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Research Article

Landscape attributes drive complex spatial microclimate configuration of Brazilian Atlantic forest fragments

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Abstract
Habitat fragmentation imposes profound impacts on the tropical forest microclimate, but the microclimatic configuration of isolated forest patches and its implications for biodiversity persistence and habitat management are not clear. In this study we assessed a set of 10 aged (> 80 years) fragments (3.0 – 3,500 ha in size) of the Atlantic forest to examine to what extent fragment microclimatic attributes are correlated with distance to the nearest edge as frequently proposed in the literature. We used 129 sampling points and took a total of 516 measures of air temperature and humidity, vapor pressure deficit and light incidence to characterize the microclimate of forest fragments in terms of their relative deviation from the surrounding matrix. Fragments as a whole presented strong internal variation and strongly differed from the microclimate exhibited by the open matrix of sugar-cane fields. Distance to nearest edge, percentage of forest cover around the measurement point, percentage of edge-affected area, and geographical orientation of the nearest edge all proved to have minor effects on the microclimate of forest fragments. Conversely, we identified percentage of forest cover and fragment area as the most significant explanatory variables driving their microclimatic configuration: as forest cover increases at landscape scale, forest microclimate deviates less from the open matrix (a forest-mediated matrix buffering). Our results suggest that microclimatic conditions are spatially complex, as they do not correlate with the distance to the nearest forest edges; rather, they are driven by a forest-mediated buffering of the surrounding matrix that minimizes heat and humidity exchanges between forest and non-forest habitats, thus shaping the microclimatic signature of isolated forest fragments.

Keywords: edge effects; habitat fragmentation; hyper-fragmented landscapes; microclimate; tropical forest.

Resumen
La fragmentación del hábitat tiene importantes impactos en el microclima de los bosques tropicales, pero los determinantes del microclima en fragmentos aislados y sus efectos sobre la biodiversidad y el manejo de estos ecosistemas aún son mal comprendidos. En este estudio, analizamos un total de 10 fragmentos de bosque (3 – 3,500 ha) aislados por más de 80 años para entender como los parámetros microclimáticos responden a características del paisaje, de los fragmentos, a la distancia al borde más próximo. Para ello, en un total de 129 puntos tomamos 516 mediciones de temperatura del aire, humedad relativa del aire, déficit de presión de vapor e incidencia de luz difusa para caracterizar el microclima de estos fragmentos en relación a los valores de la matriz adyacente. Como esperado, los fragmentos presentaron fuerte variación interna y diferirán largamente del microclima encontrado en la matriz no-forestal. La distancia al borde y otras tres variables no presentaron efectos muy significativos sobre el microclima de los fragmentos como un todo. Por otro lado, identificamos que el porcentaje de cobertura forestal alrededor de los fragmentos y su tamaño (ha) son las variables explicativas más importantes en la configuración microclimática, es decir, si la cobertura forestal aumenta en el paisaje, es menor su diferencia del microclima se diferencia del microclima en relación a la matriz no-forestal. Nuestros resultados sugieren que el microclima de los fragmentos de bosque son espacialmente complejos y no se correlacionan con la distancia al borde de los mismos; pero son influenciados por la cobertura forestal del paisaje como un todo que reduce los cambios de calor y humedad entre matriz y bosque influenciando, por lo tanto, el microclima de fragmentos de bosque.

Keywords: Efecto de borde; fragmentación del hábitat; paisajes híper-fragmentados; microclima; bosque tropical

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Introduction

Deforestation and habitat fragmentation represent the most pervasive and conspicuous anthropogenic disturbances in tropical forest landscapes [1]. In the near future, a relentless increase in human population of some tropical countries will reduce large blocks of old-growth forests to archipelagos of small fragments [2], which tend to become progressively embedded into human-managed, environmentally harsh matrices, such as pastures, croplands, and urban areas [3]. Therefore, habitat fragmentation will invariably expose an increasing portion of the remaining forest habitats to edge effects—the diverse physical and biotic changes resulting from differences in the structural complexity and biomass between juxtaposed ecosystems, i.e., the patch contrast *sensu* Harper *et al.* [4]. Creation of artificial forest edges may have serious consequences for the microclimate configuration of forest remnants embedded in non-forested habitats. Nowadays, an increasing portion of the tropical forests in fragmented landscapes are experiencing profound shifts in the structure of biological communities, with perceivable shifts in species composition regardless of whether forest patches are newly configured as a variegated, a truly fragmented, or a relictual stage [see 5, 6]. Therefore, it is reasonable to expect that the creation of edges and its relation with the microclimate configuration in isolated forest patches may be one of the main causes of the rearrangement of the biota in fragmented landscapes.

It is now clear that the negative and highly pervasive effects produced by habitat fragmentation result from a myriad of processes (such as habitat loss and disruption of biological connectivity), but much of the ecological alteration faced by the forest ecosystems can be assigned as edge-driven [6-9]. Fragment desiccation, biomass collapse, invasion of exotic species, and pervasive proliferation of early successional plants along forest edges and across small forest fragments suggest that direct edge effects (e.g., microclimatic changes) and cascade effects represent the major driving force shaping the nature of fragmented landscapes and operate as a huge catalytic source of ecosystem degradation, including biodiversity loss [7, 10]. In fact, the conspicuous impoverishment of tree assemblages along aging forest edges [11, 12] suggests that edge effects represent a permanent rather than an ephemeral force driving the spatial distribution of biodiversity in fragmented landscapes that consist largely or entirely of edge-affected habitats. In synthesis, there is no doubt that edge effects drastically affect or even drive fragments' environmental conditions as well as their internal spatial organization; however, the way fragment environments are shaped by edge-mediated influences remains poorly investigated and controversial [13].

Microclimate of forest fragments is affected by a myriad of variables including both patch and landscape metrics, such as fragment age, form, and matrix type [4, 30]. However, most studies that account for changes in the physical environment of forest fragments adopt the edge-interior cutoff in a patch scale. From this perspective, recent syntheses about edge effects in tropical forest landscapes support two major patterns. Edge-effects are greatly variable in terms of intensity and magnitude [*sensu* 4], and most of these effects penetrate less than 300 m into forests [7]. Additionally, the magnitude of many effects (particularly the abiotic ones) correlates strongly with the distance to forest edges (i.e., in a linear or exponential relationship fashion), such as the microclimatic shifts and the consequent plant population responses [6]. For example, both tree mortality [14] and air temperature [15] appear to drop steadily from forest edge toward forest interior. This basic pattern of edge to-interior changes implies a logical corollary—edge-equidistant spots within the same fragment tend to exhibit similar physical/biological conditions (a sort of edge-interior paradigm). Consequently, fragments are expected to show an internal concentric zonation in both biological and physical terms. The second and less documented pattern suggests that edge-effect expression in any single fragment is likely to be modulated by a myriad of structural and spatial attributes such as edge geographical orientation and age [16-18], fragment shape and isolation level [19], and harshness of the surrounding matrix [20-21]. These influences probably lead edge effects to be much more asymmetric in terms of intensity and magnitude, likely preventing fragments from being concentrically zoned in terms of both physical and biological characteristics; it imposes, in fact, a more spatially irregular arrangement of the biodiversity inhabiting them. To elucidate whether microclimatic configuration of forest fragments follows a concentric or irregular organization has profound implications for conservation/restoration planning in the context of hyper-fragmented landscapes, particularly for reintroduction/management of highly edge-sensitive species at local and landscape scales.

Unfortunately, studies on microclimatic configuration of tropical fragmented landscapes are still relatively rare, and most have been carried out in recently fragmented landscapes [22], which imposes some limits to anticipating long-term/persistent patterns of microclimate as well as their expressions and the definitive effects on forest fragments. The Atlantic forest of northeast Brazil is now reduced to archipelagos of small forest fragments [23], which have been embedded into sugar-cane plantations during the last four centuries [19, 24]. Old-forest fragments surrounded by this structurally homogeneous and stable matrix offer an excellent opportunity to examine the nature of forest fragments in anthropogenic landscapes and the implications for biodiversity conservation [12]. In this study we assessed a set of 10 aged (> 80 years), completely isolated fragments of Atlantic forest (3.0 – 3,500 ha in size) to investigate to what extent fragment microclimatic attributes are linearly correlated to distance to the nearest edge (i.e., edge-to-interior orientated changes or just edge effects) as largely proposed in the literature. First, we describe fragment microclimate and its relative deviation from the surrounding matrix of sugar-cane fields. Further, a small set of six patch and landscape metrics (*e.g.*, percentage of forest cover, fragment area, etc.) that apparently drive fragment microclimate is examined. Finally, we address some of the processes shaping the microclimatic configuration of forest fragments and discuss plausible implications of our uncovered patterns for the management of aging, hyper-fragmented landscapes. In summary, we expect to demonstrate that the "edge-interior" paradigm is too simple and inappropriate to draw robust conclusions on the spatial configuration of microclimate in forest fragments. Therefore, we offer a new and comprehensible approach to the understanding of the microclimate configuration of forest fragments and propose a set of practical implications for biodiversity conservation and the management of hyper-fragmented landscapes.

Methods

Study Area

The study was carried out from October 2005 to April 2006 and took place at Usina Serra Grande—a large private sugar company located in the State of Alagoas, northeastern Brazil (8º30'S, 35º50'W). This landholding still retains approximately 9,000 ha of forest assigned to a unique biogeographic region of the Atlantic forest, the Pernambuco Center of Endemism [25]. We selected a large (667 km^2), severely fragmented landscape containing 109 forest fragments (range in size = 1.67 to 3,500 ha), all of which are entirely surrounded by a uniform, stable, and inhospitable matrix of sugar-cane monoculture (Fig. 1; Table 1). This landscape comprises a low-altitude plateau (300-400 m above sea level) covered by a lowland forest (< 400 m a.s.l.). Annual rainfall is ~ 2,000 mm with a 3-month dry season (< 60 mm per mo) from November to January.

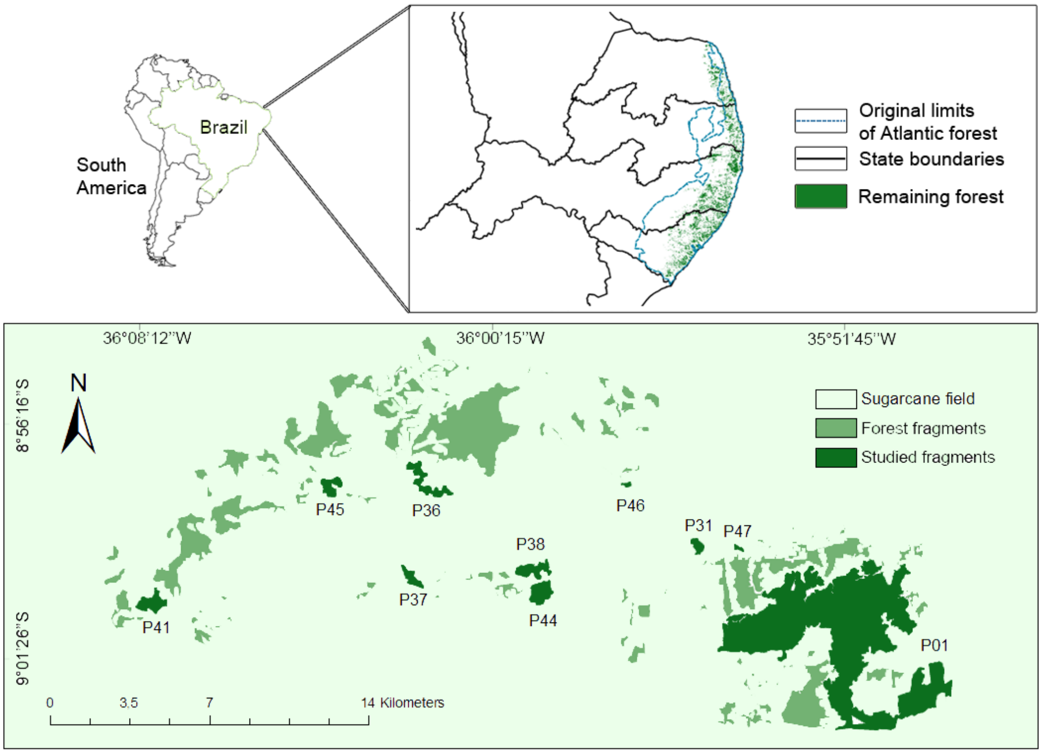

Fig. 1. Study site comprising an aged hyper-fragmented landscape at the Usina Serra Grande, Brazil.

Conservatively, sugar-cane cultivation in this landscape dates back to the 19th century and was the original motivation for clearing large tracts of pristine old-growth forests [12]. Current forest fragments, including the Coimbra forest, have been protected against fire and logging in order to preserve the watershed and guarantee a water supply for sugar-cane irrigation [22]. Such protection has guaranteed the stability of fragment perimeters, and consequently forest edges have been covered by reproductive pioneer and shade-tolerant trees [26], i.e., post-closure forest edges. This landscape, therefore, provides an interesting opportunity for fragmentation-related studies.

Microclimatic attributes

We selected a set of 10 forest fragments ranging in size from 3 to 3,500 ha, and within each of them 10 to 39 measurement points were randomly positioned for microclimate measurements (Table 1). The 129 resulting points were from 2.6 m to 600 m away from the nearest forest edge, thereby covering a large range of distances from edges over which edge effects are expected to manifest. The random locations were set in a georeferenced digital map of the study site with the help of the ArcView 3.2 software.

Table 1. Basic characteristics of each of the 10 forest fragments studied at Usina Serra Grande

Studied Fragments	FragmentArea (ha)	% of forest cover (1 km radius)	Measurement points
P01	3500.0	6.7	39
P36	91.2	8.2	10
P44	83.6	15.0	10
P38	79.6	17.1	10
P45	50.0	9.6	10
P40	43.7	1.2	10
P52	27.5	19.1	10
P47	10.2	26.1	10
P46	8.3	5.5	10
P37	3.5	5.4	10

We obtained a single measure across the 129 stations of each of the following microclimatic attributes: light incidence, air temperature, air relative moisture, and vapor pressure deficit (VPD). With the exception of the 129 light-incidence measures, the resulting 387 air-related and VPD measures were all taken between 12:00- 13:00h, under similar weather conditions of sunny sky or few clouds during the dry season of 2005/2006 (i.e., November to April). In the dry season, microclimate differences between the matrix and fragments are more perceivable, and consequently the edge effects are believed to be more tangible [27]. Briefly, light incidence was expressed as the percentage of diffuse light reaching the forest understory; it was characterized *via* leveled, hemispherical photographs taken at 1 m above ground level. Photographs were taken by a Nikon Coolpix 990 camera with a FC-E8 fisheye converter at dawn before sunrise, at dusk after sunset, or during overcast sky conditions to avoid direct solar radiation in any part of the canopy. Camera configuration and photograph analysis via the Gap Light Analyzer software followed the same procedures adopted by Wirth et al. [28]. Relative humidity and air temperature were measured using a portable thermo-hygrometer (model MTH-1380- Winner®), and such measures permitted us to obtain estimates for VPD [29].

Microclimate measurements are highly sensitive to general weather conditions and are only exclusively comparable if obtained simultaneously. Because of this (1), within-fragment measures were taken almost simultaneously, and furthermore (2) the 387 air-temperature and moisture measures, as well as VPD estimates, were expressed and examined as a relative (positive or negative) deviation from 387 paired measures taken simultaneously in the close matrix, i.e., 20 m outside fragments in the sugar-cane fields and respecting the geographical orientation of each measurement station. This sort of standardization and time-paired measurement has been adopted elsewhere in the literature [27]. In summary, these procedures offered an acceptable guarantee that within- and between-fragment differences on microclimatic parameters were not influenced by measurement techniques.

Explanatory variables

Here we assigned six plausible explanatory variables within two mutually exclusive categories. Patch-scaled metrics (PSM) are those variables that vary independently across the 129 measurement stations, regardless of whether they are located in the same fragment or not. These are: (1) edge geographical orientation (i.e., north, south, west, and east), (2) distance to nearest forest edge, (3) percentage of forest cover within a 600-m radius of each measurement station, and (4) percentage of edge-affected habitat (i.e., adopting an edge effect of 50 m adopted for the fragments, the percentage of forest cover within a 600-m set radius from each measurement station lying within the first 50 m from the border). Landscape-scaled metrics (LSM) are those attributes that vary at the landscape scale but remain constant for all the stations within the same fragment; they were percentage of forest cover around each forest fragment and fragment area. Percentage of forest cover was defined as the percentage of forested area within a 1-km external buffer set from the perimeter of each fragment. These LSM varied independently in our study site (Pearson´s correlation test = -0.13; p = 0.7; N = 10), thus ensuring independence between them. All LSM were quantified via a georeferenced digital map of the study site, which was obtained by combining (1) three images of Landsat and Spot (years 1989, 1998, 2003) and (2) a group of 160 aerial photos (1: 8000) taken by helicopter flights commissioned in April 2003.

Data analysis

Description of fragment microclimate as a deviation of matrix microclimate and its relationships with explanatory variables were examined using the following complementary approaches. First, we estimated to what extent the microclimate measures within each forest fragment deviated from their respective average values, here defined as a relative individual variation of microclimatic attributes, i.e., within-fragment microclimatic variation. Second, linear regressions and one-way ANOVAs were applied individually for each fragment alone to examine possible effects from PSM variables on the four microclimatic attributes. Third, general linear mixed models (GLMM) were used to examine the influence of PSM variables on the microclimatic configuration of forest fragments considering the entire set of 129 locations within the 10 fragments. The four PSM variables were assigned as fixed effects, and to control for variation among fragments an additional categorical variable called “fragment” was used as a random factor in the models. This technique allowed us to separate the effects by the higher order factors (PSM) from those caused by between-fragment variation. Finally, the variance not explained by the GLMM models considering the PSM variables as factors (model residuals) was assigned as a response variable in general linear models (GLM) with the two LSM variables (i.e., percentage of forest cover and fragment area) as factors as well as their interactions. Prior to all analyses, response and explanatory variables were log (absolute) or arcsine transformed (proportions) according to their nature in order to stabilize variance, improve normality of data, and consequently increase the explanatory power of models as adopted elsewhere (Santos et al., 2008). We assumed that this pool of analyses and data transformation was sufficiently robust to identify any microclimatic attribute responding linearly or even exponentially to the distance to nearest edge. All analyses were run in JMP 7.0, and the R^2 values reported always refer to the adjusted R^2.

Results

As expected, the microclimate of fragments presented strong internal variation (Fig. 2) and strongly differed from the relatively open matrix of sugar-cane fields (Fig. 3) with an average deviation of ca. 10% in air temperature, relative humidity, and VPD. When we analyzed data per fragment (through 40 ANOVA, four per forest fragment), eight significant relationships were found between the PSM variables and microclimatic attributes of forest fragments. Distance to nearest forest edge was negatively correlated with VPD (R^2 = 45.3%) and positively correlated with relative air moisture (R^2 = 40.2%) in a single fragment of 43.7 ha, while the percentage of edge-affected habitat was positively correlated with relative air moisture in a small forest patch of 3.48 ha (R^2 = 45.9%) and negatively correlated with light incidence in the largest 3,500 ha forest patch (R^2 = 8.7%). Yet, contradictory patterns were found for percentage of forest cover around measurement stations as it correlated positively with relative air moisture in a 91-ha forest fragment (R^2 = 43.6%), but these same parameters were negatively correlated in a 3.48-ha fragment (R^2 = 46.6%). Such a metric also negatively affected the light incidence in the 79.6-ha fragment (R^2 = 50.2%) and VPD in another forest patch of 83.6 ha (R^2 = 39.5%). Finally, edge geographical orientation proved to have no effects on the microclimatic configuration of forest fragments.

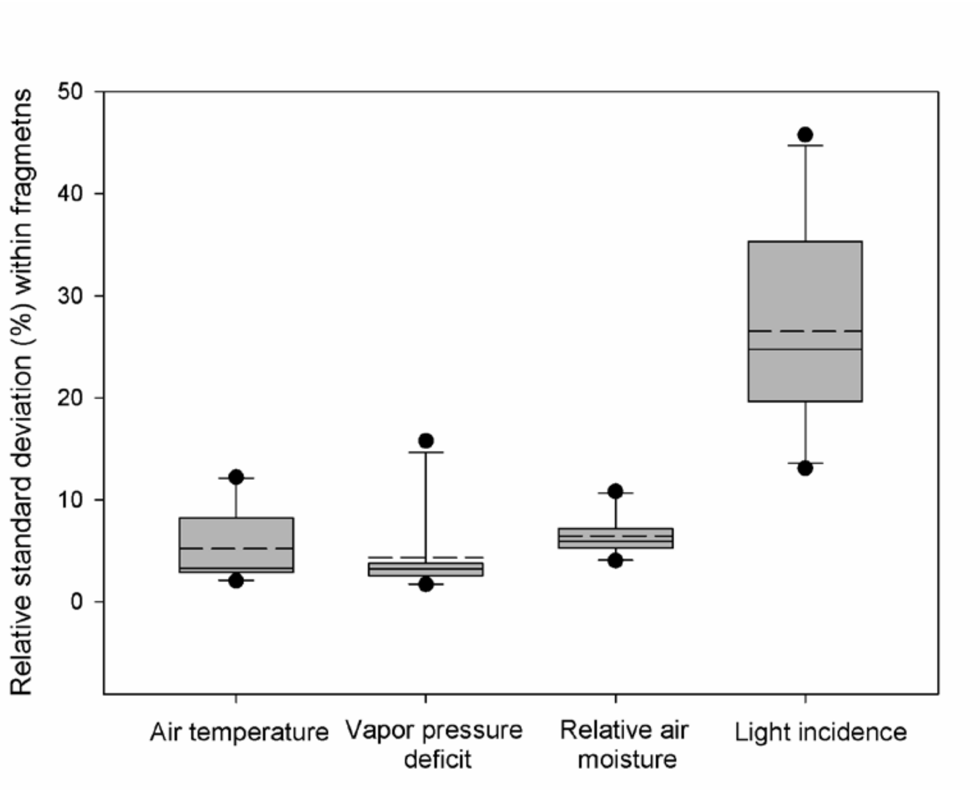

Fig. 2. Mean individual variation exhibited by four microclimatic attributes of forest fragments at Usina Serra Grande, Brazil. Median (solid line) and mean (dashed line) with 25th and 75th (boundaries of boxes); 5th and 95th percentiles (whiskers above and below box-plots) and outliers (points) are also indicated. (*n* = 10 forest fragments, 129 measures per attribute).

When we treated all fragments as a whole, GLMMs also failed to detect any significant effect of PSM variables on the microclimatic configuration of forest fragments as a whole (Table 2). Moreover, between 3% and 53% of the non-explained variance in physical environment was due to idiosyncratic characteristics of the fragments, i.e., variance explained by the random effect “fragment.” On the other hand, GLMs for landscape-scale metrics (LSM) clearly identified fragment area and its interaction with percentage of forest cover (LSM variables) as significant explanatory variables driving the microclimate of forest fragments (Table 3). Relative change in air temperature and moisture were all correlated with the logarithm of forest fragment area, but responses were mediated by the percentage of forest cover of forest fragments. In this case, the microclimate of larger fragments and those embedded in a more forested portion of the landscape deviated less from the close matrix (Fig. 4). Finally, VPD responded neither to forest area nor to percentage of forest cover, and light incidence was positively correlated with the interaction between fragment area and percentage of forest cover (Table 3).

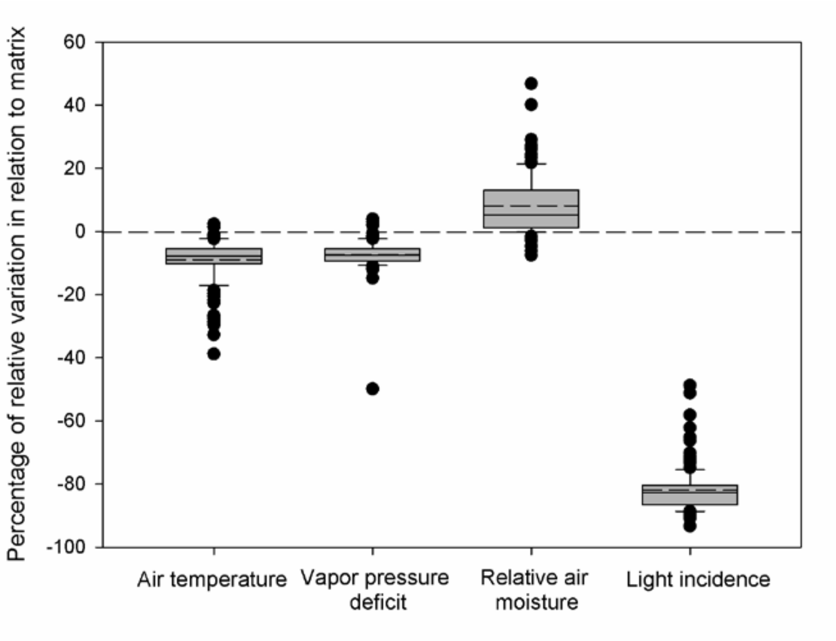

Fig. 3. Mean deviation exhibited by four microclimatic attributes of forest fragments as compared to the surrounding sugar-cane matrix at Usina Serra Grande, Brazil. Median (solid line) and mean (dashed line) with 25th and 75th (boundaries of boxes); 5th and 95th percentiles (whiskers above and below box-plots) and outliers (points) are also indicated. (*n* =10 forest fragments and 129 measures per attribute).

Discussion

Here we adopted a robust (i.e., 129 measurement stations within 10 fragments) and replicable study design in order to assess the spatial microclimatic configuration of forest fragments embedded within an aging and hyper-fragmented forest landscape. Our results suggest that fragment microclimatic conditions are highly variable and spatially complex, as they do not correlate with the distance to the nearest forest edge, i.e., no forest-edge microclimate gradient was detected. Moreover, each fragment appears to exhibit a particular or even idiosyncratic pattern of spatial microclimatic configuration in response to fragment size and percentage of forest cover around it. It implies that the simple cutoff—edge vs. core area—is not sufficiently robust to explain the environmental changes faced by old-forest fragments, even in a highly homogeneous matrix consisting of sugar-cane fields. Our findings also suggest that landscape-scale variables represent a driving force for microclimate configuration of forest fragments and reinforce the notion that edge effects and the microclimate of fragments are greatly affected by the structural attributes of the surrounding matrix at both local and landscape level [4, 7, 10].

Creation of forest edges triggers noticeable and persistent shifts along the edges of forest fragments, particularly in terms of microclimate conditions [31-33]. Specifically, forest edges are expected to be highly impacted by increased light availability in response to a high incidence of treefall gaps (at least in the aftermath of forest fragmentation) and lateral light penetration [13, 34]. Enhanced light penetration increases air temperature and its correlated attributes such as air-moisture and vapor-pressure deficit [15, 31, 34]. However, the intensity/magnitude and the spatiotemporal nature of these edge-mediated shifts may be highly variable and modulated by a set of patch and landscape metrics, such as fragment location, edge characteristics, plant-stand attributes, and biotic factors [4]; however, these shifts have been proposed to invariably express themselves as edge-microclimate gradients. Collectively, these edge-interior gradients are believed to produce an internal belt of harsh environment, i.e., a more illuminated, desiccated, and wind-exposed habitat, which parallels forest edges [33]. Such an environment, although highly sensitive to changes of edge vegetation structure and temporarily inconstant [35], is likely to persist as long as forest edges border open-habitat matrices [36].

Table 2. Results from general linear mixed models (GLMM) examining four microclimate attributes and four explanatory variables across 10 forest fragments at Usina Serra Grande, Brazil (n = 529 scores).

Microclimate and PSM variables	*d.f.*	*F - Ratio*	*p*
Air Temperature			
Edge geographical orientation	4	1.1702	0.3276
Edge-affected habitat (%)	1	0.253	0.6159
Forest cover (%)	1	0.2114	0.6465
Distance to the nearest edge	1	2.3743	0.1269
Vapor Pressure Deficit			
Edge geographical orientation	4	0.1859	0.9453
Edge-affected habitat (%)	1	0.038	0.8465
Forest cover (%)	1	3.8235	0.0838
Distance to the nearest edge	1	0.4246	0.5171
Relative Air Moisture			
Edge geographical orientation	4	0.9012	0.4658
Edge-affected habitat (%)	1	0.1388	0.7101
Forest cover (%)	1	0.3776	0.5411
Distance to the nearest edge	1	2.3548	0.1217
Light incidence			
Edge geographical orientation	4	0.3682	0.8309
Edge-affected habitat (%)	1	1.4394	0.2328
Forest cover (%)	1	0.8373	0.3627
Distance to the nearest edge	1	0.0019	0.9653

In the Serra Grande landscape, microclimatic configuration of forest fragments did not linearly correlate to distance to nearest edges whether fragments were analyzed individually or collectively. This general pattern apparently marked by the lack of forest-edge linear gradients may be the result of a myriad of processes. First, aging small forest fragments may not count with core areas that would differ from forest edges [36]. Second, edge effects became less pronounced or imperceptible as fragment ages and edges achieved the post-closure phase [4, 13]. Third, natural heterogeneity of vegetation structure (e.g., treefall gap distribution) may be strong enough to hide edge-mediated shifts [37]. A more plausible mechanistic process is that every fragment edge has its particular microclimatic gradient in terms of shape, intensity, and magnitude in response to landscape-level influences such as structural connectivity.

Another key finding from our study refers to the fact that large fragments and those more connected deviated less than smaller fragments from the surrounding matrix in terms of air temperature and moisture. It implies that as forest cover increases at landscape scale, forest microclimate deviates less from the open matrix. A plausible explanation for this landscape-scaled phenomenon is the ability of the forest ecosystem to maintain low-amplitude temperature regimes and retain elevated moisture in comparison with the non-forested and open surrounding matrix. The higher forest area at fragment scale, the greater may be the heat and moisture exchanges among fragments and the surrounding matrix, thus smoothing microclimatic discrepancies (the patch contrast) among these habitats, i.e., a forest-mediated matrix buffering. This buffering may operate via "vegetation breeze," whereby moisture from the forest is pulled away by winds into surrounding open areas [38]. Conversely, small isolated forest patches do not provide enough "vegetation breeze" to buffer the matrix, thereby enhancing microclimatic differences between forest and non-forest habitats [39].

Table 3. Results of the general linear models (GLM) examining the effect of landscape metrics (LSM) in four microclimate attributes across 10 forest fragments at Usina Serra Grande, Brazil (n = 529 scores). Bold numbers indicate significant effects and signal of t-ratios the type of relationship negative (-) or positive (no sginal).

Landscape metrics (LSM)	**t-ratios for the four microclimatic response variables**			
	Air Temperature	**Vapor Pressure Deficit**	**Relative air moisture**	**Light incidence**
Intercept	-1	-0.89	2.2	-1.36
Log fragment area	**4.27**	0.74	**-4.12**	0.21
Percentage of forest cover	-0.3	0.89	-1.3	1.77
Log fragment area * Percentage of forest cover	**2.42**	1.04	**-3.05**	**3.19**

The hypothesis of an irregular rather than concentric spatial configuration of fragment microclimate driven by landscape-level attributes receives empirical support from tree species distribution (a fragmentation-sensitive group) in our study landscape. Abundance of large trees in forest fragments has been proven to be positively correlated to the amount of forest cover around fragments [22]. Distance to nearest edge has low explanatory power regarding tree-assemblage attributes, such as species richness and functional composition, although tree-assemblage structure in forest edges and small fragments greatly differs from that in core forest interior areas [12, 40]. Whatever the driving force, our group of aging and truly isolated forest fragments is not shaped according to the "edge *vs.* core area" tradeoff, which poses interesting implications for conservation planning in hyper-fragmented landscapes. Habitat fragmentation and the consequent creation of forest edges impose tangible impacts on the biota of tropical forests [10, 41]. As soon as forest edges are created, fragments experience a rapid hyper-proliferation of short-lived pioneer trees, particularly along their edges [42]. Concomitantly, several groups of shade-tolerant/old-growth tree species (e.g., large-seeded, long-lived emergent hardwood tree species) are disfavored, and these species gradually become rare and eventually may be driven to extinction at the landscape scale [43-45]. Fragments largely or entirely consisting of edge-affected habitats cannot retain a full complement of life-history traits in plant communities, and consequently the plant-animal interaction webs constitute distorted communities.

Therefore, the conservation value of small forest fragments will largely depend on the mitigation of edge effects (and their cascades of species extirpation) via a combination of landscape-scale land-use regulations, e.g., keeping landscape structural connectivity via protection of gallery forest [8], plus fragment-scale assisted interventions such the control of liana populations [46], species reintroduction and enrichment [47-48], assisted seedling recruitment [49], and fragment buffering via second-growth vegetation [48, 50]. Such interventions may be rendered ineffective by a priori assumptions that aging fragments immersed in open-habitat matrices are concentric-shaped in terms of microclimatic/biological configuration. As fragments tend to be irregularly-shaped in response to structural variations in the surrounding matrix, a landscape perspective for management must be adopted in order to identify (1) those portions of fragment/landscape that still retain suitable habitats for fragmentation-sensitive species and (2) those that require human intervention to ameliorate edge effects and enhance the conservation value/services provided by severely fragmented landscapes. Further studies should validate both the generality of the patterns and the underlying mechanisms we documented in the Atlantic forest, as they have clear implications for biodiversity persistence and the effective management of hyper-fragmented landscapes.

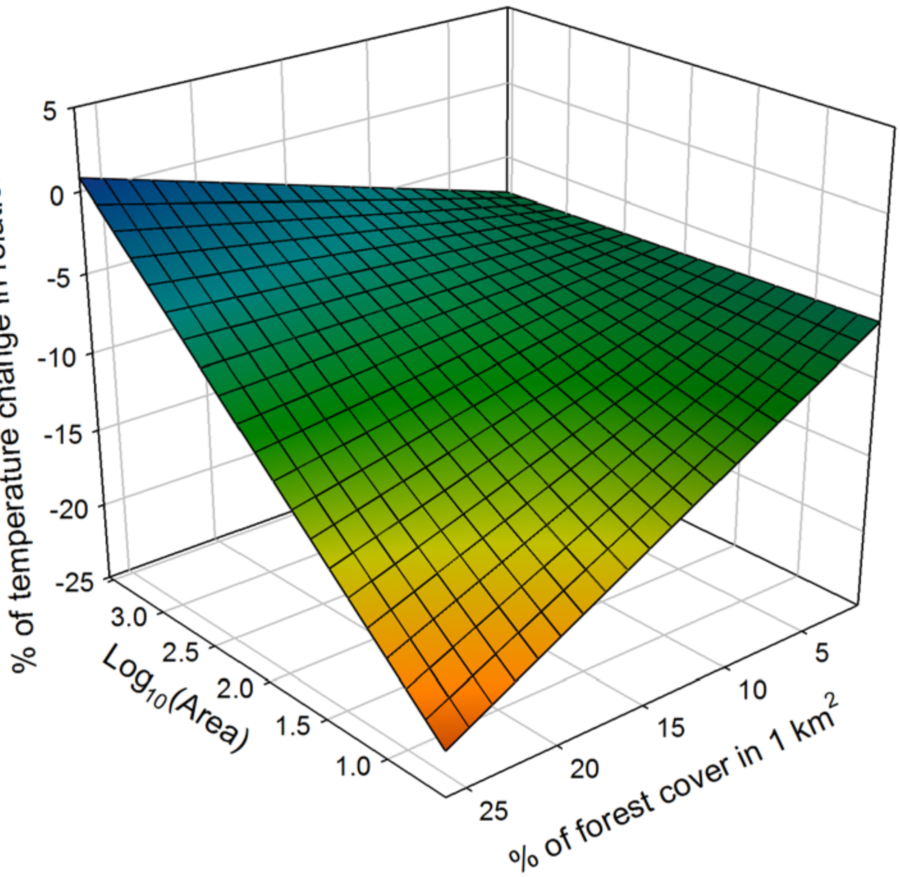

Fig. 4. Surface plot of model-predicted values of relative change of air temperature inside forest fragments with respect to surrounding matrix as a function of the logarithm of forest fragment area and its interaction with percentage of forest cover (percentage of forested area around forest fragments).

Implications for Conservation

- Within- and between-fragment microclimatic heterogeneity is a conspicuous feature of hyper-fragmented landscapes and must be taken into account in conservation/restoration planning.
- The simple cutoff "edge *vs.* core area" is a misleading approach to examining the microclimatic configuration of forest fragments in hyper-fragmented landscapes. The landscape context, especially the spatial configuration of remaining forest cover, has noticeable influences on local microclimatic patterns.
- Conservation practices aiming at mitigation of edge effects should be planned at landscape scale by identifying those portions highly modified in terms of microclimatic conditions and thus more susceptible to supporting distorted assemblages and ecological processes, i.e., landscape portions requiring human intervention.
- Protecting large areas and preventing further fragmentation of continuous large patches remain key recommendations to avoid ecological deterioration of fragmented landscapes, as increased forest cover and structural connectivity may reduce macroclimate extremes in the matrix (forest-mediated matrix buffering) and thus reduce the patch contrast—the mechanism leading to edge effects and their cascade of both community- and ecosystem-level disruptions.

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