the emergence, recruitment, and mortality of some of the most abundant species, including *Actinostemon concolor* (Spreng.) Müll.Arg. and *Psychotria leiocarpa* Cham. & Schltdl. The reduction in individuals between evaluation periods was also associated with seasonality effects, particularly

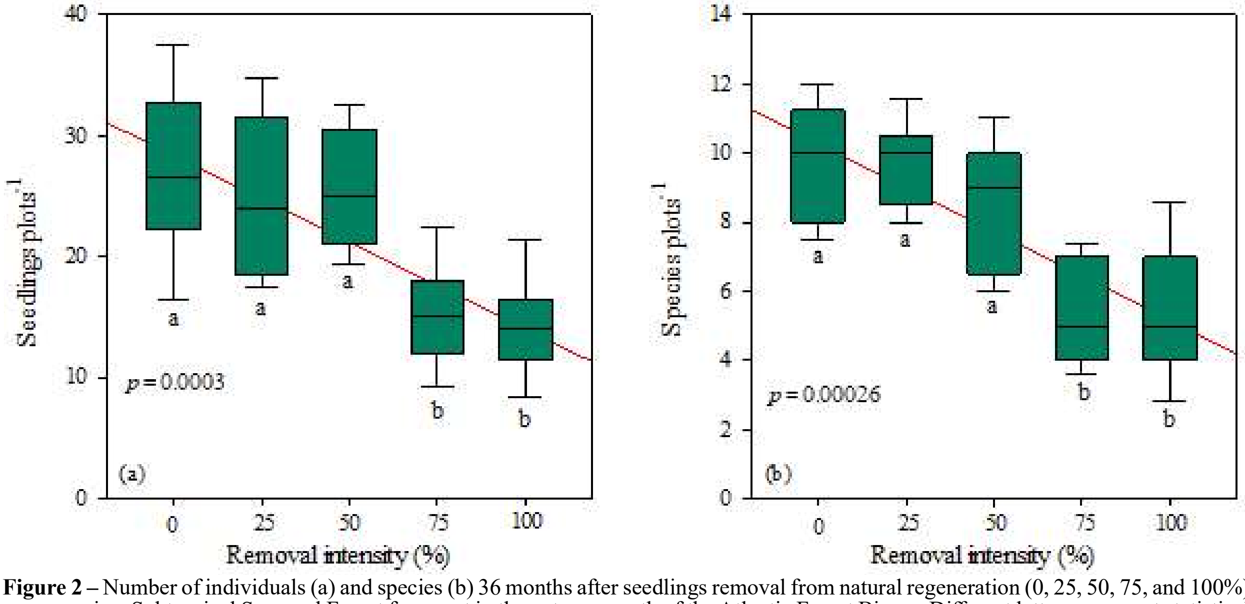

Figure 2 – Number of individuals (a) and species (b) 36 months after seedlings removal from natural regeneration (0, 25, 50, 75, and 100%) in a Subtropical Seasonal Forest fragment in the extreme south of the Atlantic Forest Biome. Different letters represent statistical differences by estimated marginal means.

Figura 2 – *Número de indivíduos (a) e espécies (b) 36 meses após a retirada das mudas da regeneração natural (0, 25, 50, 75 e 100%), em um fragmento de Floresta Estacional Subtropical no extremo sul do Bioma Mata Atlântica. Letras diferentes representam diferenças estatísticas por médias marginais estimadas.*

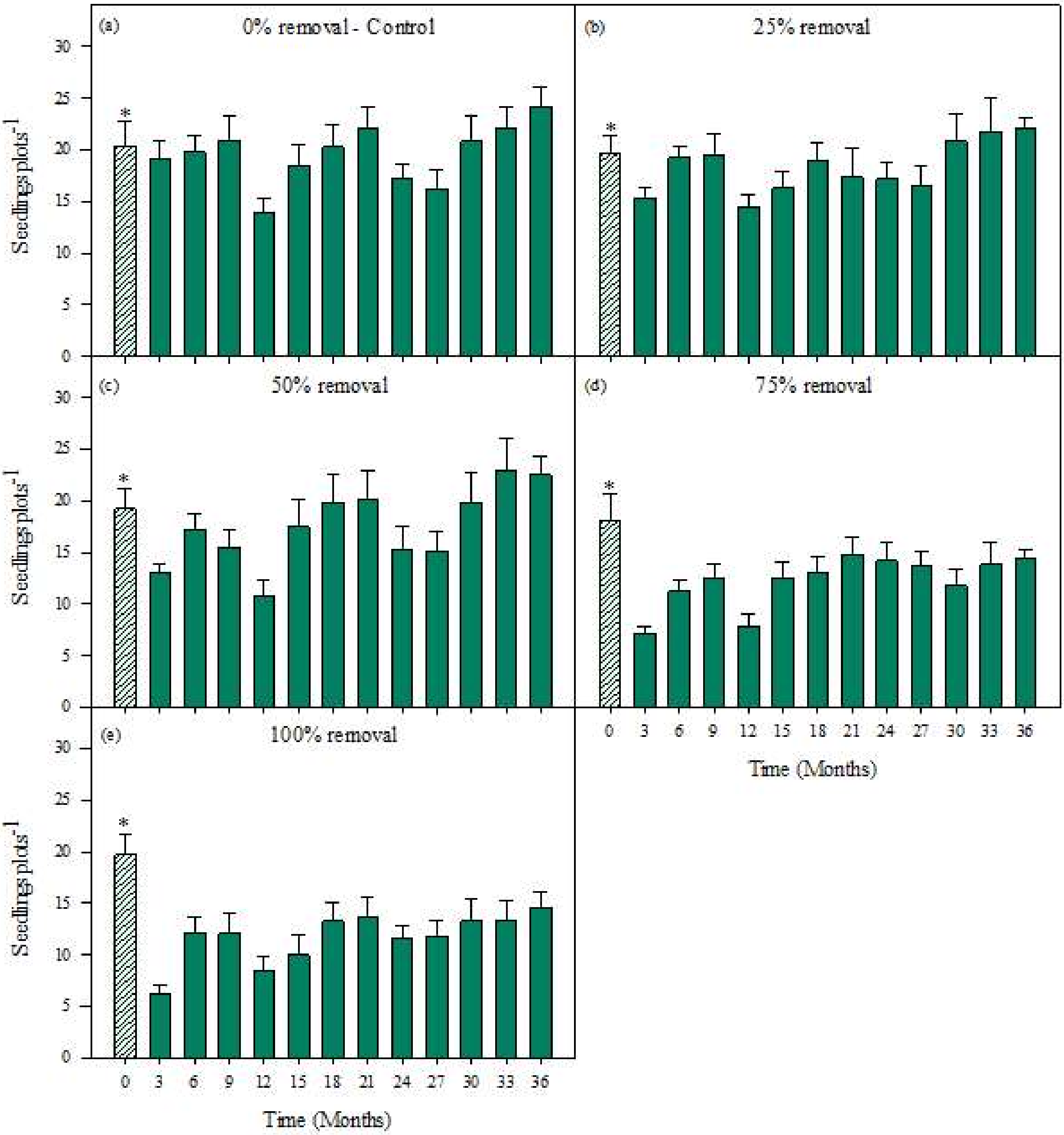

Figure 3 – Comparison of the average number of individuals observed in natural regeneration in the initial evaluation and the evaluations made after seedling removal for each intensity. 0% removal (a); 25% removal (b); 50% removal (c); 75% removal (d) and 100% removal (e). *Dunnett test at 5% probability of error. Vertical bars indicate the standard error.

***Figura 3** – Comparação do número médio de indivíduos observados na regeneração natural, na avaliação inicial com as avaliações posteriores a remoção das plântulas, para cada intensidade. 0% de remoção (a); 25% de remoção (b); 50% de remoção (c); 75% de remoção (d) e 100% de remoção (e). *Teste de Dunnett a 5% de probabilidade de erro. Barras verticais indicam o erro padrão.*

during summer, when temperatures are elevated and precipitation is less frequent (Figure 1).

For the most abundant species in the seedling bank, as determined by the number of individuals

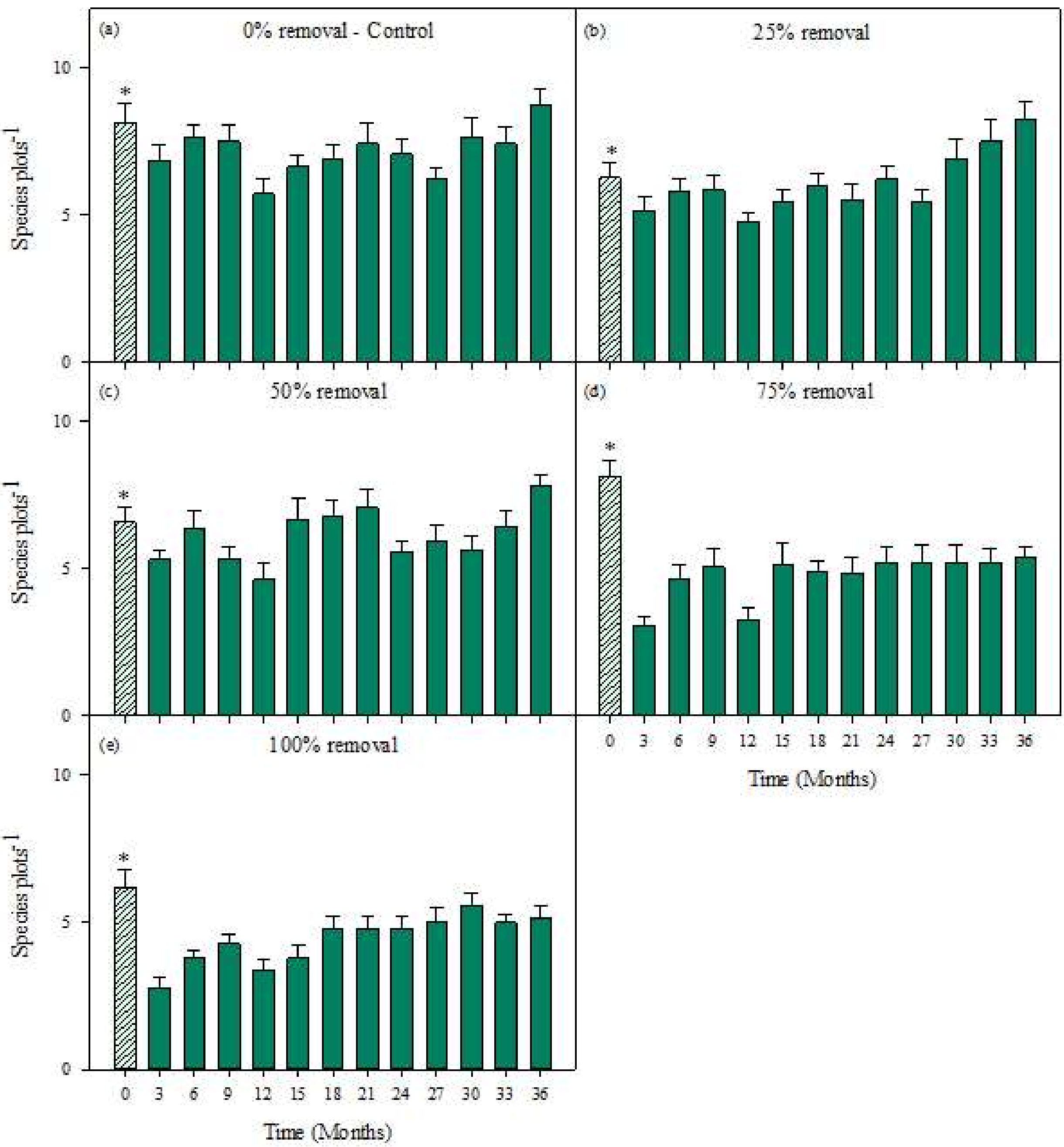

Figure 4 – Comparison of the average number of species observed in the natural regeneration in the initial evaluation with the evaluations after seedling removal for each intensity. 0% removal (a); 25% removal (b); 50% removal (c); 75% removal (d) and 100% removal (e). *Dunnett's test at 5% probability of error. Vertical bars indicate the standard error.

Figura 4 *– Comparação do número médio de espécies observadas na regeneração natural, na avaliação inicial com as avaliações posteriores a remoção das plântulas, para cada intensidade. 0% de remoção (a); 25% de remoção (b); 50% de remoção (c); 75% de remoção (d) e 100% de remoção (e). *Teste de Dunnett a 5% de probabilidade de erro. Barras verticais indicam o erro padrão.*

counted in each evaluation (Figure 5a) and removal intensity (Figure 5b), different recruitment strategies were observed in response to the removal of regenerating individuals.

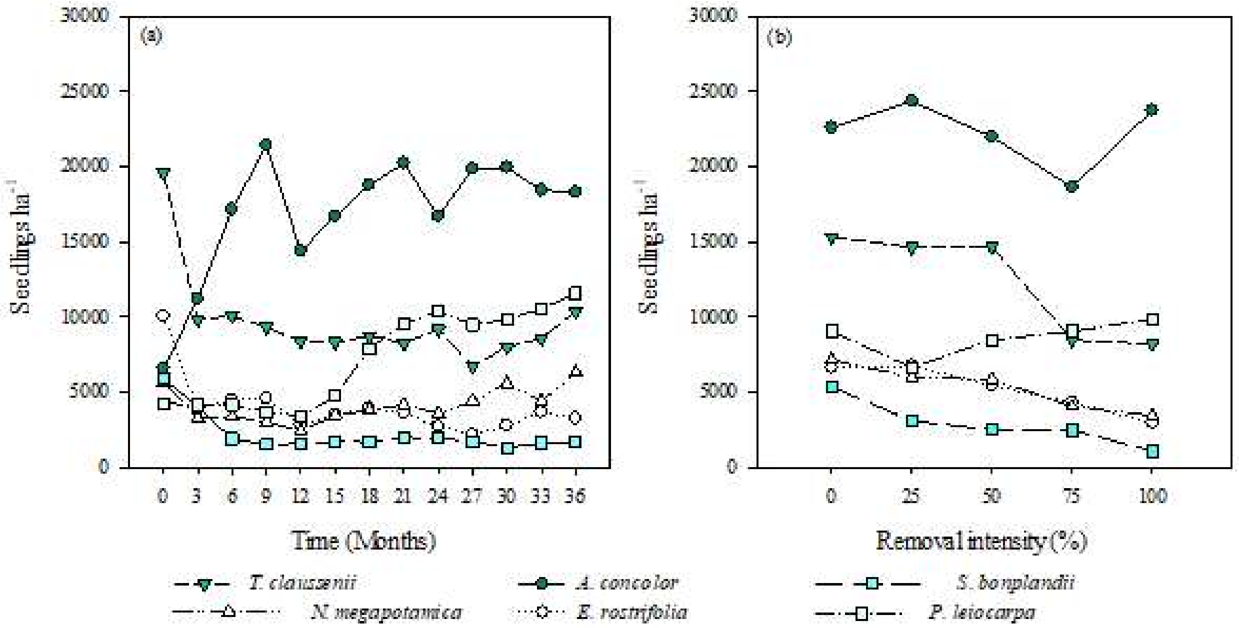

Figure 5 – Analysis of the number of individuals of the species with the highest density (*Actinostemon concolor* (Spreng.) Mull. Arg., *Eugenia rostrifolia* O. Legrand., *Sorocea bonplandii* (Baill.) WC Burger, Lanjouw & Boer, *Nectandra megapotamica* (Spreng.) Mez., *Trichilia claussenii* C. DC. and *Psychotria leiocarpa* Cham. & Schltdl.), as a function of evaluation time (a) and seedling removal intensities at 36 months after removal (b) in the extreme south of the Atlantic Forest Biome.

***Figura 5** – Análise do número de indivíduos das espécies com maior densidade (**Actinostemon concolor** (Spreng.) Mull. Arg., **Eugenia rostrifolia** O. Legrand., **Sorocea bonplandii** (Baill.) W.C. Burger, Lanjouw & Boer, **Nectandra megapotamica** (Spreng.) Mez., **Trichilia claussenii** C. DC. e **Psychotria leiocarpa** Cham. & Schltdl.), em função do tempo de avaliação (a) e das intensidades de remoção de plântulas aos 36 meses após a remoção (b) no extremo Sul do Bioma Mata Atlântica.*

A. concolor, Nectandra megapotamica (Spreng.) Mez, and *P. leiocarpa* were more abundant at the initial evaluation (time 0) than at 36 months following seedling removal. Of these, *A. concolor* was the only species equally abundant after three months of seedling removal as at the start.

Considering the effect of seedling removal on species with higher densities, *A. concolor* and *P. leiocarpa* were the only species that, 36 months after seedling removal, had higher numbers of individuals in plots where all seedlings were removed (100% removal). Individuals of *Eugenia rostrifolia* D.Legrand, *N. megapotamica*, and *Trichilia claussenii* C.DC. were reduced in number as removal intensity increased; however, at removal intensities of 25% and 50%, the numbers of individuals of these species were similar to those observed in the control plots (0% removal). Notably, the number of individual *Sorocea bonplandii* (Baill.) W.C.Burger et al. decreased by as much as 60% in treatment plots compared to controls, even under relatively low removal intensities (i.e., 25%) (Figure 5 b).

4. DISCUSSION

The results of our seedling removal experiment suggest that using seedling banks to produce seedlings from forest tree species for use in forest restoration efforts may be sustainable. Seedling removal intensities of up to 50% did not compromise the characteristics or structure of the regenerating community, as evidenced by the fact that treatment plots subjected to these intensities remained similar to the control (0% removal). Other studies on different forest typologies also found that low removal intensities (below 50%) do not interfere with plant community dynamics (Viani and Rodrigues, 2008; Turchetto et al., 2018).

However, the removal of 50% or more of seedlings reduced both the number of individuals and species richness, indicating that this level represents a threshold for the sustainability of regenerating individuals. As intensities rose, fewer species constituted the seedling bank, probably because of the need to maintain a "stock" with some species whose dispersion and/or regeneration is more difficult. This scenario demonstrates that removing individuals from seedling banks can significantly impact some species, especially those with a low regeneration density.

Therefore, a thorough understanding of species dynamics in each habitat is urgently needed, including the causes, mechanisms, and factors that drive the natural regeneration process. However, at present, little is known about the regenerative capacity and population structure of the species that comprise Brazil's forests, especially in terms of their response to the impacts of anthropogenic activities (Omondi et al., 2016).

Of the most abundant species in our forest fragment, only seedlings of *A. concolor* were more abundant at the time of the second evaluation (i.e., the first following removal, December/2013) than at the time of the initial evaluation. *A. concolor* flowers and develops fruit in October and November (Andreis et al., 2005), suggesting that a higher number of individuals of this species would be expected in subsequent evaluation periods given the dispersal of propagules and/or seed drop during this time; moreover, according to Scipioni et al. (2011), this species thrives in the understory, a characteristic that makes it a prime candidate for seedling banks.

On the other hand, the seedling abundance of the species was considerably lower in the evaluations carried out at 12 months (December/2014) and 24 months (December/2015), most likely attributable to the higher average maximum temperature and reduced rainfall characteristic of this season. Although most individuals were less than 10 cm tall, a functional root system is required if they are to establish, given that, as noted by McLaren and McDonald (2003), high temperatures combined with water deficits can lead to desiccation and plant death. Thus, because *A. concolor* is a typical understory species that adapts to mild temperatures, newly emerged individuals are more susceptible to mortality.

Seedlings of *E. rostrifolia*, *N. megapotamica*, *T. claussenii*, and *S. bonplandii* were reduced in abundance across all treatments, regardless of removal intensity. Sccoti et al. (2011), who examined the mechanisms of natural regeneration in a Deciduous Seasonal Forest remnant, reported that the dispersal of *E. rostrifolia* propagules was greatly reduced over two consecutive years, demonstrating the reproductive seasonality of this species. Lower rates of regeneration exhibited by *N. megapotamica*, *T. claussenii*, and *S. bonplandii* may also be due to a rapid loss of viability, relatively lower fruit production, and seasonality effects.

Differing tolerance levels to removing regenerating individuals were also observed among species. For instance, *A. concolor* and *P. leiocarpa* exhibited high regeneration capacity, tolerating 100% removal, whereas *E. rostrifolia*, *N. megapotamica*, and *T. claussenii*—despite their populations eventually being restored in the seedling bank—only maintained regeneration capacity at 50% or lower removal intensities. Similarly, *S. bonplandii* abundance did not show signs of rebounding even at 36 months after removal. As Andrew et al. (2015) point out, even plants that grow in the same community typically differ in their requirements, and as such, responses to human disturbances will vary among species.

For several species, individual abundances were significantly reduced compared to the initial evaluation, and in some cases had disappeared altogether. Viani and Rodrigues (2008), who analyzed the impact of seedling removal in a forest remnant, observed that both species with lower regeneration densities and locally rare species were extirpated from the experimental area, demonstrating the detrimental effects of seedling removal on populations of such species. As such, removing species with low population densities should be avoided when the objective is to produce forest species seedlings from natural regeneration.

The results of the present study indicate that *Picrasma crenata* (Vell.) Engl. and *Diospyros inconstans* Jacq., both rare late secondary species with discontinuous distributions (Carvalho, 2006), vanished from the experimental area following the removal of regenerating individuals, indicating that seedling removal reduced the capacity of these populations to regenerate sustainably.

Populations of *Prunus myrtifolia* (L.) urb. and *Cordia americana* (L.) Gottschling JSMill., which require high levels of light during development (Leonhardt et al., 2008; Vaccaro et al., 1999), were significantly lower in the seedling bank following the removal of regenerating individuals. Developing and maintaining soil seed banks is an essential adaptive strategy for early-successional species (Dalling et al., 1998). Regeneration occurs after significant disturbances lead to increased light exposure in the understory and cause seeds to translocate to the upper strata of the forest soil. Because of this, excessive removal of these species from the plant community can hamper forest successional processes following disturbances (e.g., clearings that form after trees fall).

During this experiment, it was possible to identify seasonality in the recruitment of seedlings from the shrub-arboreal component. Previous research on seedling banks in Seasonal Tropical Forests have also indicated species density and richness variations over time during regeneration (McLaren and Mcdonald, 2003; Venturoli et al., 2011). Both richness and density are influenced by climatic factors.

We observed marked seasonal effects on species density and richness of species during natural regeneration, accounting for the reduction in both individuals and species in the evaluations conducted at 12 months (December/2014) and 24 months (December/2015) following removal. These assessments were performed in summer when temperatures were considerably higher (Figure 1). Previous studies have shown that natural regeneration rates of seasonal forests are greatly affected by ambient temperatures (McLaren and McDonald, 2003), and that environmental conditions influence a wide range of plant physiological processes, including seed production patterns, seedling germination, survival, and development (Khurana and Singh, 2001). For instance, Gerhardt et al. (1992) reported a reduction in the number of individuals during warmer periods of the year, while Metz et al. (2008) noted that seedling communities are more susceptible to higher temperatures and seasonal water deficits because of their shallower root systems restricted to the surface layer of the soil. Moreover, periods of infrequent precipitation can result in water deficits, exacerbated by higher temperatures and more intense solar radiation, leading to plant desiccation and mortality (McLaren and McDonald, 2003).

The results of our analysis suggest that using seedlings taken from natural areas as a source of propagules for subsequent use in forest restoration projects through the transplantation of regenerating individuals may be sustainable if undertaken at moderate removal intensities (up to 50% of individuals). However, restoration efforts for which this technique might be used should rely only on species with abundant natural regenerative capacity and that develop seedling banks as an adaptive strategy. As Souza et al. (2018) observed, of the thousands of seedlings in a forest, only a handful of individuals complete their life cycles, while the majority succumb to abiotic and biotic filters and stochastic events.

5. CONCLUSION

Our experiments show that removing regenerating individuals at high intensities (>50% of seedlings) compromises the recruitment of new individuals and seriously threatens successional continuity.

Late secondary species generally have a high density of individuals in the seedling bank, and are thus generally resilient to anthropogenic intervention. However, the potential for recovery varies greatly among plant species. Our analysis indicates that removing up to 50% of individuals in the seedling bank is tolerable for *A. concolor*, *E. rostrifolia*, T. *claussenii*, *N. megapotamica*, and *P. leiocarpa*.

In addition, any level of seedling removal from natural banks can greatly impact or even lead to the local extirpation of rare or low-density species, and therefore, removal of seedlings is recommended only for species with high densities of individuals in the seedling bank.

AUTHOR CONTRIBUTIONS

FT and MMA conceived and designed the study; FT, AMG, RMC and JCM conducted the experiment; FT and FOF analyzed the data; FT and MMA wrote the first manuscript draft; AMG, RMC, JCM and FOF reviewed and edited the manuscript; All authors read and approved the final manuscript.

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