Long-Term Impact of Forest Fragmentation on Tree Functional Diversity, Trait Composition and Aboveground Biomass.

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Research

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Abstract

Background: Community composition on fragmented forest remnants has been shown to diverge from their natural successional path, revealing an alternative state which has been known as retrogressive succession. Here we show the long-term monitoring of a small forest fragment concerning community structure, species richness, functional diversity and composition throughout 17 years to offer a means to generalize community performance under the impacts of forest fragmentation.

Results: The adult tree community showed shifts on its functional composition: reduction in species’ maximum height and percentage of simple leaves, indicating an investment in resource-acquisitive and disturbance adapted traits. However, we also found a gradual increase in wood density throughout the years for the adult community. For the overall community, functional composition analysis indicated a gradual reduction in the percentage of simple leaves and a significant increase in aboveground biomass. The decrease in Hmax and simple leaves, especially for the adult tree community, are mostly related to microenvironmental conditions caused by edge effects, as desiccation and tree canopy damage.

Conclusion: Our results show that natural regeneration is being negatively affected, except for aboveground biomass. Although these findings could have resulted from a transient dynamic, they constitute a warning to future conservation policies around the ecological integrity of small forest fragments.

Background

The high rates of forest degradation and fragmentation across tropical rain forests have led to a scenario where most forest remnants are reduced in size and inserted in a human transformed matrix (Magnano et al. 2014; Matos et al. 2016; Valdés et al., 2019; Zambrano et al., 2020). These fragmented remnants are usually surrounded by pastures and arable lands beyond other human settlements (Valdés et al. 2019). Consequently, fragmentation promotes the reduction of forested areas, isolation of remnants and creation of edges (Kupfer et al. 2006; Matos et al. 2016), and threatens the long-term persistence of species (Turner and Corlett 1996; Pereira et al. 2010; Rands et al. 2010), as well as the goods and services provided by those ecosystems (Foley et al. 2007; Zambrano et al. 2020). Small and isolated fragments are exposed to a variety of edge effects (hotter and drier microclimate, increased light intensity, wind turbulence) and immigration of alien species (Murcia 1995; Turner and Corlett 1996; Laurance et al. 2006b, a; Haddad et al. 2015). Thus, the sustainability of tree communities under such environmental pressures has motivated studies on the mechanisms by which species coexistence is maintained in a local-scale habitat.

The reduction of forest remnants’ area drives biodiversity loss directly through the removal of species and indirectly by changes in environmental conditions at forest edges which favour the performance of early successional species (Laurance et al. 2002, 2006a; Tabarelli and Santos 2008; Lôbo et al. 2011). Community composition from fragmented forests has been shown to diverge from their natural
successional path, revealing an alternative state which has been known as retrogressive succession (Santos et al. 2008; Tabarelli et al. 2008a, 2012; Magnago et al. 2014; Rocha-santos et al. 2016; Ewers et al. 2017). This altered successional trajectory is characterized by increased rates of mortality (Lindenmayer et al. 2012), species-poor communities with a proliferation of disturbance-adapted tree species (Laurance et al., 2006b; Tabarelli and Lopes 2008), loss of large trees (due to physiological stress and wind turbulence; Oliveira et al., 2008, increase of small-seeded softwood species (Laurance et al. 2006b), lower biomass storage potential (Van Der Sande et al. 2016) and impacts phylogenetic diversity (Matos et al. 2016; Zambrano et al. 2020). Overall, the shift in successional trajectories caused in a great part by the edge creation promotes a functional simplification of plant communities affecting late-successional trees (Suding et al. 2008).

Species respond to changes in environmental conditions through their functional traits, represented by plant community functional composition (defined by community weighted trait means, CWMs) and functional diversity (i.e. the distribution of traits within a community) (Diaz and Cabido 2001; Candido et al. 2020). Functional traits represent physiological trade-offs in plant strategies (Wright et al. 2004; Reich 2014), being greatly useful to summarize changes in community composition in response to selective pressures and in relation to forest succession trajectories (Poorter et al., 2019). Therefore, long-term monitoring of functional diversity and composition throughout time offer a means to generalize community performance under the impacts of forest fragmentation.

Habitat fragmentation can lead to major changes on species community composition, yet little is known about its long term impacts, especially on functional traits composition and aboveground biomass (Laurance et al. 2006b; Santos et al. 2008; Magnano et al. 2014). Old-growth forest fragments surrounded by human-modified landscapes offer an excellent opportunity to examine the long-term effects of habitat fragmentation on diversity, functional composition and ecosystem services potential of such small forest remnants. Thus, understanding how these effects influence forest regeneration and successional processes over time is of crucial importance to ensure forest persistence in fragmented landscapes.

Here we investigated how species richness, functional diversity and composition and aboveground biomass change over 17 years in a small tropical forest remnant surrounded by human-modified landscapes. We hypothesized that the tree community will show altered succession trajectory signs such as i) high mortality rate (superior to the recruitment rate); ii) decrease in species diversity and aboveground biomass throughout time and iii) shifts in functional composition toward a prevalence of species with highly colonization ability and early-successional traits (abiotic dispersion, small seed size, lower stature and wood density and compound leaves) throughout time. Finally, we also tested for shifts in functional composition within the adult and juvenile trees, as different forest stratum face different environmental constraints.

Materials And Methods
Study area

The study was conducted in the southeast region of Minas Gerais, Brazil (21°13’11” S – 44°58’15” W), on a remnant of the endangered Brazilian Atlantic Rain Forest, classified as Semideciduous Seasonal Forests (IBGE 2012). The mean altitude is 884 meters. The regional climate is classified as Cwb (Mesothermic climate of Köppen), defined by dry winters and mild summers. Mean annual rainfall and temperature are 1493 mm and 19.3°C, respectively (Vilela and Ramalho 1979). Soil types in the region are primarily argisols and nitosols (Machado and Oliveira-Filho 2010). Fragment area is currently around 4.0 hectares (ha) and it is surrounded by a low biomass landscape matrix, composed mostly by coffee plantations, pastures and a small dawn drainage canal.

Data collection

Data for this study was derived from 17 years (2000 to 2017) of forest survey from the 29 permanent plots of 0.4 ha each (20 m x 20 m), a total of 1.16 ha sampled (data were obtained from ForestPlots.net; Lopez-Gonzalez et al. 2009; Lopez-Gonzalez et al. 2011). All trees with a diameter at breast height (DBH) ≥ 5 cm were identified to species level. All plots were first measured in 2000, re-measured in 2005, 2011 and 2017, when surviving, dead and recruiting (individuals that met the inclusion criterion) were evaluated. Species identities were checked for nomenclatural synonyms using the online tool Taxonomic Name Resolution Service (TNRS) ver. 3.2 (Boyle et al. 2013).

To analyze the changes in species richness of the trees between the four surveys (2000, 2005, 2011 and 2017), we computed species rarefaction curves using the platform R (R Core Development Team 2018) and the vegan package (Oksanen et al. 2015).

Demographic metrics

The changes in the tree community over time were determined for each plot by calculating the following mean annual abundance rates: Mortality (M = (1 - [(N0 - Nm) / N0] 1 / t) * 100) and recruitment (R = (1 - (1 - Nr / Nt) 1 / t)*100, whereas biomass dynamics were described by basal area loss (P = (1 - ((AB0 - (ABm + ABd)) / AB0) 1 / t) *100) and gain (G = (1 - (1 - (ABr + ABg) / ABt) 1 / t) * 100), where: t is the time elapsed between censuses; N0 and Nt the initial and final tree counts; Nm and Nr are dead trees and recruit counts; AB0 and ABt are the initial and final tree basal area; ABm is the basal area of dead trees; ABr is basal area of recruits; and ABd and ABg are the increment and decrement in the basal area from the surviving trees (Sheil et al. 2000; Sheil and May, 1996).

Functional traits

The functional traits considered in the study are related to natural successional trajectories of forests (Van Der Sande et al. 2016), species stress resistance, and species standing biomass (Attri et al. 2015; Lohbeck et al. 2015; Poorter et al. 2015): Maximum height, wood density, leaf type, seed size and dispersal mode were obtained following standardized protocols (Cornelissen et al. 2003; Pérez-Harguindeguy et al. 2013).
Species maximum height (Hmax, m) is an indicator of the adult stature of species, potentially related to the species longevity and life-history strategy (King et al. 2006), and was calculated as the 95th-percentile height of all trees of the species. Species wood density (WD, g.cm-3) represents biomass per wood volume constructed and was obtained from the Global Wood Density Database (filtered by Tropical South America, Zanne et al. 2009). For the species with WD not available, we used mean values for the WD of the genus or family. The leaf type (LT, categorical data) reflects the species heat balance. In other words, leaf size profoundly affects a variety of biological water and energy processes and has particularly important implications for understanding the adaption strategy of plants to environmental changes (Wang et al. 2019). All species were categorized: compound and simple leaves. Seed size (SS, categorical data), although usually related to the competitive vigour of the seedlings (Kitagima 2007), is also an important life-history trait for trees, correlated to a suite of morphological and physiological traits of pioneer species (small seeds) and shade-tolerant species (large seeds) (Poorter and Rose 2005; Osuri and Sankaran 2016). Qualitative data for species SS were obtained from herbarium specimens, and the species were classified as small seeds species (seed length < 1.5 cm) and large seeds species (seed length > 1.6 cm), following Tabarelli and Peres (2002) and Santos et al. (2008).

Dispersal mode (DM, categorical data) is an indicator of the ability of plants to colonize habitats and is especially important in fragmented landscapes because they can improve predictions of dispersal probability and seed bank composition (Kraft et al. 2015). All species were categorized: biotic dispersion and abiotic dispersion.

Community weighted mean traits and functional diversity indices

Community weighted mean (CWM) trait values (Maximum height, wood density, leaf type, seed size and dispersal mode) and functional diversity indices were calculated per plot and per inventory (2000, 2005, 2011 and 2017) for the overall community, juveniles (5 cm ≤ DBH < 10 cm) and adults (DBH ≥ 10 cm). Both were weighted by species abundance to equally weight recruiting and dying trees on changes in CWM values (van der Sande et al. 2016). Adult survivors respond slowly to disturbance and tend to make a large contribution to community biomass because they are large (Chazdon et al. 2007), while recruits (smaller individuals) respond fast to disturbance and contribute more to abundance (Van Breugel et al. 2007).

For functional diversity, we checked the functional richness (FRic), an indicator of the species volume occupying the niche space of a community (Villéger et al. 2008) which measures the extent to which the trait space is filled. The functional richness and the CWM values were calculated using Gower's distance (that allows mixed traits types: continuous, ordinal and categorical). The functional analyses were calculated using the 'FD' package in R (Laliberté et al. 2015).

Biomass estimates

For every tree with DBH ≥ 5 cm, the aboveground biomass (AGB) was calculated using the allometric formula of Chave et al. 2014: AGB = exp[-1.803-0.976E + 0.976ln(DBH) + 2.673ln(DBH)-0.0299[ln(DBH)]^2]
and the parameters, DBH (cm), species wood density (WD, g cm$^{-3}$) and E, which is a measure of environmental stress (retrieved from Rejou-Mechain and Chave, 2014).

**Statistical analysis**

We used generalized linear mixed models (GLMM) to assess the differences in species richness, functional diversity and composition (SR, FRic, CWM Hmax, CWM WD, CWM LT, CWM SS and CWM DM) and aboveground biomass among the four forest inventories (2000, 2005, 2011 and 2017). Measures from the plot from the different years of monitoring were considered as a random factor, to account the lack of independence within the plots among the four inventories (Bates et al. 2014a).

When necessary, data were log10 or square root transformed prior to analysis to meet the assumptions of normality and homoscedasticity. Tukey post-hoc tests were used to assess the differences between the forest surveys (2000, 2005, 2011 and 2017).

To test for potential spatial nonindependence of plots, we assessed the degree of spatial autocorrelation in our linear mixed model residuals using the Moran's I test. A $p$-value < 0.05 would indicate that the model residuals show spatial autocorrelation, which was not found for any of our models (Kissling and Carl 2008) (Table S1).

All analyses, figures and graphs were performed using the platform R (R Core Development Team 2018) and the following packages: multcomp (Bretz et al. 2015), lme4 (Bates et al. 2014b), lmerTest (Kuznetsova et al. 2016), MuMIn (Barton 2016), and ggplot2 (Wickham and Chang 2016).

**Results**

We found that the annual mortality in the tree community was higher than recruitment for all forest inventories, except for the last one, resulting in a net decrease in total tree abundance (Table 1). In 2000, 1275 individuals were recorded consisting of 151 species within 46 families (Table S2). In 2005, 1234 individuals were recorded, a reduction caused by the higher mortality rate (3.28% year$^{-1}$) in comparison with the recruitment rate (2.65% year$^{-1}$) for the survey interval. A similar pattern was found for 2011 when the lower recruitment rate (2.86% year$^{-1}$) and high mortality rate (4.00% year$^{-1}$) resulted in a reduction of tree abundance (1150). In 2017 there was a small increase in abundance (1153 individuals), a result from the slightly higher recruitment rate (2.48% year$^{-1}$) in comparison with the mortality rate (2.43% year$^{-1}$). Overall, from 2000 and 2017, we found a decrease in 9.56% in tree abundance (Table 1).

The higher rates of annual basal area loss compared to the gain rates in the basal area in the community within the first three intervals resulted in a loss of basal area (34.01 m$^2$, 32.81 m$^2$, and 31.64 m$^2$ for 2000, 2005 and 2011, respectively). However, a strong increase in the total basal area was recorded in 2017 (39.40 m$^2$), resulting in a positive net change of 13.68% between 2000 and 2017 (Table 1). Indeed, we found an increase in AGB for the last survey, resulting in a net gain in 18.61% in biomass (Table 2).
The small reduction found in species richness was not significant (Table 2, Table S3), as also suggested by the rarefaction curves as there is an overlap of the standard deviation of the four richness curves (Fig. 1). Species functional richness showed a small but not significant reduction (Table 2).

**Table 1**
Tree community dynamics components of a Semideciduous Forest in Lavras, Minas Gerais State, Brazil.

| Survey interval | 2000–2005 | 2005–2011 | 2011–2017 |
|-----------------|------------|------------|------------|
| Number of plots | 29         | 29         | 29         |
| Number of trees:|            |            |            |
| Initial         | 1275       | 1234       | 1150       |
| Final           | 1234       | 1150       | 1153       |
| Survivals       | 1079       | 966        | 992        |
| Deads           | 196        | 268        | 158        |
| Recruits        | 155        | 184        | 161        |
| Mortality rate (% year\(^{-1}\)) | 3.28 | 4.00 | 2.43 |
| Recruitment rate (% year\(^{-1}\)) | 2.65 | 2.86 | 2.48 |
| Basal Area:     |            |            |            |
| Initial         | 34.01      | 32.81      | 31.64      |
| Final           | 32.81      | 31.64      | 39.40      |
| BA loss rate (% year\(^{-1}\)) | 2.67 | 3.03 | 2.52 |
| BA gain rate (% year\(^{-1}\)) | 1.97 | 2.44 | 6.03 |
| Dead (m\(^2\)) | 3.78       | 4.69       | -3.56      |
| Recruits (m\(^2\)) | 0.72 | 0.70 | 2.13 |
| Survival (m\(^2\)) | 1.87 | 2.81 | 9.19 |

 BA Basal Area
Table 2
Species richness, functional richness and aboveground biomass per plot for the overall community fitted from generalized linear mixed models.

|                  | 2000  | 2005  | 2011  | 2017  |
|------------------|-------|-------|-------|-------|
| Species richness | 22.06a| 21.44ab| 20.13b| 20.48ab|
| Functional richness | 20.62a| 20.56a| 20.53a| 20.16a|
| Aboveground biomass (Mg/ha) | 255.05b| 249.94b| 242.02b| 313.36a|

Different letters indicate significant differences among mean values (p < 0.05) based on pairwise comparisons in mixed linear models (Tukey’s HSD).

For the overall community, functional composition analysis indicated a gradual reduction in the percentage of simple leaves (Fig. 2, Table S4). The adult tree community showed a reduction in Hmax and the percentage of simple leaves, indicating an investment in resource-acquisitive and disturbance adapted traits. However, we also found a gradual increase in wood density through the years for the adult community (Fig. 2). The juvenile tree community did not show any shifts in functional trait composition.

**Discussion**

This study has provided relevant insights into the successional trajectory effects of fragmentation on the tree community of a small forest remnant surrounded by human-modified landscapes. Under 17 years of community monitoring, the dynamics' analysis revealed a continuous reduction in the overall tree abundance and shifts in trait composition favouring adult species with resource-acquisitive, pioneer life-strategies (reduction in tree maximum height and in species with simple leaves and a slight increase in the percentage of small seeds). However, for the adult tree community (DBH > 10 cm), we found a significant increase in wood density. Indeed, the last monitoring interval (2011–2017) showed a strong increase in total basal area and a significant increase in aboveground biomass (reaching higher values than found for the first survey). Based on these findings, our hypothesis was partly accepted, as natural succession is being negatively affected, except for aboveground biomass.

Other studies in Neotropical small forests have shown tree communities dominated by a small set generalist species in forest fragments with one to 10 hectares (Laurance 2001; Laurance et al. 2006b). After analyzing the long-term dynamics of a forest fragment with 4 ha, we found a decrease in Hmax and simple leaves for the adult tree community and a decrease in simple leaves for the overall tree community. During succession, pioneer species are expected to be replaced by shade-tolerant ones, with the community gradually accumulating species diversity and ecological functions (Guariguata and Ostertag 2001). This trajectory is changed when strong environmental filters lead to the selection of species that share the adaptation strategies required to colonize and survive in a changed post-disturbance habitat (Tabarelli et al. 2008).
In disturbed habitats, the establishment of late-successional species is compromised until the stressful conditions had reduced to an acceptable state (Lebrija-Trejos et al. 2010). Edge creation, e.g., promotes microclimatic and structural changes within the forest with severe consequences to tree communities (Murcia 1995), such as desiccation which act as a climate filter favouring mostly generalist pioneer species (Pierce et al. 2017). Leaf type reflects adaptations to reduced water availability and therefore a gradual increase in species with simple leaves is expected in the course of succession towards more mature and undisturbed forests (Wright et al. 2017; Gei et al. 2018). Consequently, we found a gradual increase of trees with compound leaves, a strategy to prevent the excessive water loss as plants with pinnate or bipinnate leaves can release individual leaflets (and not complete leaves) during severe water stress, increasing heat dissipation and regulating temperature (Wright et al. 2017; Gei et al. 2018).

When considering the adult tree community, we also found a decrease in species Hmax. The reduction of adult trees’ Hmax is also expected in communities under disturbance (Carreño-Rocabado et al. 2012). The tree canopy damage allows trees to get more access to light, which no longer consists of a limiting-resource (Ruiz-jaen and Potvin 2011). These results suggest the presence of strong post-fragmentation edge effects, leading to an increase in pioneer species while shade-tolerant species are negatively impacted (Zambrano et al. 2020). As a consequence, adult tree species may not invest in increasing their height as much as other life strategies (King et al. 2006). Besides, it is also expected a great loss of large trees due to physiological stress and wind turbulence (Oliveira et al., 2008, also see Laurance et al., 1988, 2000).

The increase in wood density throughout time in the adult tree community can also be related to disturbed habitats as it guarantees trunk resistance to physical damages by herbivores, pathogens and woody debris (Van Gelder et al. 2006; Mccarthy-Neumann and Kobe 2008) and also an indication of hydraulic safety (Sterck et al. 2006). Previous studies have shown the lack of wood density variation with fragmentation and fragment forest size, even for secondary forests (Magnago et al. 2014; Liu et al. 2019). However, since wood densities of species can be affected by environmental changes due to fragmentation (Laurance et al. 2006a, b; Nock et al. 2009), the average wood densities we used from the literature (Chave et al. 2009; Zanne et al. 2009) would miss any such variation. Our functional diversity analyses could be refined in future analyses using wood densities derived from in situ measurements, and also, when herbarium collections permit, fruit and seed sizes as continuous rather than categorical variables.

The gain in basal area in the community indicates their species’ high productivity (Finegan et al. 2015). Indeed, the higher basal area is translated in gains in biomass, which showed a significant increase through time. The values for AGB found in this study are comparable to large undisturbed rainforests (Pyles et al. 2018). Previous studies have reported that fragmentation has no significant effect on biomass, with the productivity of the shade-intolerant trees having a high role in the accumulation of biomass (Magnago et al. 2014; Liu et al. 2019).
Proximity to edge and small fragment size favours a turnover with trees typical from late-successional stages being replaced by pioneer and especially the short-lived species (Nascimento and Laurance 2004; Tabarelli et al. 2004; Laurance et al. 2006a; Michalski et al. 2007; Santos et al. 2012). Consequently, forest regeneration potential might be lower in these fragments, with detrimental consequences for tree diversity and regeneration dynamics in the long term. However, the process of forest succession can take many years of centuries, therefore longer monitoring is needed to check whether the conditions found in the studied fragment matches the retrogressive succession hypothesis or is rather a transient, regeneration dynamic in human-modified landscapes that might lead to advanced successional stages (Guariguata and Ostertag 2001; Letcher and Chazdon 2009; Ewers et al. 2016; Muscarella et al. 2016).

**Conclusion**

This study provides important contributions to the influence of fragmentation on the successional trajectory of tree communities on small forest remnants surrounded by human-modified landscapes. Based on our findings, natural succession is being negatively affected, except for aboveground biomass. The decrease in Hmax and simple leaves, especially for the adult tree community, are mostly related do microenvironmental conditions caused by edge effects, as desiccation and tree canopy damage. Although those findings could have resulted from a transient dynamic, they constitute a warning to future conservation policies around the ecological integrity of small and isolated forest fragments.

**Abbreviations**

DBH: Diameter at breast height; Hmax: Species maximum height; WD: Species wood density; LT: Leaf type; SS: Seed size; DM: Dispersal mode; CWM: Community weighted mean; FRic: Functional richness; AGB: Aboveground biomass.

**Declarations**

**Ethics approval and consent to participate**

Not applicable

**Consent for publication**

Not applicable

**Availability of data and materials**

The datasets generated during and/or analysed during the current study are available in the ForestPlots repository, www.forestplots.net.

**Competing interests**
The authors declare that they have no competing interests.

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**Authors’ contributions**

Study concept and design: Borges E, Pyles, M. Analysis and interpretation of data: Borges E, Pyles, M. Drafting of the manuscript: Borges E, Bueno, M. Critical revision of the manuscript for important intellectual content: Pyles, M, Bueno, M. Statistical analysis: Borges E, Pyles, M. Obtained funding: Borges E, Fontes M, Santos R. Study supervision: Oliveira-Filho A, Bueno, M. The author(s) read and approved the final manuscript.

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Figures

![Species rarefaction curves for species richness in a semidesiduous tropical forest tree community at Lavras, Minas Gerais, southeast Brazil in 2000, 2005, 2010 and 2017.](image)

**Figure 1**

Species rarefaction curves for species richness in a semidesiduous tropical forest tree community at Lavras, Minas Gerais, southeast Brazil in 2000, 2005, 2010 and 2017.
Figure 2

Community trait composition for the four years of forest inventories (2000, 2005, 2011 and 2017) for the overall community, adult tree community and juveniles. Different letters indicate significant differences among mean values (p < 0.05) based on pairwise comparisons in mixed linear models (Tukey’s HSD).

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