

## Natural and anthropic forest fragments have distinct ecological behavior due to their different origin and landscape context

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**Abstract:** We tested the hypothesis that plant populations in natural fragments have distinct ecological behavior in relation to anthropic fragments. We selected the species *Myrcia splendens* (SW.) DC. in 2 forest fragments located in southeastern Brazil that present different origins and landscape contexts. The natural fragment originates from landscape relief variations and is inserted in a native grassland matrix, while the anthropic fragment originates from fragmentation due to area conversion and is inserted in an agricultural matrix. We established transects covering an area from one border to the other in each fragment, and we established subunits of 400 m<sup>2</sup> within them. Within each subunit we measured all individuals of *M. splendens* at all establishment stages (seedlings to established trees). We monitored population behavior in the two fragments for 4 years, evaluating their spatial structure, temporal behavior, and age structure. The two populations present distinct ecological behaviors associated with their different origins and landscape contexts; the natural fragment is exposed to disturbances it has adapted to throughout the evolutionary process, whereas the anthropic fragment is subject to new evolutionary disturbances, such as effect edge, cattle, and recurrent fire.

**Key words:** Natural forest patches, *Myrcia splendens* (SW.) DC., capões de mata, matrix influence

### 1. Introduction

Ecosystem fragmentation has been identified as the main current cause of biodiversity loss and environmental degradation, which puts the provision of several essential ecosystem services at risk (Haddad et al., 2015). The process of fragmentation describes the conversion by an anthropic agent of continuous areas into smaller, dispersed spots separated by an anthropic matrix (Wilcove et al., 1986; Collinge, 2009). This has diverse consequences including habitat reduction, alteration of habitat quality through modification of both conditions and resources, and modification of the fragment spatial configuration (Collinge, 2009; Wilson et al., 2016; Pardini et al., 2018). These consequences alone affect the ecological patterns of populations and communities at different scales and from different perspectives, and each has a particular set of effects (Collinge, 2009; Wilson et al., 2016; Pardini et al., 2018). Landscapes submitted to this process are characterized by fragments of varied shape and size that are dispersed in an anthropic matrix composed of pastures, agricultural crops, roads, and urban centers (Pert et al., 2012; Matte

et al., 2015). Edge effect (Murcia, 1995; Tabarelli et al., 2008), reproductive isolation due to lack of connection and an impermeable matrix (Jules and Shahani, 2003; Thompson et al., 2017), an increase in nonnative species in the anthropic matrix due to changes in conditions and resources (Jauni et al., 2015), and a modification of richness patterns through the habitat reduction process (Fahrig, 2003; Hadadd et al., 2015) are consequences of the sensu lato fragmentation process.

In contrast to fragmentation by anthropic activity, in some places it is possible to observe naturally fragmented landscapes in which an archipelago of forest islands occurs inside a native grassland matrix (Matte et al., 2015; Coelho et al., 2018a). Although most studies of this fragment type have been carried out in the region between the Atlantic and Cerrado Domain in the Brazilian Southeast, it is expected that this type of landscape will always occur in regions of contact between savanna and forest formations associated with mountain chains, where topographic variables play an essential role in the differentiation of soil and microclimate environmental conditions (Coelho et al.,

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2016, 2018a, 2018b). Due to these topographic variations, sites at the same altitude and macroclimate may be subject to different edaphic and microclimatic constraints (Coelho et al., 2016; Coelho et al., 2018a, 2018b). Such variations increase the complexity of these environments and potentiate biological diversity at the landscape level (Coelho et al., 2016).

In these landscapes most of the matrix is composed of shallow and poorly-drained soil, is subject to high temperatures via direct luminosity, and contains sclerophyllous vegetation recurrently submitted to fire, as in the *Campos rupestres* (Coelho et al., 2016; Morellato and Silveira, 2018). The natural fragments inserted in this landscape (called *capões de mata* in Brazil) represent points of greater environmental suitability formed by specific soil and climate conditions that are obligatory for its existence and thus characterize edaphoclimatic formations (Meguro et al., 1996; Valente, 2009; Coelho et al., 2016, 2018a). These patches are of forest size and structure. Floristic composition occurs at points of greater soil depth and moisture, such as valley bottoms, drainage lines, and areas adjacent to watercourses (Meguro et al., 1996; Coelho et al., 2016; Coelho et al., 2018a, 2018b). Their occurrence in the landscape is limited mainly by the availability of soil, for the development of larger trees, and water. Although they are more fertile than the grassland matrix, the soils in natural fragments tend to have a deficient nutritional supply when compared to the forest formations in different landscape contexts (Meguro et al., 1996; Valente, 2009; Coelho et al., 2016; Coelho et al., 2018a, 2018b).

According to the literature, while anthropic fragments originate through the continuous fractionation of forest areas, colonization and the establishment of natural fragments occurred through propagule dispersion along drainage lines and in humid areas of mountain chains by animals that are associated with these landscape points during their life cycle (Meguro et al., 1996; Coelho et al., 2016). The continuous occurrence of this process would give rise to a successive colonization sequence that ended in forest formation (Meguro et al., 1996; Coelho et al., 2016). The high representation of dispersal by animal species in these islands and the link between islands along thin bands of trees associated with drainage lines suggest the validity of this colonization and establishment model (Meguro et al., 1996; Coelho et al., 2016). Once established, expansion into adjacent areas would be limited by edaphic and climatic constraints and by fire in adjacent grassland where it is an important component (Coelho et al., 2016; Coelho et al., 2018a; Morellato and Silveira, 2018). The natural fragments would have their limits strongly influenced by fire, due to the effect of fire on individual mortality and modification of environmental conditions (Araújo et al., 2017; Coelho et al., 2018a, 2018b).

As in landscapes fragmented by anthropic action, attributes such as the shape, size, and spatial configuration of natural fragments are important to their ecological patterns (Matte et al., 2015; Coelho et al., 2016). Natural fragments are also subject to the fragmentation consequences commonly addressed in anthropic approaches, such as edge effect and problems with connectivity between fragments (Souza, 2009; Matte et al., 2015; Coelho et al., 2016). The edge effect would have originated in soil differentiation and the microclimatic conditions of temperature, luminosity, and humidity, which also provide corresponding structural and floristic variation in the border–interior direction (Souza, 2009; Coelho et al., 2016). The connectivity between populations in different fragments would be hampered by the distinct matrix, but in a context that differs from anthropic fragments associated with urban and agricultural matrices (Matte et al., 2015; Coelho et al., 2016).

Unlike the functioning of anthropic fragments, natural fragment functioning is still relatively unknown. The few studies carried out addressed important ecological aspects which represented the first step towards understanding these fragments (Meguro et al., 1996; Souza, 2009; Valente, 2009; Coelho et al., 2016; Coelho et al., 2018a, 2018b). However, the general characteristics of these fragments are discussed mainly based on qualitative assessments that do not allow for deep knowledge of important ecological aspects (Meguro et al., 1996; Coelho et al., 2016). This lack of knowledge impairs initiatives addressing natural fragment conservation; in the absence of information, patterns associated with anthropic fragments are applied to natural fragments. However, the level of similarity between the two types of fragments is not clear, and there are substantial differences in restrictive factors and landscape context (Matte et al., 2015; Coelho et al., 2018). In addition, these fragments provide important ecosystem services related to the protection of headwaters, water springs, and watercourses and provide resources for ecologically important animals in the face of pollination and the dispersal of plant species (Coelho et al., 2016; Coelho et al., 2018a, 2018b). Studies that elucidate the relationship between the ecological behavior of natural and anthropic fragments are urgently required to address our need for knowledge of vegetation, to facilitate conservation plans and political action in an intensively modified world, and to help us understand how fragmentation interacts with such changes (Wilson et al., 2016).

We adopted study of populations as a method of comparing the ecological behavior of natural and anthropic fragments. Thus, in this work we tested the hypothesis that populations in natural fragments present distinct ecological behavior compared to the same populations in anthropic fragments. We chose a species that occurs widely

in the Brazilian Atlantic domain and that is present in an anthropic fragment and a natural fragment with the same climatic conditions. We followed this species for 4 years (seedlings to established individuals), evaluating the spatial structure, population structure, dynamic aspects, and age structure. The population level of the study was selected to allow a level of clarity about ecological behavior that is not usually available in community studies (Rockwood, 2015). All population life stages were monitored in order to obtain clear results regarding ecological patterns in the two types of fragments, a resolution that is not common in works limited to arboreal individuals.

## 2. Materials and methods

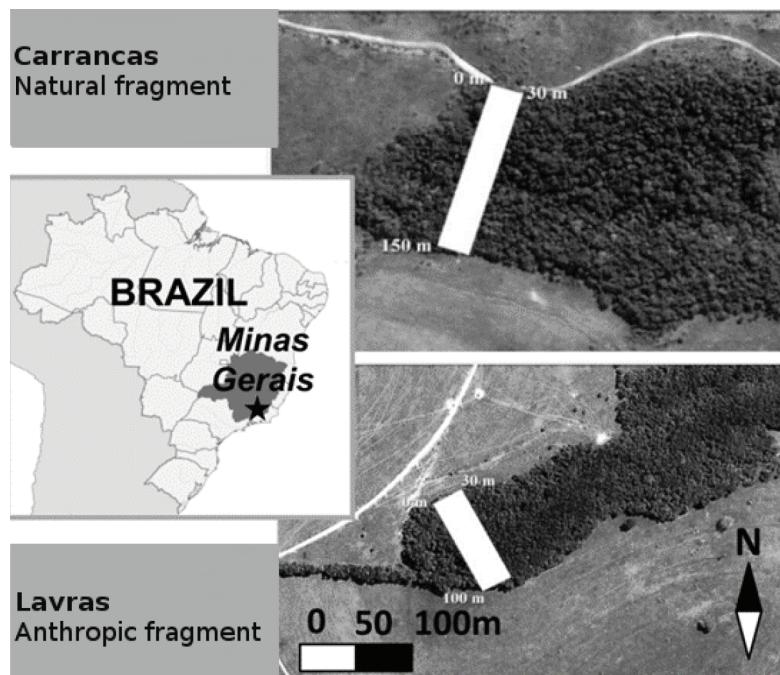
### 2.1. Study area and species

We studied one natural and one anthropic rainforest fragment in Minas Gerais in Southern Brazil (Figure 1). Both forests are tropical and semideciduous, with an average canopy height of 10 m (undisturbed fragment) and 13 m (disturbed fragment) and are classified as Atlantic Forest (Mata Atlântica; IBGE, 2012). The climate of both forest fragments is mesothermic, characterized by wet summers and dry winters, with two clear seasons (Köppen's Cwa type) (Dantas et al., 2007).

Our natural forest fragment is located in Carrancas ( $21^{\circ}27'12''S$ ,  $44^{\circ}7'31''W$ ; 1200 m a.s.l.), is 14 ha, and is surrounded by a matrix of rocky fields and native grasses

(*campo rupestre*). This forest patch is naturally occurring due to intrinsic factors such as slope and soil; it was spared from clearance due to inaccessibility and its use as a local source of occasional, selective wood extraction. Nevertheless, other than the access road that comes close to some edges of the fragment, we did not find any signs of previous clearing (tree stumps, etc.) or evidence that the surrounding vegetation matrix had been severely modified by human activity. Our anthropic forest fragment is located in Lavras ( $21^{\circ}18'15''S$ ,  $44^{\circ}59'21''W$ ; 1000 m a.s.l.), is 9 ha, and is surrounded by a matrix of soybean plantations and cattle ranches. The relief is flat in the greater part of the fragment, with an increase in slope in the lower portion where there is a watercourse with deficient drainage that entails flooding. This forest patch has been fragmented due to anthropogenic activities, and during the current study signs of cattle trampling and walking trails were observed.

We selected *Myrcia splendens* (SW.) DC. (Myrtaceae) as our target species due to the abundance of individuals from all life stages present at both study sites. The genus *Myrcia* represents the most species-rich tree genus in the Atlantic Forest and the savannas of South America (Lucas et al., 2011). Our target species *M. splendens* is a light-demanding canopy species of the rainforest (Higuchi et al., 2008) that reaches more than 15 m at maturity and produces small, fleshy fruits that are dispersed by animals (Gressler et al., 2006). The species occurs from Southeastern Brazil to



**Figure 1.** Location of sampling sites within Atlantic Forest fragments in (a) Carrancas and (b) Lavras in Minas Gerais, Brazil. White rectangles denote the location of the sampling plots in the forest fragment.

Mexico and is also found in Panama, Belize, Puerto Rico, and Costa Rica (Amiguet et al., 2005; Cole et al., 2008). It is an important fleshy-fruit-producing tree utilized by a wide variety of bird and animal life throughout its range in the Atlantic rain forest and is considered an important species for secondary rainforest succession and forest restoration (Lorenzi, 1998; Arantes et al., 2014).

## 2.2. Data sampling

To sample *M. splendens* we marked out a vegetation plot within each forest fragment from the edge to the interior of each fragment in 2010. Due to size and shape differences between the two fragments, we used a 30 × 150 m transect in the undisturbed fragment in Carrancas and a 30 × 110 m transect in the disturbed fragment in Lavras. To conduct sampling, we subdivided each transection lengthwise every 10 m, forming subplots of 30 × 10 m. Within each subplot we measured height (cm) and diameter at the base (DAB) of all living individuals of *M. splendens*. We also collected the relative location of each individual, thus obtaining spatial coordinates (X and Y) for each. We repeated these measurements in 2011, 2012, and 2013; recorded the individuals that died; and measured new recruit individuals.

## 2.3. Data analysis

In order to evaluate whether the two populations presented different spatial structures, we made two comparisons. First, we evaluated whether the abundance of species individuals presents a spatially structured distribution in each year using a Mantel test (Anderson and Walsh, 2013) at a 5% significance level using abundance and the coordinates of the upper right corner of each sample unit. Next, from each year of individual spatial measurement data we conducted K-Ripley tests (Ripley, 1981) in each fragment to evaluate the spatial structure of the population as a whole.

In order to evaluate whether populations in different contexts present different temporal behavior, we evaluated both fragments for changes in *M. splendens* individual density and basal area over time. In sequence we also evaluated the numbers of dead individuals and recruits (individuals that reached the inclusion criteria in a posterior mensuration) by total values over time for each fragment. Finally, we performed Kaplan–Meier curves (Kaplan and Meier, 1958) constructed to estimate the survival of individuals in each fragment, using the Survival package in R 3.4.1 (R Core Team, 2017). The Kaplan–Meier procedure is based on estimated conditional probabilities at each time interval, using the product limit of those probabilities to estimate the survival rate at each point in time (Hosmer and Lemeshow, 1999). Differences in the survival estimative for each fragment were verified using a logrank test.

Finally, in order to evaluate whether the two populations differ according to age structure, we performed two comparisons. First, we subdivided the populations of each year into height classes to represent different developmental stages of the species: <15 cm (seedling), >15 to 30 cm (regenerating), >30 to 100 cm (juvenile), >100 to 300 cm (preestablished), and >300 cm (established) (Morel et al., 2014). From the data distributions, we evaluated whether the two populations differ in relation to age structure through chi-square at the 5% significance level (Zar, 2010). We presented only height class data for this analysis, because height was strongly correlated with diameter (Pearson's correlation:  $P < 0.0001$ ). Next, we constructed Kaplan–Meier curves for each height class to look for differences in survival estimative according to phase of development. Differences among height class were also verified using a logrank test.

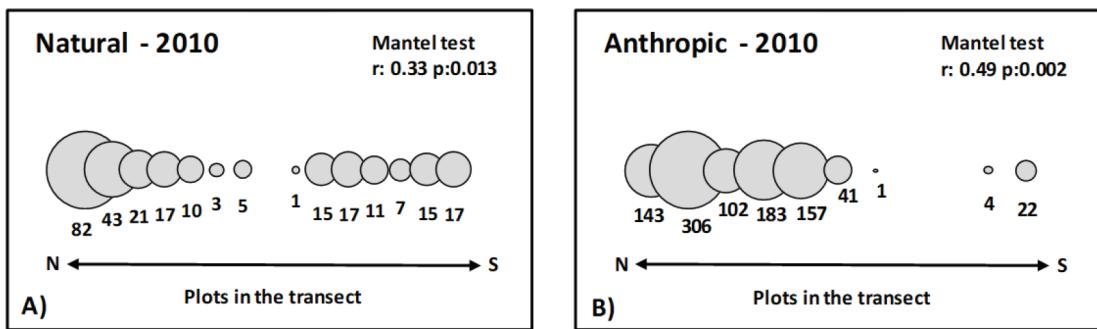
## 3. Results

### 3.1. Population structure

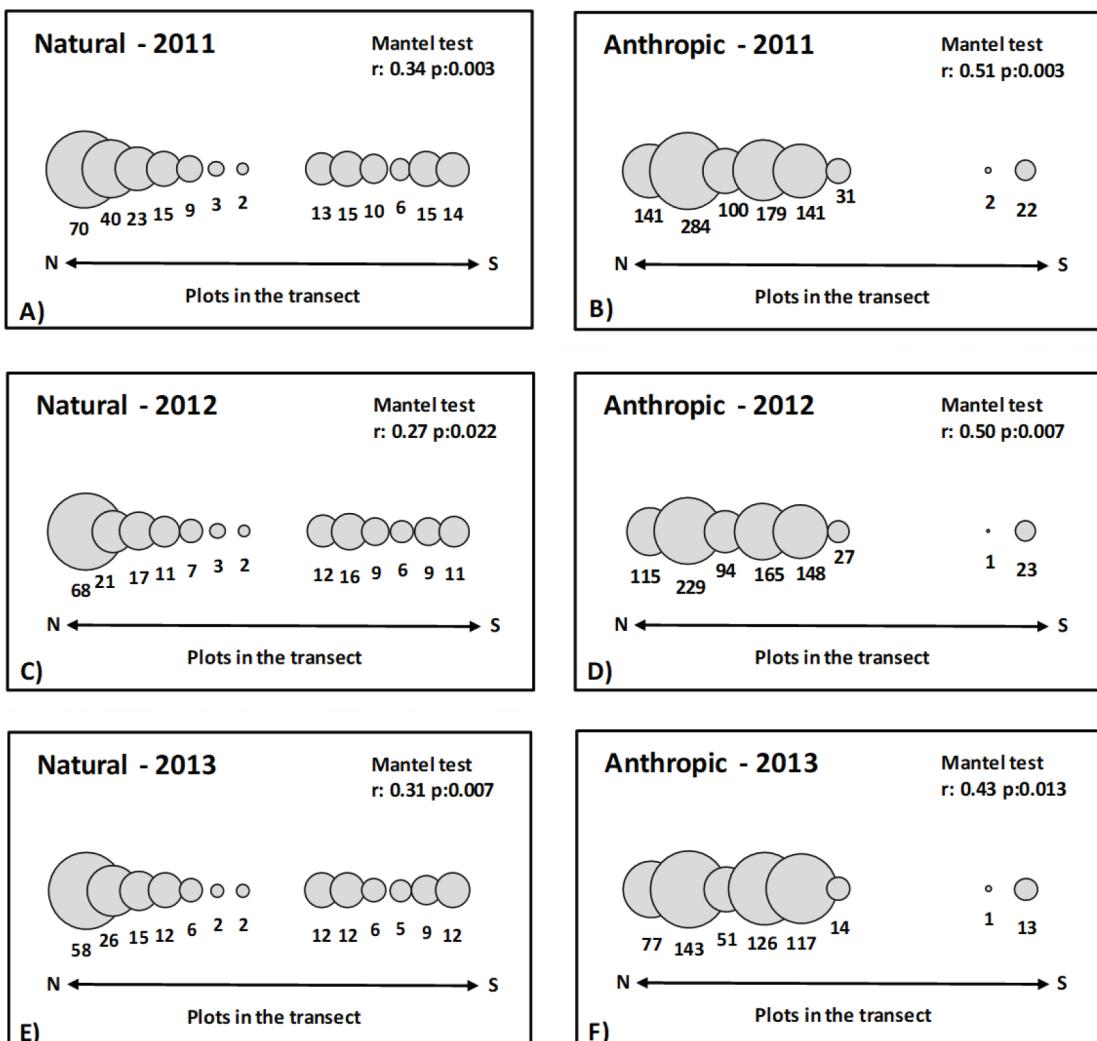
The two *Myrcia splendens* populations presented spatial patterns that were significantly related to abundance in all measurement years (Figures 2 and 3). The correlation between abundance and space was positive in the two fragments, with closer plots tending to present similar abundance values. However, while the abundance is greater at both ends and decreased towards the center in the natural fragment, in the anthropic fragment it is concentrated at one end. The populations in the two fragments presented an aggregate occurrence pattern regardless of distance between individuals in all measurement years (Figures 4 and 5).

### 3.2. Temporal behavior

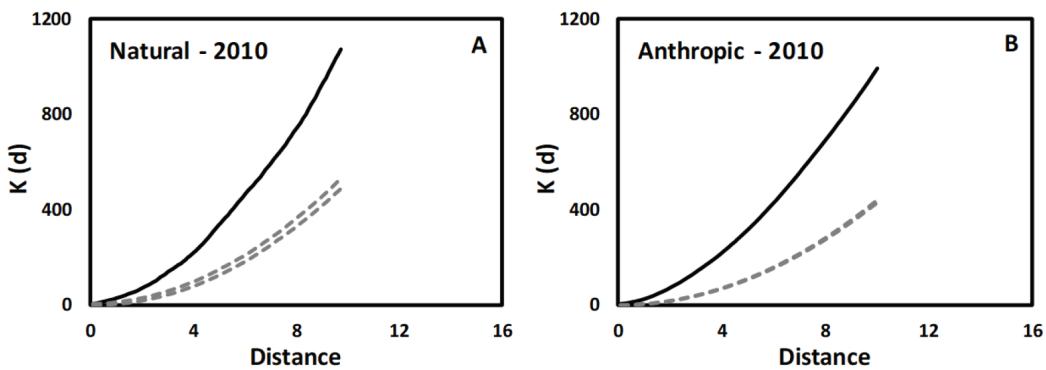
The two *Myrcia splendens* populations differed by density of individuals and basal area; they also differed in temporal variation for these attributes, number of dead individuals and recruits, and survival chances. The anthropic fragment population presented greater density of individuals and basal area in relation to the natural fragment population, and there were expressive temporal variations towards the reduction of these values (Figure 6). In agreement with this result, mortality increased in the anthropic fragment and recruitment decreased over the measurement years, reaching values of 1000 individuals (mortality) and recruitment equal to 0 in the last two intervals (Figure 7). In contrast, the natural fragment population had stable temporal behavior with small changes in density, basal area (Figure 6), mortality, and recruitment of individuals (Figure 7). Survival chances were not similar between fragments over the measurement years according to logrank test ( $P < 0.001$ ), although this probability was similar in the first two intervals and became smaller in the anthropic fragment in the last interval (Figure 8). Thus, the



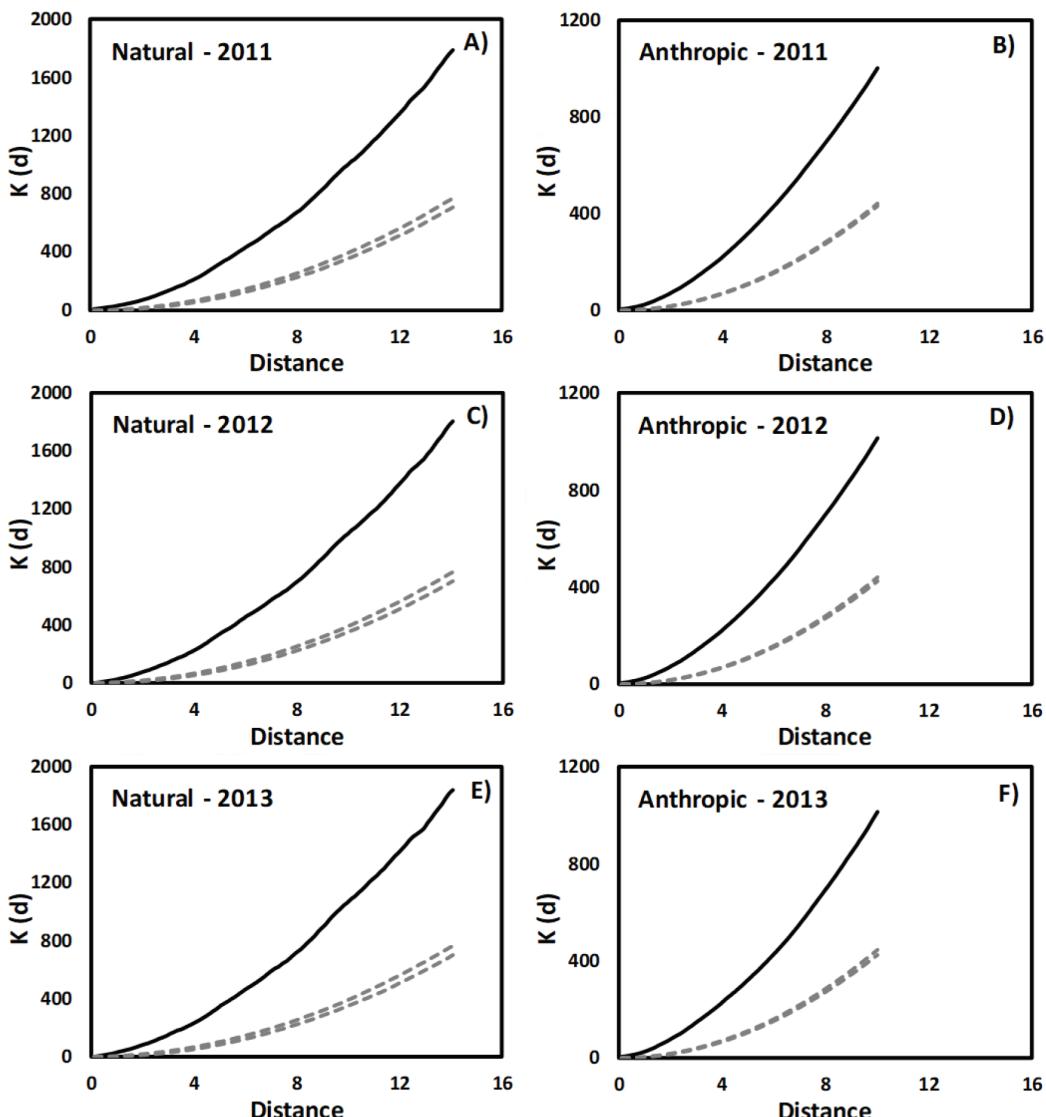
**Figure 2.** Representation of the abundance spatial structure of *Myrcia splendens* in plots in 2010 for the natural (A) and anthropic (B) fragments in Minas Gerais, Brazil. The circles refer to the plots, and their arrangement represents the arrangement within the transect. The circle sizes are proportional to the corresponding plot abundance and are calibrated according to the other values inside the diagram. The arrows represent the north-south transect axe.



**Figure 3.** Representation of the abundance spatial structure of *Myrcia splendens* in the year of measurement for the natural fragment (A, C, and E) and the anthropic fragment (B, D, and F) in Minas Gerais, Brazil. The circles refer to the plots, and their arrangement represents the location within the transect. The circle sizes are proportional to the corresponding plot abundance and are calibrated according to the other values inside the diagram. The arrows represent the north-south transect axe.



**Figure 4.** K-Ripley for the whole population of the natural fragment (A) and the anthropic fragment (B) in 2010. The continuous black line above the range of the null distribution (2 dashed gray lines) indicates a pattern of aggregation in *Myrcia splendens* distribution in this moment.



**Figure 5.** K-Ripley for the whole population of the natural fragment (A, C, and E) and the anthropic fragment (B, D, and F) in 2011, 2012, and 2013. The continuous black line above the range of the null distribution (2 dashed gray lines) indicates a pattern of aggregation in the distribution of *Myrcia splendens* in all years of measurement in both locations.

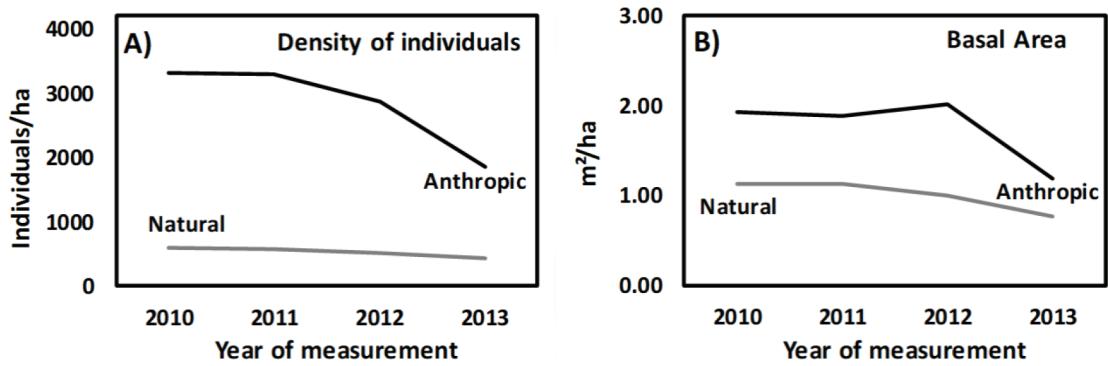


Figure 6. Density of individuals (ind/ha) (A) and basal area ( $m^2/ha$ ) (B) of *Myrcia splendens* during the years of measurement in the 2 fragments (natural and anthropic) at Minas Gerais, Brazil. Gray line: natural fragment, dark line: anthropic fragment.

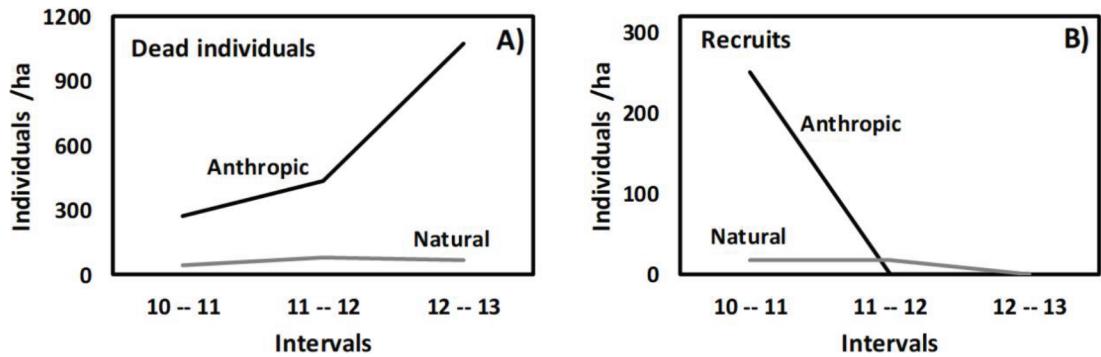


Figure 7. Number of dead (ind/ha) (A) and recruit (ind/ha) (B) *Myrcia splendens* individuals during the years of measurement in the 2 fragments (natural and anthropic) at Minas Gerais, Brazil. Gray line: natural fragment, dark line: anthropic fragment.

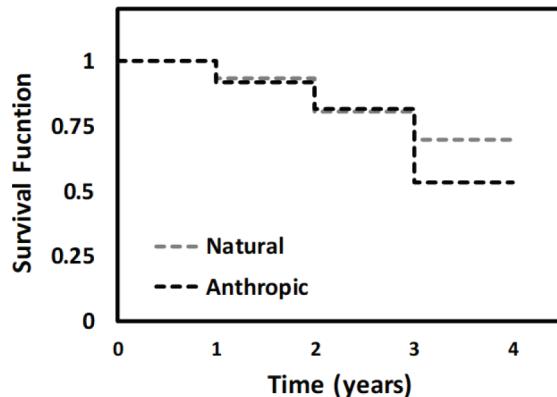


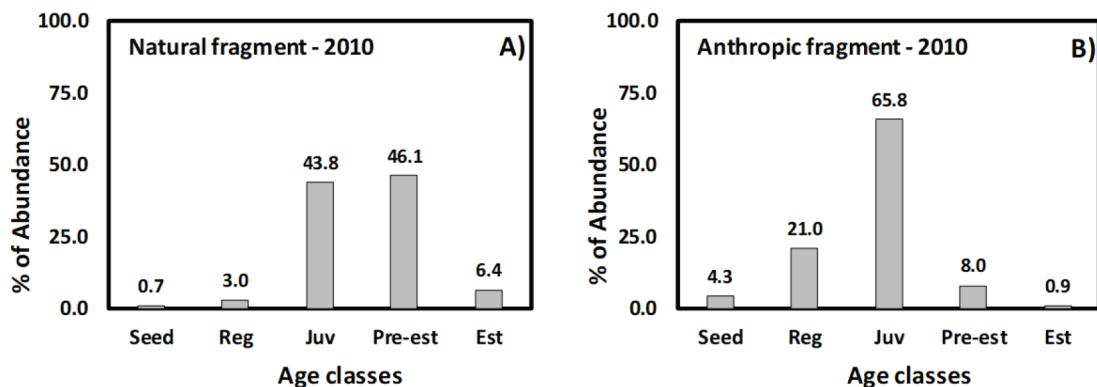
Figure 8. Kaplan-Meier survival curves for *Myrcia splendens* individuals in the natural and anthropic fragments at Minas Gerais, Brazil.

two populations present distinct dynamic patterns, with the anthropic fragment population presenting accelerated dynamics, in relation to stable behavior in the natural fragment population, as well as an association with high mortality, low recruitment, and lower survival chances.

### 3.3. Age structure

The two *Myrcia splendens* populations presented distinct age structures, with distinct distribution of individuals in the establishment phases during all measurement years ( $P < 0.001$ ; Figures 9 and 10). While in the natural fragment the preestablished and juvenile classes accounted for almost 90% of individuals in 2010, the juvenile class of individuals alone represented approximately two-thirds of the total abundance in the anthropic fragment, followed by regenerating phase individuals with 21% of abundance. In the other years, the two populations presented similar behaviors (Figure 10). Thus, in the anthropic fragment, individuals of the initial establishment phases presented greater representativeness, while in the natural fragment population, individuals of more advanced phases were of greater importance.

The class behavior regarding survival chances was similar between the two *Myrcia splendens* populations in relation to hierarchy of class but different according to survival chance magnitude and temporal variation (Figure 11). In both populations the lowest survival chances were found in the lower classes (seedling and regenerating) and the highest in the upper classes (preestablished



**Figure 9.** Percentage abundance by age class of *Myrcia splendens* in the first year of measurement (2010) in the natural fragment (A) and anthropic fragment (B) at Minas Gerais, Brazil. The 2 distributions are significantly different according chi-square ( $P < 0.001$ ). Seed: seedling, Reg: regenerating, Juv: juvenile, Pre-est: preestablished, and Est: established.

and established). However, survival chances decreased more significantly in the anthropic fragment population throughout the measurement years, reaching lower levels for all classes in comparison to the natural fragment population. In the seedling class, for example, the survival chances decreased in the first year and stabilized in the other years for the natural fragment, while in the anthropic fragment a steady decline occurred (Figure 11).

#### 4. Discussion

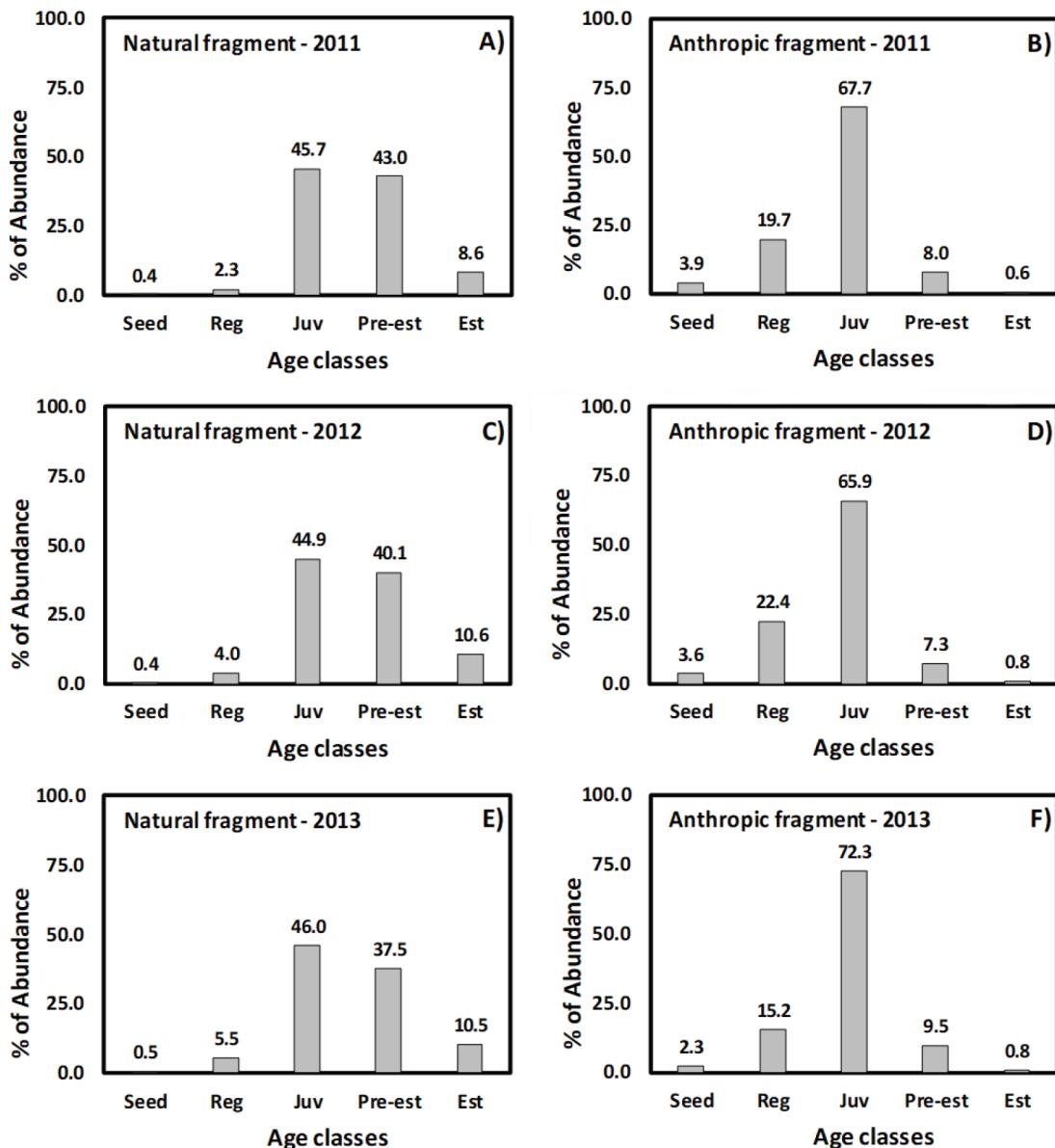
Our results support the hypothesis that the natural fragment population of *Myrcia splendens* differs from the anthropic fragment population in all addressed perspectives. Thus, the two populations have distinct spatial structures, temporal behavior, survival probability, and age structure.

The presence of spatial structure in the abundance distribution and aggregate occurrence pattern for the two populations indicates the existence of diverse factors in the two sites. However, the different fragments may be subject to different restrictive factors. In the natural fragment it is possible to observe an abundance gradient in the border-interior direction, suggesting the existence of differences in environmental suitability along the transect for *Myrcia splendens*. Such differences are probably related to the differences in environmental conditions associated with luminosity, temperature, soil depth, and humidity that are known to occur along natural fragments (Souza, 2009; Morel et al., 2014; Matte et al., 2015; Coelho et al., 2016). Due to the presence of a small valley and a watercourse in the central part of the fragment, conditions and resources tend to vary from the two ends of the transection towards the central areas. In this way, *Myrcia splendens* individuals would have their occurrence and abundance controlled by the internal environmental variation of the fragment, and greater success tends to be associated with areas closer to

the limits. The aggregate pattern of population occurrence can also be explained by environmental variation, as individuals develop in places where conditions, resources, and competition with other species allow for establishment (Hart and Marshall, 2013; Barraclough, 2015). Thus, in the natural fragment, environmental variation in the edge-interior direction would explain the spatial population patterns.

In the anthropic fragment, distribution of individuals is concentrated in the transect north end, configuring an aggregate occurrence pattern and differences between edge and interior in only one direction, but without gradual value modification. This pattern can also be explained by variations in environmental conditions that configure differences in site suitability for *Myrcia splendens*, but in a manner different than in the natural fragment. Low occurrence of individuals in this portion may be associated with environmental differences such as the watercourse at the southern end and adjacent areas that present conditions unfavorable to the species. However, the absence of an abundance gradient in the interior-edge direction where individuals occur and are abundant, similar to the upper portion as a whole, may be associated with the broad cattle occupation in the fragment. Cattle action occurs in order to modify environmental conditions and hinders the success of less resistant species (Trimble and Mendel, 1995; Raffaele et al., 2011; Benítez-Malvido, 2014; Ondei et al., 2017). Thus, occurrence would be limited by the natural variation in the fragment, while the pattern of abundance would be associated with the influence of the anthropic context.

In relation to the dynamics patterns, the natural fragment presents stable behavior, and the anthropic fragment presents temporal variations associated with the reduction of both density and basal area, increase in mortality, decrease in recruitment, and lower probability

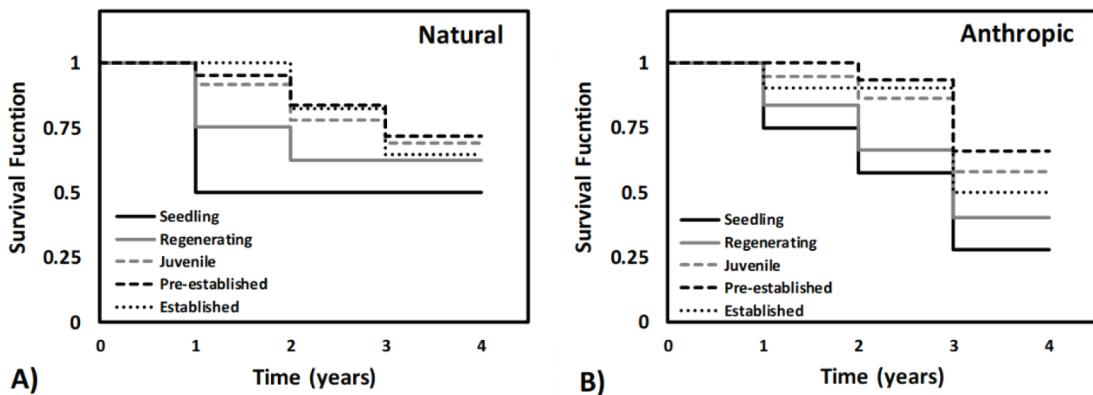


**Figure 10.** Percentage abundance of age classes of *Myrcia splendens* in the years of measurement in the natural fragment (A, C, and E) and anthropic fragment (B, D, and F) at Minas Gerais, Brazil. There are significant differences between natural and anthropic fragments in each year by chi-square at 5% significance level ( $P < 0.001$ , for all comparisons). Additionally, there are no significant differences between years of measurement for each fragment (natural and anthropic) by chi-square at 5% significance level ( $P > 0.05$  for all comparisons). Seed: seedling; Reg: regenerating; Juv: juvenile; Pre-est: preestablished; and Est: established.

of survival; differences between the two fragments are related to the conditions and context of each. As the two fragments are subject to different influencing factors, the constraints in each one will be different and this will reflect on dynamic patterns and survival chances (Meguro et al., 1996; Wilson et al., 1996). In the natural fragment environmental conditions are relatively stable, and the formation presents an evolutionary relationship with the factors present, including native grassland matrix,

native fauna, sporadic fire, and internal environmental differentiation (Coelho et al., 2016; Coelho et al., 2018a, 2018b). Thus, in naturally fragmented environments the population is subject to the variation it has been interacting with throughout the evolutionary process (Coelho et al., 2016; Coelho et al., 2018a, 2018b).

The anthropic fragment represents a portion of a past continuous forest that was subjected to changes in environmental conditions and external agents associated



**Figure 11.** Kaplan–Meier survival curves for *Myrcia splendens* individuals of different height classes in the natural fragment (A) and in the anthropic fragment (B) at Minas Gerais, Brazil.

with the anthropic matrix, such as cattle, frequent fire, and the influence of herbicides used on nearby agricultural crops (Murcia, 1995; Fahrig, 2003; Ondei et al., 2017; Pardini et al., 2018). The presence of these disturbances makes conditions and resource availability more variable over time and makes it difficult to develop stable behavior, which increases mortality and decreases recruitment and the survival chances of individuals (Collinge, 2009; Brando et al., 2014; Hadadd et al., 2015; Pardini et al., 2018). We observed the modification of the anthropic matrix between 2012 and 2013, as cattle were replaced by soy production. We believe that the mortality increase, low recruitment maintenance, and reduction in survival chances during the last interval may be associated with this event and the application of plant herbicides common to soy production. Thus, the fragmentation context influences the dynamic behavior and population survival, with greater dynamism and chances for individual survival in natural fragments, compared to anthropic fragments.

The differences in age structures between populations and the greater representativeness of different stages of establishment between fragments is probably due to the conditions and context of each fragment. In the natural fragment, the major importance of the preestablished followed by juvenile-phase individuals may also be associated with the conditions of temporal stability in natural fragments which are associated with the absence of restrictive factors throughout the evolutionary process (Meguro et al., 1996; Coelho et al., 2016). Such stability allows for development of individuals throughout the establishment phases, with the dynamic processes and the age structure varying within the common pattern of natural fragments (Morel et al., 2014; Coelho et al., 2016).

In the anthropic fragment, disturbances related to the fragmentation process and anthropic matrix, such as the presence of cattle, frequent fire, and herbicides from associated agricultural crops represent a restrictive

factor for the development of individuals throughout the establishment phases (Fahrig, 2003; Brando et al., 2014). These factors explain the high representativeness of juvenile and regenerating individuals in the anthropic fragment, since their frequent occurrence hinders growth, and also explains the increasing representativity of individuals of more advanced phases (Fahrig, 2003; Hu et al., 2016; Arroyo-Rodríguez et al., 2017; Pardini et al., 2018). The difference in conditions and context between fragments also explains the results for individual survival chances in the establishment phases, where the chances decrease more strongly over the years in the anthropic fragment, especially in the initial phases. In the anthropic fragment, individuals have a lower chance of developing into higher phases, which forms an age structure marked by young individuals of low longevity.

The differences in population ecological behavior between the two fragments as a whole highlight the distinction between natural fragmentation and anthropogenic fragmentation associated with the origin and landscape context of each. Evolution of natural fragments is associated with the particular fragment context, as it occurs due to natural agents associated with the topographic variation that synthesizes variations in soil and microclimate conditions (Meguro et al., 1996; Coelho et al., 2016). In this way, ecological behavior of natural fragments has adapted to all the common factors in the landscape in which they developed, thus presenting an associated ecological structure (Meguro et al., 1996; Morel et al., 2014; Coelho et al., 2016). In contrast, anthropic fragmentation submits portions of forest to conditions and disturbances that did not occur through the evolutionary process (Murcia, 1995; Fahrig, 2003; Collinge, 2009; Hadadd et al., 2015). Thus, interior portions are subjected to edge conditions and to all agents related to an anthropic matrix that can abruptly change the environment and,

consequently, influence the ecological behavior of populations and communities (Murcia, 1995; Fahrig, 2003; Collinge, 2009; Hadadd et al., 2015). Although the landscapes in the two fragments seem similar, origin and landscape context are essential to their differentiation and vegetation responses (Morel et al., 2014; Matte et al., 2015; Coelho et al., 2016; Wilson et al., 2016).

The distinction between the two fragment types draws attention primarily to the need for greater knowledge of the ecological behavior of natural fragments. These fragments are an important part of landscapes in transitional regions and account for important ecosystem services associated with the protection of watercourses and biodiversity shelter (Meguro et al., 1995; Coelho et al., 2016; Coelho et al., 2018a, 2018b). Thus, understanding the structural and

floristic patterns, origin, evolution, and possible responses to environmental modifications in fragments are all essential to fragment conservation in a changing world (Wright et al., 2005; Wilson et al., 2016). Considering the distinctions presented here, fragments with different origins that are inserted into different landscape contexts should be considered distinct units of singular behavior for the purposes of conservation and environmental policies.

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