Abstract
Environmental characteristics are among the most important triggers and regulators of plant phenophases, so that the abiotic and biotic changes driven by habitat loss and fragmentation can result in alterations of plant phenological patterns. We investigated whether forest edge and interior have differences in phenological pattern of tree communities. We followed the reproductive phenologies of tree communities in seven forest fragments on a monthly basis for two years (in 200 m² edge and interior plots per fragment). We sampled a total of 0.28 ha of anthropic forest fragments, comprising 313 trees (180 in edge, 133 in interior) belonging to 103 species and 34 families. Our results evidenced reproductive phenological changes between edge and interior tree communities, with: (i) phenological activities differing temporally between the two habitats (edge and forest interior) in all tree communities; (ii) greater phenological intensity at the forest edge than in the forest interior among tree species common to both habitats; (iii) more tree species showed phenological activity at the forest edge in 2010 and interior in 2011, when considering only those exclusive to each habitat.

Habitat fragmentation can therefore alter microenvironmental characteristics and influence biologic processes, including the reproductive phenologies of trees, through edge formation.

Key words: flowering, fragmentation, fruiting, seasonality.

Resumo
Características ambientais estão entre os gatilhos mais importantes e reguladores das fenofases das plantas. Portanto, mudanças abióticas e bióticas resultantes da perda de habitat e fragmentação podem resultar em alterações no padrão das espécies vegetais. Nós investigamos se a borda e interior de florestas possuem diferenças no padrão fenológico das comunidades de árvores. Nós acompanhamos a fenologia reprodutiva da comunidade de árvores em sete fragmentos mensalmente por dois anos (em 200 m² de parcelas no interior e borda por fragmento). Nós amostramos um total de 0,28 hectares de fragmentos florestais antrópicos, compreendendo 321 árvores pertencendo a 103 espécies. Nossos resultados evidenciaram mudanças na fenologia reprodutiva da comunidade de árvores da borda e interior, com: (i) atividade fenológica diferindo temporalmnte entre os dois habitats (borda e interior) em toda comunidade vegetal; (ii) maior intensidade fenológica na borda do fragmento do que no interior dentre as espécies de árvores comuns aos dois habitats; (iii) mais espécies de árvores apresentaram atividade fenológica na borda em 2010 e interior em 2011 quando considerando apenas aquelas exclusivas de cada habitat. A fragmentação de habitat pode, portanto, alterar características microambientais e influenciar processos biológicos, incluindo a fenologia reprodutiva das árvores, através da formação de bordas.

Palavras-chave: floração, fragmentação, frutificação, sazonalidade.

See supplementary material at <https://doi.org/10.6084/m9.figshare.14167013.v1>
Introduction

Studies of tree reproductive phenology can aid ecosystem conservation and management efforts by elucidating many aspects of plant community organization and maintenance (Chambers et al. 2013). The timing of flowering and fruiting (plant reproductive phenophases), can have significant implications for tree community structure, functioning, and regeneration, as well as the qualities and quantities of resources available for consumers (Vilela et al. 2018). While tree vegetative and reproduction schedules may be determined by specific genetic factors, climatic and environmental conditions can control the possibility of their expression (Seghieri et al. 2009). Indeed water availability (e.g., Pires et al. 2018) and temperature (e.g., Peñuela et al. 2019) have been described as phenophase triggers, shaping phenophase initiation and intensity (e.g., Cascante-Marín et al. 2017; Olubode 2019).

Forest habitat losses and fragmentation have greatly increased in recent years due to agricultural expansion (Driscoll et al. 2013) and are threatening many forest species (Morellato et al. 2016). Edge formation resulted from forest fragmentation can change microenvironmental conditions (Ewers & Banks-Leite 2013; Ziter et al. 2014) and impact species survival and their interrelationships. Recent studies have revealed marked abiotic differences between forest edges and interiors (Riutta et al. 2012). We recorded the reproductive phenologies (1) tree community phenological patterns will show seasonality, and that activity intensity peaks will be asynchronous among forest edges and interiors (Temporal Hypothesis); (2) phenological intensity at the forest edge will be greater than in the forest interior among tree species present in both habitats (Intensity Hypothesis); and (3) the percentage of tree species will show higher phenological activity and intensity at the forest edge among tree species exclusive of each habitat (Composition Hypothesis). We reinforce here the importance of proactive mitigating actions in controlling edge effects, especially in highly fragmented landscapes, and suggest possible future instabilities of ecological interactions in forest fragment communities.

Material and Methods

Study area

We sampled forest fragments inserted in submontane Semidecidual Atlantic Forest, southern of Minas Gerais state. These areas have already fragmented in our oldest register, in 1979 (ESRI 2016), with predominance of anthropogenic matrices (i.e., pasture, annual and perennial cultures). The region experiences dry winters with a mean temperature of 16.9 ºC and, mean precipitation rate of 26 mm during the winter months, and a mean aurstral summer temperature of 21.5 ºC and a precipitation rate of 290 mm during the summer months (1,500 mm annually, Koppen climate classification Cwb, Alvares et al. 2014). The region elevations ranging from 720 to 1,350 m, where predominate hilly relief. The vegetation landscape there is highly fragmented due to anthropogenic disturbances, with only 9% of the original seasonal semi-deciduous forest cover remaining. The most common land use types there are: pastures (51%), coffee plantations (17%), and annual crops (principally sugarcane and corn, 7%) (Olivetti et al. 2015).

Data survey

We sought here to verify whether the phenological patterns of tree communities are different among edge and interior forest habitats for flowering and fruiting, and tested the hypothesis that: (1) tree community phenological patterns will show seasonality, and that activity intensity peaks will be asynchronous among forest edges and interiors (Temporal Hypothesis); (2) phenological intensity at the forest edge will be greater than in the forest interior among tree species present in both habitats (Intensity Hypothesis); and (3) the percentage of tree species will show higher phenological activity and intensity at the forest edge among tree species exclusive of each habitat (Composition Hypothesis).
Table 1 – The seven studied fragments in the region of Alfenas (MG), their area (hectares), coordinates (decimal degrees), altitude (meters above the sea level), and tree diversity information (Sp. Richness = number of tree species; Sp. abundance = number of tree individuals). Bray-Curtis and Jaccard indexes indicates dissimilarity of species composition among edge and interior for all studied fragments. Beta diversity indexes (turnover and nestedness) indicates a higher turnover contribution for overall beta diversity than Nestedness, indicating high species substitution rate among habitats.

| Fragment          | Area (ha) | Longitude  | Latitude     | Elevation (m a.s.l.) | Sp. richness | Sp. abundance | Bray-Curtis | Jaccard | Turnover | Nestedness |
|-------------------|-----------|------------|--------------|----------------------|--------------|---------------|-------------|---------|----------|------------|
| Monte Alegre      | 5         | -45.961944 | -21.751389   | 825                  | 17           | 23            | 0.68        | 0.80    | 0.70     | 0.24       |
| Vista Alegre      | 7         | -45.876944 | -21.338611   | 791                  | 28           | 48            | 0.66        | 0.79    | 0.6      | 0.35       |
| Pedreira          | 11        | -46.159722 | -21.411944   | 821                  | 22           | 49            | 0.96        | 0.98    | 0.8      | 0.16       |
| São Tomé          | 49        | -45.988889 | -21.470556   | 793                  | 31           | 54            | 0.83        | 0.9     | 0.57     | 0.38       |
| Gaspar Lopes      | 70        | -45.927778 | -21.381944   | 847                  | 36           | 62            | 0.67        | 0.81    | 0.6      | 0.35       |
| Florence          | 96        | -45.848056 | -21.331944   | 835                  | 28           | 45            | 0.91        | 0.95    | 0.5      | 0.46       |
| Parque Municipal  | 205       | -45.966389 | -21.224167   | 775                  | 24           | 32            | 0.87        | 0.93    | 0.6      | 0.35       |
| **All fragments** | **103**   | **313**    | **0.57**     | **0.73**             | **0.61**     | **0.33**      |

We recorded the flowering (flower buds and/or open flowers) and fruiting (unripe and/or ripe fruits) of each tree on a monthly basis during two years (January/2010 to December/2011). We evaluated flowering and fruiting phenological patterns based on their presence or absence, and their intensities. Phenological intensities were based on a phenological score scale from 0 (absence of phenological activity) to 4 (maximum phenological activity for that tree / species), with 25% intervals between each class. From this phenological intensity scores we calculated the Intensity Percentage monthly using Fournier’s method (Fournier 1974), by the formula: % Fournier = (Σ phenological scores / 4N) × 100, where Fournier Intensity Percentages (% Fournier) is defined by the sum of the phenological score of all trees inserted in one community (Σ phenological scores), divided by the higher score possible in that community (number of trees multiplied by four - 4N), accessed in percentage. From Fournier Intensity Percentage we obtained: the (a) pattern of phenological intensity during the year; (b) the mean date of activity intensity; as well as (c) the percentages of species showing phenological activity during the year.

Analyses

We analyzed the phenological patterns using circular analyses in ORIANA software, version 4.02 (Kovach Computing Services), and all other analyzes we used the free software R (R Core Team)
(Tab. 2). To calculate circular statistics parameters, the months of the two study years (2010 and 2011) were converted into angles, $0^\circ = \text{January/2010 (1)}$ and $330^\circ = \text{December/2011 (24)}$, at $15^\circ$ intervals. All final analyses in both habitats (edges and forest interior) were carried out considering the years together. Flowering and fruiting statistics were conducted separately in both approaches.

The species composition dissimilarity, beta diversity partition and phenophase durations analyses were carried out in the R software (R Core Team 2019). We used the function “vegdist” from “vegan package” (Oksanen et al. 2019) to calculate species composition dissimilarity, considering Jaccard (richness) and Bray-Curtis (abundance) dissimilarity indices, bounded between 0 (edge and interior shares the same species composition) and 1 (edge and interior species compositions are distinct in their entirety). We used the package “betapart” (Baselga et al. 2018) to explore the beta diversity (i.e., turnover and nestedness) partition among habitats.

Temporal Hypothesis
To test the Temporal Hypothesis (phenological asynchronicity between forest edges and interiors), we calculate the Fournier Intensity Percentages (i.e., phenological intensity) for each tree (sample unit). We aggregated the tree phenological intensity from all edge and interior plots to compare the general temporal pattern for each habitat. We verify the phenological seasonality both at edge and interior using the Rayleigh Test of Uniformity ($z$). The Rayleigh Test of Uniformity takes into account the distribution of angles (e.g., phenological data by months) around the circle, testing if that distribution is uniform (null hypothesis) or concentrated. If the $p$-value is smaller than the significance level chosen (0.05), the data are not uniformly distributed, leading to higher $z$ value (Fisher 1993). We defined the phenological mean date by Mean Vector ($\mu$) and intensity peak with the aid of the graphical representations of Fournier Intensity Percentages pattern from both habitat.

Table 2 – Description of the methodology for all hypothesis. The data structure was defined as the data used to answer each question, as well as the data organization. A sample unit was defined as the applied unit for each response variable described. Aim define our objective and applied tests what was the statistical test used for each analysis.

| Hypothesis           | Data structure                                    | Sample unit       | Response variable                  | Aim                                      | Applied tests                           |
|----------------------|---------------------------------------------------|-------------------|-----------------------------------|------------------------------------------|------------------------------------------|
| Temporal hypothesis  | Edge and interior data aggregated in one single   | Tree              | Fournier Intensity Percentages    | Seasonality in each habitat              | Rayleigh Test of Uniformity ($z$)         |
|                      | community per habitat                             |                   |                                   | Mean date and intensity peaks of each    | Mean Vector ($\mu$) and graphics         |
|                      |                                                    |                   |                                   | habitat                                  |                                          |
| Intensity hypothesis | Edge and interior data aggregated in one single   | Tree              | Fournier Intensity Percentages    | Phenological intensity difference among   | Mardia-Watson-Wheeler ($W$)               |
|                      | community per habitat, considering tree species   |                   |                                   | habitat                                  |                                          |
|                      | common for both habitat                           |                   |                                   |                                          |                                          |
|                      |                                                    |                   | Phenophase Duration of phenophases| Difference of phenophase duration         | One-sample Wilcoxon Signed Rank Test     |
|                      |                                                    |                   |                                   | among habitats                           |                                          |
| Composition hypothesis| Edge and interior data aggregated in one single   | Tree              | Percentages of species in         | Percentage of species in                 | Mardia-Watson-Wheeler ($W$)               |
|                      | community per habitat, considering tree species   |                   | phenological activity             | phenological activity difference among    |                                          |
|                      | exclusive of each habitat                         |                   |                                   | habitat                                  |                                          |
|                      |                                                    |                   | Phenophase Duration of phenophases| Difference of phenophase duration         | One-sample Wilcoxon Signed Rank Test     |
|                      |                                                    |                   |                                   | among habitats                           |                                          |
Intensity Hypothesis

To test the Intensity Hypothesis (higher phenological intensity at the forest edge among tree species present in both habitats) we analyzed only species common to edge and interior habitats (at least two individuals in each habitat). Considering only common species (occurring in both habitat), the edge and interior tree communities have few differences in species composition (Jaccard 0.34, Bray-Curtis 0.21 all plots together). We calculate the Fournier Intensity Percentages (phenological intensity) for each tree (sample unit), as well as quantified the amount and duration of phenophases, considering each phenophase period as sample unit. We aggregated the tree phenological intensity of common species from all edge and interior plots to compare the general intensity pattern among habitats. We compare the phenological intensity between habitats (edge and interior plots) by Mardia-Watson-Wheeler (W) test. The Mardia-Watson-Wheeler test compare if two or more data distribution around the circle are identical (null hypothesis) or differents. If the p-value is smaller than the significance level chosen (0.05), the data are not identical distributed, leading to a large W value (Fisher 1993). We used One-sample Wilcoxon Signed Rank Test to compare the mean of phenophase duration among habitat because the phenophase duration data are non-parametric. Wilcoxon Signed Rank Test determine if non-parametrics samples are equal to a known standard value (null hypothesis) (Bauer 1972). If the p-value is smaller than the significance level chosen (0.05), the mean of phenophase duration is equal among habitats.

Composition Hypothesis

To test the Composition Hypothesis (higher phenological intensity at the forest edge among tree species exclusive of each habitat), considering all phenological differences due to different species compositions among edge and interior, we analyzed the tree community excluding species held as common to both habitats. Considering only that exclusive species, the edge and interior tree communities are remarkably dissimilar (Jaccard 0.87, Bray-Curtis 0.78 all plots together). We quantified the percentages of species in phenological activity, considering tree as sample unit, as well as, quantified the amount and duration of phenophases considering each phenophase period as sample unit. We used the phenological activity presence/absence of each tree to calculate the percentage of species in phenological activity. We aggregated the percentages of species in phenological activity of exclusive species from all edge and interior plots to compare the general activity pattern among habitats. We compared the percentages of species in phenological activity between the habitats (edge and interior plots) by Mardia-Watson-Wheeler (W) test, and we compare the duration of phenophases among habitats by One-sample Wilcoxon Signed Rank Test.

Results

Temporal Hypothesis

We found asynchrony only for flowering activity between the two habitats (forest edge and interior) (Tab. 3; Fig. 1). Temporal differences of flowering period between the habitats were evidenced by the seasonality only in the forest interior (z = 6.951, p =< 0.001) (Fig. 2a). The flowering mean date (interior: May/2010; edge June/2010) and intensity peak (interior: between September and October of 2010; edge: between October and November of 2010) were early in interior than at the forest edge (Fig. 2a: flowering; Fig. 2b: fruiting).

Intensity Hypothesis

We identified 13 species common to both habitats (with two or more individuals in each habitat), representing nine plant families and a total of 125 trees (Tab. S1, available on supplementary material <https://doi.org/10.6084/m9.figshare.14167013.v1>). Tree flowering activity was different among habitats, generally more intense in the forest edge than in the interior (W = 7.03; p = 0.03) (Fig. 3a). The mean of phenophase duration among habitat were similar (flowering: W = 624.5, p = 0.44; fruiting: W = 227.5, p = 0.54).

Composition Hypothesis

The percentages of tree species demonstrating phenological activities were different across the years. The percentage of species flowering was similar among habitats (Fig. 4a). On the other hand, the percentage of species fruiting was higher at the forest edge in 2010, and higher at the interior in 2011 (W = 11.59, p = 0.003) (Fig. 4b). The mean of phenophase duration among habitat were similar (flowering: W = 207.5, p = 0.45; fruiting: W = 227.5, p = 0.54).
All of our hypotheses were confirmed, as: (i) the tree communities in the two habitats examined (forest edge and interior) showed phenological patterns at different times (Temporal Hypothesis); (ii) considering the same tree species, tree phenological intensities were higher at the edge than in the forest interior (Intensity Hypothesis); and (iii) more tree species showed phenological activity at the forest edge (Composition Hypothesis).

It is widely known that forest fragmentation process alters microclimatic conditions (Ewers & Banks-Leite 2013; Ziter et al. 2014; Couto-Santos et al. 2015), so that biological processes like reproductive phenology and productivity will be affected, as well ectothermic arthropod abundance (Barahona-Segovia et al. 2019). Species or individual changes at a forest edge, driven by microclimatic changes, could alter community phenological patterns (Athayde & Morellato 2014; Laurance et al. 2003; Reznik et al. 2012). As such, individuals of the same tree species growing at the forest edge show different phenological patterns than those located in the interior (Herrerías-Diego et al. 2006). Those phenological changes may reflect higher light levels at the forest edge, as light is an important limiting factor, mainly for flowering (Athayde & Morellato 2014; Herreries-Diego et al. 2006; Pires et al. 2013; Vogado et al. 2016). Higher light levels can increase primary productivity.

### Table 3 – Temporal hypothesis test results.

| Phenophase | Local  | Mean vector (µ) | Mean date     | Rayleigh test (z) | Rayleigh test (p) |
|------------|--------|-----------------|---------------|-------------------|------------------|
| Flowering  | Edge   | 158.139°        | 2010: October | 4.352             | 0.605            |
|            | Interior| 147.46°         | 2011: September| 6.951             | 9.58E-04         |
| Fruiting   | Edge   | 138.187°        | 2010: October | 2.409             | 0.09             |
|            | Interior| 144.301°        | 2011: September| 1.747             | 0.174            |

### Figure 1 – a-b. Linear representation of Fournier Intensity Percentage for all tree community (temporal hypothesis) – a. to flowering; b. to fruiting. Only flowering in forest interior (highlighted in red) showed seasonal distribution. Note intensity peak of interior early and higher than edge.
and new leaf (Czapiewska et al. 2019) and flower (Nishikawa 2009) production, or harm certain shade-adapted species (Richards et al. 2003). The observed increases of phenological intensities at the forest edge were generated by light tolerant species (Cunningham 2000; Vogado et al. 2016). Changes in phenological patterns relative to the forest interior may be associated with pattern asynchrony (Herrerías-Diego et al. 2006) and/or different phenological activity intensities (Pires et al. 2013).

Temperature is another microclimatic variable associated with forest edge formation, with forest edges having higher and more variable temperatures (Laurance et al. 2001; Barahona-Segovia et al. 2019). Temperature variations are considered flowering triggers and can influence plant reproductive phenologies (Ramos & Santos 2005; Herrerías-Diego et al. 2006; Rubim et al. 2010). Generalist pollinator insects are more active during warmer periods, thus favoring

Figure 2 – a-b. Circular representation of Fournier Intensity Percentage for all tree community (temporal hypothesis) – a. to flowering; b. to fruiting. The black row indicate the beginning (0º). From 0º at 180º is represented 2010, and from 180º to the end is 2011. Note longer bars for flowering intensity (a) in edge, mainly in 2011. Surrounding bars outside indicates the confidence limits (red is confidence level unconfident).
species flowering at forest edges due to the higher temperatures there (Xiao et al. 2016; González et al. 2017). Habitat temperatures can be even higher in warmer months and favor flowering asynchrony (Andreis et al. 2004; Athayde & Morellato 2014).

As water availability can decrease with edge formation (e.g., leaf-level water content; Wright et al. 2012), that factor could also help explain the observed differences in tree phenological patterns between the forest edge and interior. Water resource differences may result from lower soil water availability (Herrerías-Diego et al. 2006), or lower relative humidity of the air (Reznik et al. 2012). Water availability is also a limiting factor for plant reproductive phenology. Both light and water must be available in order to increase primary productivity (e.g., Whitley et al. 2011), and many tree species show greater flowering and fruiting

Figure 3 – a-b. Circular representation of Fournier Intensity Percentage for species common to both habitats (intensity hypothesis) – a. to flowering; b. to fruiting. The black row indicate the beginning (0°). From 0° at 180° is represented 2010, and from 180° to the end is 2011. Note bars considerably longer for fruiting intensity (b) at edge in both years. Surrounding bars outside indicates the confidence limits (red is confidence level unconfident).
during the rainy season (Rubim et al. 2010; Vogado et al. 2016). Less water availability can also result in lower fruit yields, mainly of fleshy fruits (Reznik et al. 2012), and lower flower/fruit conversion percentages (Cunningham 2000). However, we found that the fruit production from those tree species exclusive from edge showed higher species percentage fruiting than in the interior. This result can be explained once most of the tree species at the edge are generalist, producing anemochorous fruit and/or produce small fleshy fruit that do not need much water (Razafindratsima et al. 2018).

The formation of two different habitats (edge and interior) can result in two distinct communities, with different species compositions, as seen in the present study and previous ones (Nagy et al. 2015; Kostrakiewicz-Gieralt & Zajac 2014; Matesanz et al. 2010), although similar phenological intensities

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**Figure 4** – a-b. Circular representation of species percentage in a phenological activity for tree community without species common (composition hypothesis) – a. to flowering; b. to fruiting. From 0° at 180° is represented 2010, and from 180° to the end is 2011. Considering the bars, the percentage species in fruiting was higher at edge in 2010, and higher at interior in 2011. Surrounding bars outside indicates the confidence limits.
may be seen in different communities, even if their distinct species compositions demonstrate different phenological patterns (Reznik et al. 2012). The successional stages of trees, for example, can affect the timing and intensities of their phenological activities. Pioneer plants will be more favored in forest edge habitats than in forest interiors (which favor climax species) (Kibet 2011). Pioneer tree species show greater reproductive investments in sunny environments (such as forest gaps and edges), and demonstrate greater phenophase intensities than seeing in climax environments, thus increasing phenological pattern differences between habitats (Delerue et al. 2013). Those differences can be in terms of the dates of phenophase initiation (Athayde & Morellato 2014; Pires et al. 2013), and/or higher intensities at different times (Reznik et al. 2012). Although tree flowering intensities are higher at forest edges than in forest interiors, the former communities show lower flower/fruit conversions, especially in small forest fragments (Cunningham 2000).

If flowering occurs at different times in different communities (as seen in the present study), reproduction may then be restricted to individuals closer to each other, even though both communities have essentially similar flowering intensities. In that situation, gene flow could decrease, potentially increasing the levels of endogamy, resulting in genetic drift and loss of seed genetic quality (Cascante et al. 2002; Ramos et al. 2007). Genetic drift can be compounded under those conditions if we consider that closer individuals are more likely to be related and thus have higher genetic similarity (Leonardi et al. 2012; Conson et al. 2013). Low gene flow between communities could result in populations more susceptible to diseases, disturbances, and local extinctions (Nazareno & Reis 2014). Even with similar phenological intensities, but at different times in forest edge and interior habitats, other phenophase dependent organisms (such as the pollinators and seed dispersed) may be impacted by that temporal asynchrony. Forest edge habitat tends to favor generalists and pioneer tree species (Carneiro et al. 2016), decreasing flower varieties and their quantities in edge habitats and thus compromising specialist interactions (Xiao et al. 2016). The higher flowering intensity at the forest edge may satiate pollinators and decrease their foraging areas - and thus restrict intraspecific gene flow. Similar processes impact shade specialist trees in the forest interior that depend on specific pollinators, which usually show lower abundances in forest fragments because of reduced food supplies and altered microclimatic conditions (González et al. 2017). However, the fact of trees of the same species fruit in different times between edges and fragment interior could favor some frugivorous, once they can remaining in the same fragment for a longer time because of the longer fruit supply (e.g., Reys et al. 2005).

It is well know that tree reproductive phenologies are influenced by climatic characteristics, and that forest fragmentation changes the phenological intensities and patterns of plant populations, but studies at the community level in fragmented habitat are still missing. The present study added to current knowledge of habitat fragmentation effects, especially edge effects on tree reproductive phenologies, and our results can improve conservation and management efforts in natural systems. Based on our results, highly fragmented landscapes show differences in tree reproductive phenologies in forest edge and interior communities, with potential long-term reproductive and genetic impacts. The forest edge effect therefore need to be reduced through proactive conservation and management efforts (such as the creation of transition buffer zones around forest fragments).

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References

Alvares CA, Staep JL, Sentelhas PC, Gonçalves JLM & Sparovek G (2014) Köppen’s climate classification map for Brazil. Meteorologische Zeitschrift 22: 711-728.

Andreis C, Longhi SJ, Brun EJ, Wojciechowski JC, Machado AA, Vaccaro S & Cassal CZ (2004) Estudio fenológico em três fases sucessionais de uma floresta estacional decidual no município de Santa Tereza, RS, Brasil. Revista Árvore 29: 55-63.

Athayde EA & Morellato LPC (2014) Anthropogenic edges, isolation and the flowering time and fruit set of Anadenanthera peregrina, a cerrado savanna tree. International Journal of Biometeorology 58: 443-454.

Barahona-Segovia RM, Crespin SJ, Grez AA & Veloso C (2019) Anthropogenic thermal gradient in managed...
landscapes determines physiological performance and explains the edge-biased distribution of ectothermic arthropods. Forest Ecology and Management 440: 147-157.

Baselga A, Orme D, Villeger S, De Bortoli J & Leprieur F (2018) betapart: partitioning beta diversity into turnover and nestedness components. R package version 1.5.1. Available at <https://CRAN.R-project.org/package= betapart>. Access on 19 February 2020.

Bauer DF (1972) Constructing confidence sets using rank statistics. Journal of the American Statistical Association 67: 687-690.

Carneiro MS, Campos CCF, Beijo LA & Ramos FN (2016) Anthropogenic matrices favor homogenization of tree reproductive functions in a highly fragmented landscape. PLoS ONE 11: e0164814. DOI: <https://doi.org/10.1371/journal.pone.0164814>.

Cascante A, Quesada M, Lobo JJ & Fuchs EA (2002) Effects of dry tropical forest fragmentation on the reproductive success and genetic structure of the tree *Samanea saman*. Conservation Biology 16: 137-147.

Cascante-Marin A, Trejos C & Alvarado R (2017) Association between rainfall seasonality and the flowering of epiphytic plants in a Neotropical montane forest. Biotropica 46: 912-920.

Chambers LE, Alwegg R, Barbraud C, Barnard P, Beaumont LJ, Crawford RJM, Durant JM, Hughes L, Keatley MR, Low M, Morellato LPC, Poloczanska ES, Ruoppolo V, Vanstreels RET, Woehler EJ & Wolfardt AC (2013) Phenological changes in the southern hemisphere. PloSone 8: 1-13.

Conson ARO, Ruas EA, Vieira BG, Rodrigues LA, Costa BF, Bianchini E, Prioli AJ, Ruas CF & Ruas PM (2013) Genetic structure of the Atlantic Rainforest tree species *Luehea divaricata* (Malvaceae). Genetica 141: 205-215.

Couto-Santos APL, Conceição AA & Funch LS (2015) The role of temporal scale in linear edge effects on a submontane Atlantic forest arboreal community. Acta Botanica Brasilica 29: 190-197.

Cunningham SA (2000) Effects of habitat fragmentation on the reproductive ecology of four plant species in mallee woodland. Conservation Biology 14: 758-768.

Czapiewska N, Dyderski MK & Jagodziński AM (2019) Seasonal dynamics of floodplain forest understory-impacts of degradation, light availability and temperature on biomass and species composition. Forest 10: 1-16.

Fisher NI (1993) Statistical analysis of circular data. Cambridge University Press, Cambridge. 277p.

Delerue F, Gonzalez M, Atlan A, Pellerin S & Augusto L (2013) Plasticity of reproductive allocation of a woody species (*Ulex europaeus*) in response to variation in resource availability. Annals of Forest Science 70: 219-228.

Driscoll DA, Banks SC, Barton PS, Lindenmayer DB & Smith AL (2013) Conceptual domain of the matrix in fragmented landscapes. Trends in Ecology & Evolution 28: 605-613.

ESRI - Environmental Systems Research Institute (2016) “Imagery - Landsat Explorer”. Available at <https://livingatlas2.arcgis.com/landsatexplorer/>. Access on 15 December 2019.

Ewers RM & Banks-Leite C (2013) Fragmentation impairs the microclimate buffering effect of tropical forests. PloSone 8: e58093.

Fortunato MEM & Quirino ZGM (2016) Efeitos da fragmentação na fenologia reprodutiva de espécies arbóreas presentes em borda e interior de Mata Atlântica Paraiaba. Rodriguesia 67: 603-614.

González E, Salvo A & Valladares G (2017) Natural vegetation cover in the landscape and edge effects: differential responses of insect orders in a fragmented forest. Insect Science 24: 891-901.

Herreras-Diego Y, Quesada M, Stoner KE & Lobo JA (2006) Effects of forest fragmentation on phenological patterns and reproductive success of the Tropical Dry Forest tree *Cieba aesculifolia*. Conservation Biology 20: 1111-1120.

Kibet S (2011) Plant communities, species diversity, richness, and regeneration of a traditionally managed coastal forest, Kenya. Forest Ecology and Management 261: 949-957.

Kostrakiewicz-Gieralt K & Zajac M (2014) The influence of habitat conditions on the performance of two invasive, annuals - *Impatiens glandulifera* and *Bidens frondosa*. Biologia 69: 449-462.

Oksanen JF, Blanchet FG, Kindt R, Legendre P, Minchin PR, O’Harra B, Simpson GL, Solymos P, Stevens H & Wagner HH (2019) vegan: community ecology package. R package version 2.5-6. Available at <https://cran.r-project.org/web/packages/vegan/index.html>. Access on 19 February 2020.

Laurance WF, Lovejoy TE, Vasconcelos HL, Bruna EM, Didham RK, Stouffer PC, Gascon C, Bierregaard RO, Laurance SG & Sampaio E (2001) Ecosystem decay of Amazonian Forest Fragments: a 22-years investigation. Conservation Biology 16: 605-618.

Laurance WF, Merona JMR, Andrade A, Laurance SG, D’Angelo S, Lovejoy TE & Vasconcelos HL (2003) Rain-forest fragmentation and the phenology of Amazonian tree communities. Journal of Tropical Ecology 19: 343-347.

Leonardi S, Piovani P, Scalfi M, Piotti A, Giannini R & Leonardi S, Piovani P, Scalfi M, Piotti A, Giannini R & Valladares F (2010) Global change and the evolution of phenotypic plasticity in plants. Annals of the New York Academy of Sciences 1206: 35-55.
Matias-Palafoux ML, Jimenez-Sierra CL, Golubov J & Mandujano MC (2017) Reproductive ecology of the threatened: "star cactus" *Astrophytum ornatum* (Cactaceae): a strategy of continuous reproduction with low success. Botanical Science 95: 245-258.

Morellato LPC, Alberton A, Alvarado ST, Borges B, Buissen E, Camargo MGG, Cancian LF, Carstensen DW, Escobar DFE, Leite PTP, Mendoza I, Rocha NMWB, Soares NC, Silva TSF, Staggemeier VG, Streher AS, Vargas BC & Peres CA (2016) Linking plant phenology to conservation biology. Biological Conservation 195: 60-72.

Nagy RC, Porder S, Neill C, Brando P, Quintino RM & Nascimento SA (2015) Structure and composition of altered riparian forests in an agricultural Amazonian landscape. Ecological Applications 25: 1725-1738.

Nishikawa Y (2009) Significance of intra-inflorescence variation on flowering time of a spring ephemeral, *Gagea lutea* (Liliaceae), under seasonal fluctuations of pollinator and light availabilities. Plant Ecology 202: 337-347.

Oliveira ECS, Costa Júnior EO, Fernandes PD & Quirino ZGM (2019) Phenological study of populations of *Cnidoscolus quercifolius* in the western Seridó, Paraíba state, Brazil. Rodriguésia 70: e02352016. DOI: <http://dx.doi.org/10.1590/2175-7860201970001>.

Olivetti D, Mincauto RL, Bernardes Ayer JE, Naves Silva ML & Curi N (2015) Spatial and temporal modeling of water erosion in dystrophic red latosol (oxisol) used for farming and cattle raising activities in a sub-basin in the out of Minas Gerais. Ciencia e Agrotecnologia 39: 58-67.

Olbode OO (2019) Influence of seasonal variability of precipitation and temperature on performances of pawpaw varieties intercropped with cucumber. Scientia Horticulturae 243: 622-644.

Peñuela MC, Bustillos-Lema M, Álvarez-Solás S & Núñez-Avellaneda LA (2019) Reproductive phenology variation of the multiple inflorescence-palm tree *Mettenia maynensis* in relation to climate, in a Piedmont forest in western Amazonia. Trees 33: 867-876.

Pires JPA, Silva AG & Freitas L (2013) Plant size, flowering synchrony and edge effects: what, how and where they affect the reproductive success of a Neotropical tree species. Austral Ecology 39: 328-336.

Pires JPA, Marino NAC, Silva AG, Rodrigues PJFP & Freitas L (2018) Tree community phenodynamics and its relationship with climatic conditions in a lowland tropical rainforest. Forests 9: 10.3390/f9030114.

Ramos FN & Santos FAM (2005) Phenology of *Psychotria tenuinervis* (Rubiacaeae) in Atlantic forest fragments: fragment and habitat scales. Canadian Journal of Botany 83: 1305-1316.

Ramos FN, Jose J, Solferini VN & Santos FAM (2007) Quality of seeds produced by *Psychotria tenuinervis* (Rubiacaeae): distance from anthropogenic and natural edges of Atlantic forest fragment. Biochemical Genetics 45: 441-458.

Razafindratsima OH, Brown KA, Carvalho F, Johnson SE, Wright PC & Dunham AE (2018) Edge effects on components of diversity and above-ground biomass in a tropical rainforest. British Ecological Society 55: 977-985.

Reys P, Galetti M, Morellato LPC & Sabino J (2005) Fenologia reprodutiva e disponibilidade de frutos de espécies arbóreas em mata ciliar no Rio Formoso, Mato Grosso do Sul. Biota Neotropica 5: 309-318.

Reznik G, Pires JPA & Freitas L (2012) Efeito de bordas lineares na fenologia de espécies arbóreas zoocóricas em um remanescente de Mata Atlântica. Acta Botanica Brasilica 26: 65-73.

Richards AE, Shapcott A, Playford J, Morrison B, Critchley C & Schmidt S (2003) Physiological profiles of restricted endemic plants and their widespread congeners in the North Queensland wet tropics, Australia. Biological Conservation 111: 41-52.

Riutta T, Slade EM, Morecroft MD, Bebber DP & Malhi Y (2014) Living on the edge: quantifying the structure of a fragmented forest landscape in England. Landscape Ecology 29: 949-961.

Rubim P, Nascimento HEM & Morellato LPC (2010) Variações interanuais na fenologia de uma comunidade arbórea de floresta semidecidua no sudeste do Brasil. Acta Botanica Brasilica 24: 756-762.

Seghieri J, Vescovo A, Padel K, Soubrie R, Arijounin M, Boulain N, Rosnay P, Galle S, Gosset M, Mouctar AH, Peugeot C & Timouk F (2009) Relationships between climate, soil moisture and phenology of the woody cover in two sites located along the West African latitudinal gradient. Journal of Hydrology 375: 78-89.

Vilela AA, claro VTS, Torezan-Silingardi HM & Del-Claro K (2018) Climate changes affecting biotic interactions, phenology, and reproductive success in a savanna community over a 10-year period. Arthropod-Plant Interactions 12: 215-227.

Vogado NO, Camargo MGG, Locosselli GM & Morellato LPC (2016) Edge effects on the phenology of the guamirim, *Myrcia guianensis* (Myrtaceae), a cerrado tree, Brazil. Tropical Conservation Science 9: 291-312.

Whitley RJ, Macinnis-Ng CMO, Hutley LB, Beringer J, Zeppel M, Williams M, Taylor D & Eamus D (2011) Is productivity of mesic savannas light limited or water limited? Results of a simulation study. Global Change Biology 17: 3130-3149.

Wicklein HF, Christopher D, Carter ME & Smith BH (2012) Edge effects on sapling characteristics and
microclimate in a small temperate deciduous forest fragment. Natural Areas Journal 32: 110-116.

Wright TE, Tausz M, Kasel S, Volkova L, Merchant A & Bennett LT (2012) Edge type affects leaf-level water relations and estimated transpiration of *Eucalyptus arenacea*. Tree Physiology 32: 280-293.

Xiao Y, Li X, Cao Y & Dong M (2016) The diverse effects of habitat fragmentation on plant-pollinator interactions. Plant Ecology 217: 857-868.

Ziter C, Bennett EM & Gonzalez A (2014) Temperate forest fragments maintain aboveground carbon stocks out to the forest edge despite changes in community composition. Oecologia 176: 893-902.