Original Paper

Edge creation changes the timing and intensity of phenological reproductive patterns and species activities in forest tree communities

João Pedro Costa Elias[1,3,8], Driélli Carvalho Vergne[2,4], Mariane Patrezi Zanatta[2,5],

Caroline Cambraia Furtado Campos[1,6] & Flavio Nunes Ramos[1,7]

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 fenologico 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 temporalmente 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.

[1] Universidade Federal de Alfenas, Depto. Ciências da Natureza, Lab. Ecologia de Fragmentos Florestais - ECOFRAG, Alfenas, MG, Brazil.

[2] Universidade Federal de São Carlos, Depto. Hidrobiologia, Lab. Ecologia e Conservação, São Carlos, SP, Brazil.

[3] ORCID: <https://orcid.org/0000-0001-8137-5979>. [4] ORCID: <https://orcid.org/0000-0003-3782-3476>. [5] ORCID: <https://orcid.org/0000-0002-8978-4416>.

[6] ORCID: <https://orcid.org/0000-0001-5924-8404>. [7] ORCID: <https://orcid.org/0000-0001-6689-3575>.

[8] Author for correspondence: jpcelias.bio@gmail.com

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.* 2014; Wicklein *et al.* 2012) that can affect the reproductive patterns of plant communities and their associated species (Athayde & Morellato 2014). Phenological studies in anthropogenic landscapes, however, have largely been limited to population studies (*e.g.*, Vogado *et al.* 2016; Matias-Palafox *et al.* 2017; Oliveira *et al.* 2019), whereas the few studies with a community approach have showed increased phenological intensities of trees at forest edges (Fortunato & Quirino 2016), with synchronize different from those in the forest interior (Cunningham 2000; Reznik *et al.* 2012). Phenological changes at the species level in response to habitat modifications can vary among functional groups and successional stages (Xiao *et al.* 2016). Generalists and pioneer species are usually favored by edge formation, and increased flower and fruit production are usually the main phenological changes observed in those situations (Cunningham 2000; Xiao *et al.* 2016). Instead specialist or climax species that are adapted to forest interior conditions tend to decrease their reproductive activities near the forest edge (Xiao *et al.* 2016).

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). 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 austral 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 recorded the reproductive phenologies of plant communities within 200 m² plots (10 × 20 m, or 0.02 ha). We sampled seven fragments of Semidecidual Atlantic Forest (Tab. 1), randomly selecting two plots per each fragment (14 plots, 0.28 ha total), in two different habitats: one at the edge (up to 50 m from the edge) and the other at the

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**

forest interior (at least 200 m from the edge). The edge and interior plots were situated at least 150 m apart from each other. We sampled the phenologies of 313 individual trees > 1.5 m tall (reproductive individuals) (from 17 to 36 per fragment, average 26) belonging to 34 families and 103 species (from 23 to 62 per fragment, average 44) (Tab. S1, available on supplementary material <https://doi.org/10.6084/m9.figshare.14167013.v1>). In general, the tree species composition is dissimilar among edge and interior, with turnover component as the highest cause of dissimilarity species composition, indicating high species substitution rate among habitats (Tab. 1).

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, $0° =$ January/2010 (1) and $330° =$ December/2011 (24), at $15°$ 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 take 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 (μ) 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 community per habitat	Tree	Fournier Intensity Percentages	Seasonality in each habitat	Rayleigh Test of Uniformity (z)
				Mean date and intensity peaks of each habitat	Mean Vector (μ) and graphics
Intesity hypothesis	Edge and interior data aggregated in one single community per habitat, considering tree species common for both habitat	Tree	Fournier Intensity Percentages	Phenological intensity difference among habitat	Mardia-Watson-Wheeler (W)
		Phenophase period	Duration of phenophases	Difference of phenophase duration among habitats	One-sample Wilcoxon Signed Rank Test
Composition hypothesis	Edge and interior data aggregated in one single community per habitat, considering tree species exclusive of each habitat	Tree	Percentages of species in phenological activity	Percentage of species in phenological activity difference among habitat	Mardia-Watson-Wheeler (W)
		Phenophase period	Duration of phenophases	Difference of phenophase duration among habitats	One-sample Wilcoxon Signed Rank Test

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: $W = 207.5$, $p = 0.45$; 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: $W = 624.5$, $p = 0.44$; fruiting: $W = 436$, $p = 0.84$).

Table 3 – Temporal hypothesis test results. Rayleigh Test of Uniformity highlighted in bold indicate the phenological seasonality of flowering in the interior.

Phenophase	Local	Mean vector (µ)	Mean date	Rayleigh test (z)	Rayleigh test (p)
Flowering	Edge	158.139°	2010: October 2011: September	4.352	0.605
	Interior	147.46°	2010: October 2011: September	**6.951**	**9.58E-04**
Fruiting	Edge	138.187°	2010: October 2011: September	2.409	0.09
	Interior	144.301°	2010: October 2011: September	1.747	0.174
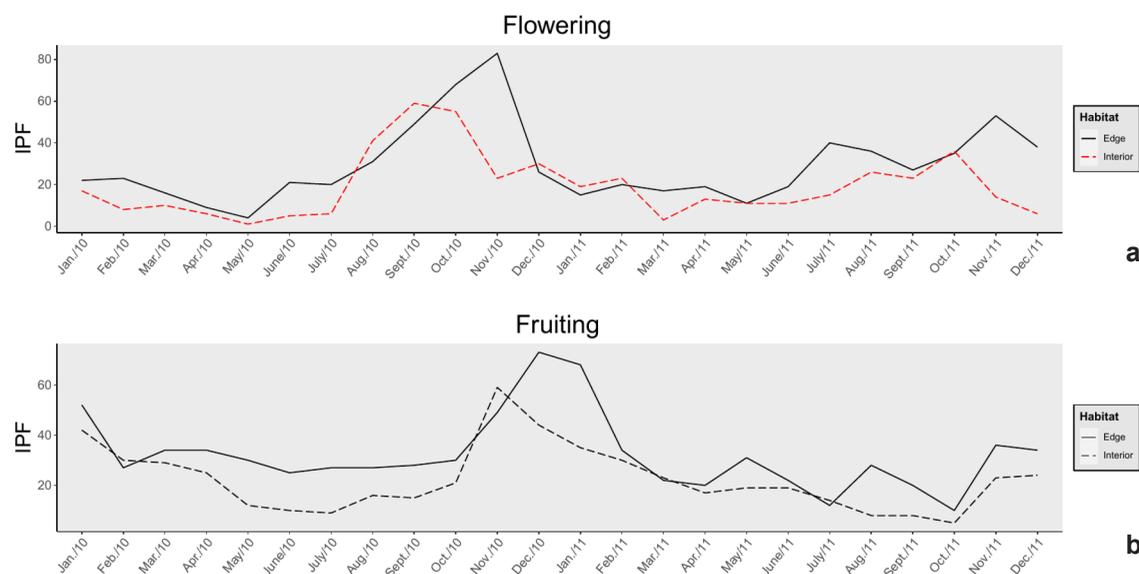
Figure 1 – a-b. Linear representation of Fournier Intensity Percentage for all tree community (temporal hypothesis) – a. to flowering; b. to fruiting. Only flowering in forest interior (highlighted in red) showed seasonal distribution. Note intensity peak of interior early and higher than edge.

Discussion

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; Herrerías-Diego *et al.* 2006; Pires *et al.* 2013; Vogado *et al.* 2016). Higher light levels can increase primary productivity

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
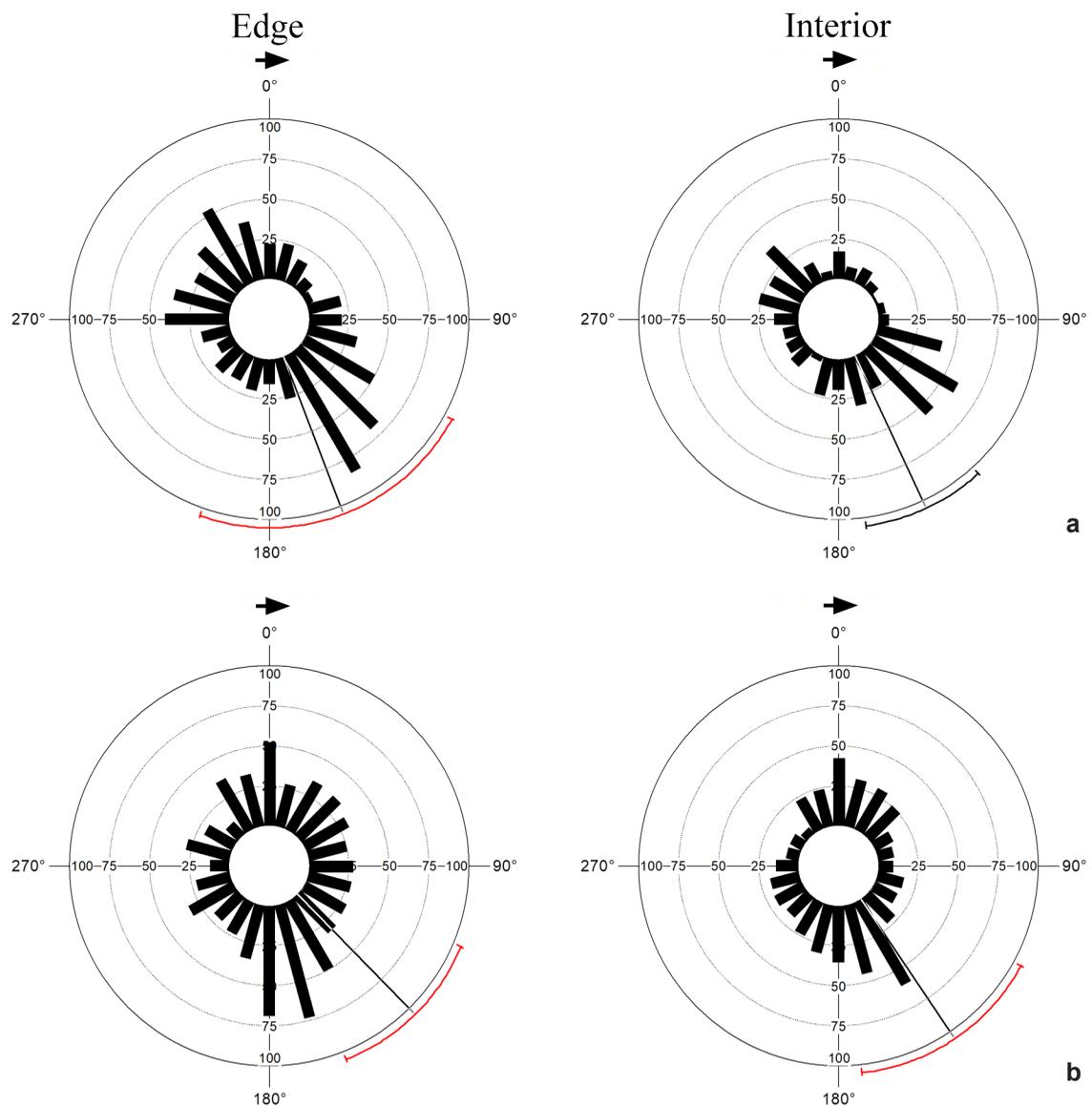
Figure 2 – a-b. Circular representation of Fournier Intensity Percentage for all tree community (temporal hypothesis) – a. to flowering; b. to fruiting. The black row indicate the beginning (0º). From 0º at 180º is represented 2010, and from 180º to the end is 2011. Note longer bars for flowering intensity (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
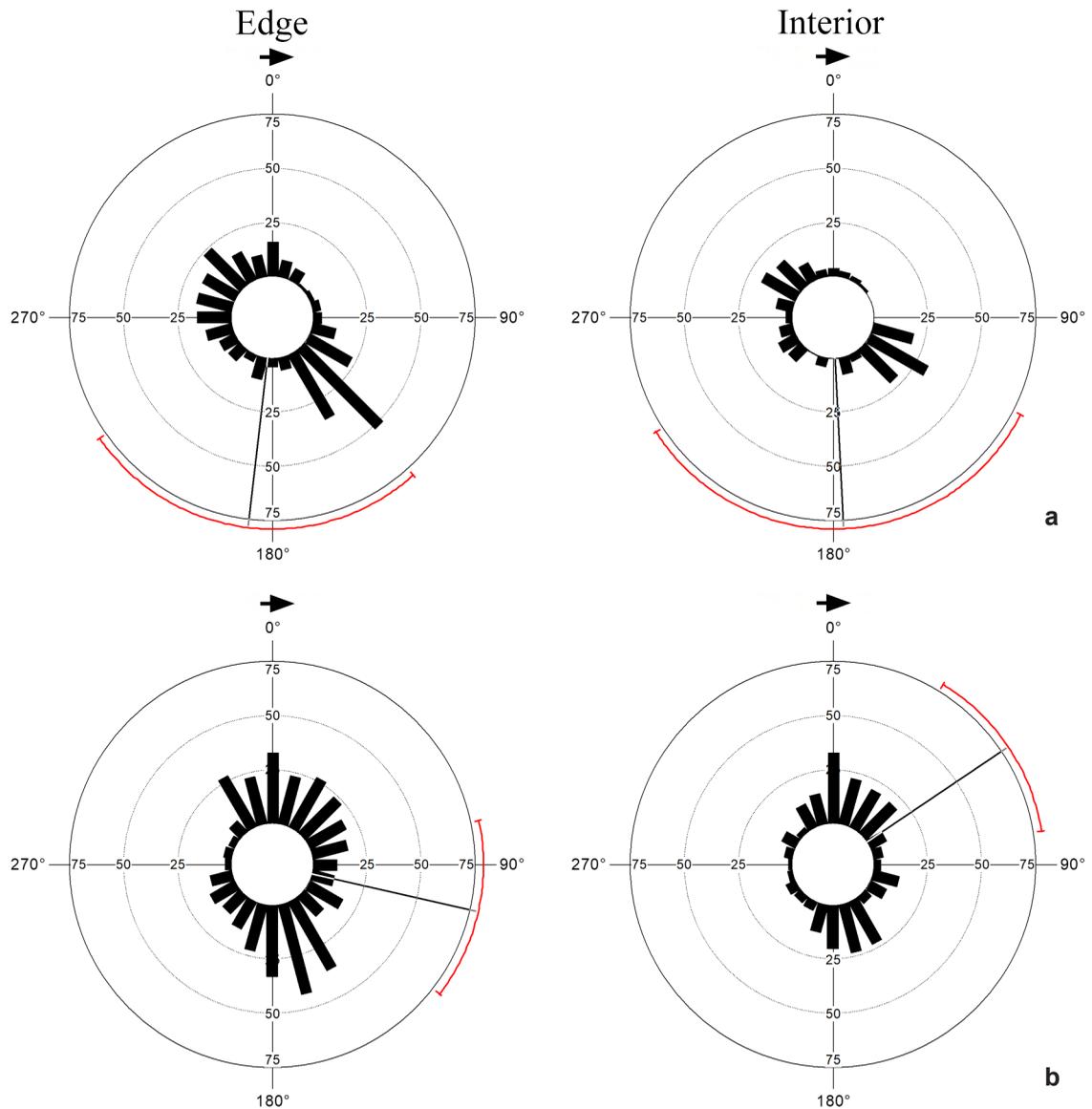
Figure 3 – a-b. Circular representation of Fournier Intensity Percentage for species common to both habitats (intensity hypothesis) – a. to flowering; b. to fruiting. The black row indicate the beginning (0º). From 0º at 180º is represented 2010, and from 180º to the end is 2011. Note bars considerable 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
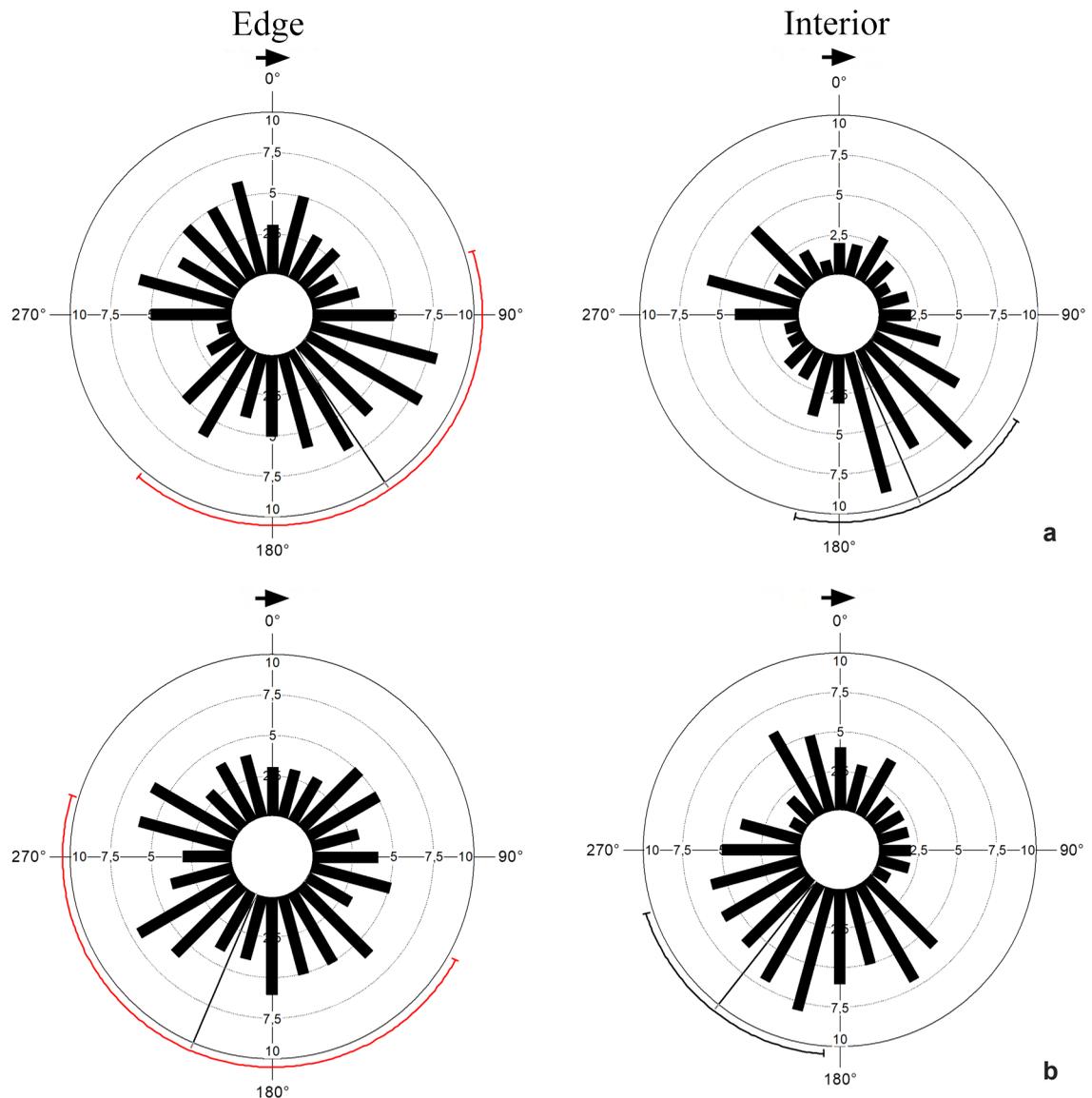
Figure 4 – a-b. Circular representation of species percentage in a phenological activity for tree community without species common (composition hypothesis) – a. to flowering; b. to fruiting. From 0º at 180º is represented 2010, and from 180º to the end is 2011. Considering the bars, the percentage species in fruiting was higher at edge in 2010, and higher at interior in 2011. Surrounding bars outside indicates the confidence limits.

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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 dispersers) 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).

Acknowledgments

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