

NOTE AND COMMENT

Víctor Arroyo-Rodríguez · Romeo A. Saldaña-Vázquez ·  
Lenore Fahrig · Bráulio A. Santos

## Does forest fragmentation cause an increase in forest temperature?

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**Abstract** Forest fragmentation is considered by many to be a primary cause of the current biodiversity crisis. The underlying mechanisms are poorly known, but a potentially important one is associated with altered thermal conditions within the remaining forest patches, especially at forest edges. Yet, large uncertainty remains about the effect of fragmentation on forest temperature, as it is unclear whether temperature decreases from forest edge to forest interior, and whether this local gradient scales up to an effect of fragmentation (landscape attribute) on temperature. We calculated the effect size (correlation coefficient) of distance from forest edge on air temperature, and tested for differences among forest types surrounded by different matrices using meta-analysis techniques. We found a negative edge-interior temperature gradient, but correlation coefficients were highly variable, and significant only for temperate and tropical forests surrounded by a highly contrasting open matrix. Nevertheless, it is unclear if these local-scale changes in temperature can be scaled up to an effect of fragmentation on temperature. Although it may be valid when considering “fragmentation” as forest loss only, the landscape-scale inference is not so clear when

we consider the second aspect of fragmentation, where a given amount of forest is divided into a large number of small patches (fragmentation per se). Therefore, care is needed when assuming that fragmentation changes forest temperature, as thermal changes at forest edges depend on forest type and matrix composition, and it is still uncertain if this local gradient can be scaled up to the landscape.

**Keywords** Climate change · Edge effects · Habitat disturbance · Microclimate · Thermal biology

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V. Arroyo-Rodríguez (✉) · R. A. Saldaña-Vázquez  
Instituto de Investigaciones en Ecosistemas y Sustentabilidad,  
Universidad Nacional Autónoma de México, Antigua Carretera a  
Pátzcuaro No. 8701, Ex-Hacienda de San José de la Huerta, 58190  
Morelia, Michoacán, Mexico  
E-mail: victorarroyo\_rodriguez@hotmail.com  
Tel.: +52 (443) 3222777

L. Fahrig  
Geomatics and Landscape Ecology Laboratory, Department of  
Biology, Carleton University, 1125, Colonel Drive, Ottawa, ON  
K1S 5B6, Canada

B. A. Santos  
Departamento de Sistemática e Ecologia, Universidade Federal da  
Paraíba, Cidade Universitária, s/n-Castelo Branco, João Pessoa,  
Paraíba 58051-900, Brazil

### Introduction

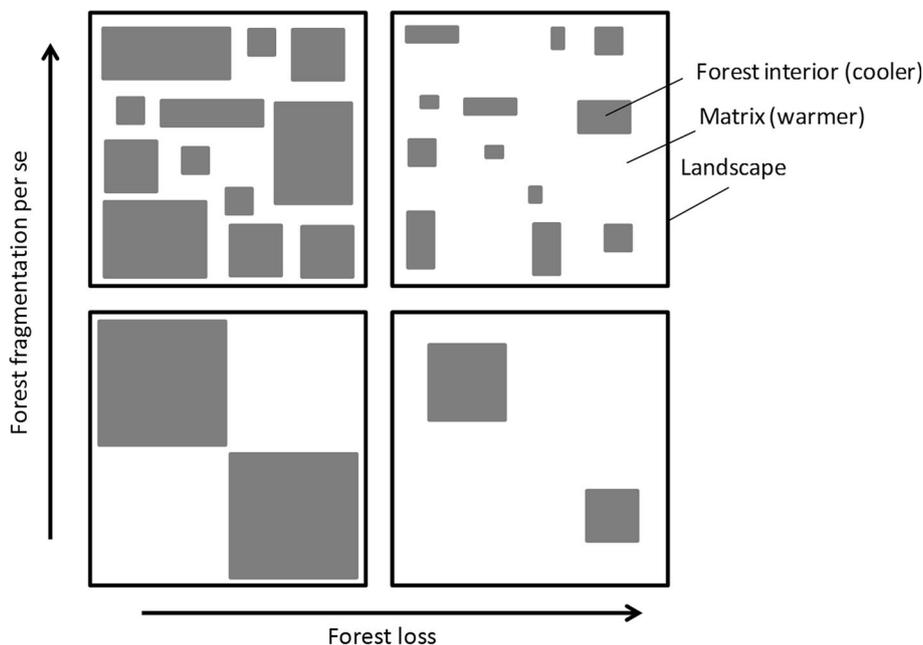
Forest fragmentation is considered by many to be an important driver of biological impoverishment worldwide (Haddad et al. 2015). Different mechanisms have been proposed to explain the causes of such impoverishment (e.g. Ewers and Didham 2006; Didham et al. 2012; Tschardt et al. 2012), and one potentially important mechanism is associated with altered microclimatic conditions within the remaining forest patches (Murcia 1995; Laurance et al. 2002; Latimer and Zuckerberg 2016; Tuff et al. 2016), particularly at forest edges (“edge influence”; sensu Harper et al. 2005). Unfortunately, our understanding about the effect of forest fragmentation on forest temperature is still very poor.

The hypothesis that temperature drives ecological responses to fragmentation has been recently reviewed by Tuff et al. (2016). In fact, they propose a framework that links thermosensitivity of individuals and species to community and ecosystem shifts following habitat fragmentation (Tuff et al. 2016). Although timely and interesting, the utility of this framework is limited by at least three main constraints. First, mean temperature (and especially variance) is rarely measured in fragmented forests (but see Latimer and Zuckerberg 2016). Second, fragmentation is typically defined as a landscape-scale process (McGarigal and Cushman 2002), but

changes in temperature in fragmented forests are mainly assessed at the patch scale—usually comparing forest edges and interiors (Murcia 1995; Tuff et al. 2016). Finally, the available evidence on thermal changes at forest edges is not conclusive. Although some studies support the premise of higher mean temperature at forest edges than interiors (Tuff et al. 2016), other studies do not find the expected negative edge-interior temperature gradient (e.g. Young and Mitchell 1994; Cadenasso et al. 1997; Gehlhausen et al. 2000; Wright et al. 2010; Dovčiak and Brown 2014).

An important challenge when assessing the importance of temperature as a mechanism underlying ecological disturbances following forest fragmentation is that thermal changes at forest edges can be highly variable, depending on multiple factors such as forest type, matrix composition, edge orientation, and forest edge age (reviewed by Tuff et al. 2016). For example, changes in mean temperature at forest edges are expected to be higher in recently created forest edges, especially when bordered by a high-contrast open-area matrix (Williams-Linera 1990; Matlack 1993; Didham and Lawton 1999; Pohlman et al. 2007). Thermal changes can also be higher in forests that receive higher solar radiation (e.g. tropical forests > temperate forests), particularly at those edges oriented to South in the northern hemisphere or edges oriented to North in the southern hemisphere (Tuff et al. 2016). Yet, because no study to date has synthesized the available information on thermal changes at forest edges, large uncertainty remains on the generality of the expected negative edge-interior temperature gradient and the potential driving forces.

Here, we evaluated whether temperature decreases from forest edge to forest interior with a global meta-analysis. To assess if such local gradients depend on forest type and matrix composition, we tested for differences in edge-interior temperature gradients among forest types surrounded by different matrices. Finally, we discuss whether this local gradient can be scaled up to make landscape-scale inferences, particularly considering the two main components of the fragmentation process: forest loss and forest ‘division’ into small patches (Fahrig 2003, 2017; Hadley and Betts 2016; Fig. 1). We focus on these two components of the fragmentation process because they can have different effects on air temperature at the landscape scale. For example, by converting large tracts of closed-canopy forest into smaller patches surrounded by open matrix, forest loss increases both the edge to area ratio and the amount of warmer, open cover in the landscape (as we move panels from a to b, and c to d; Fig. 1). Yet, when a given amount of forest is divided into a large number of small patches (i.e. fragmentation per se), the amount of forest edge also increases, but the amount of (warm) open matrix in the landscape remains constant (from panels c to a, and d to b; Fig. 1). This implies that, with increasing the number of forest patches in the landscape, fragmentation per se increases the proportion of the matrix that is exposed to (cool) forest air, potentially increasing air temperature in the matrix (see the “vegetation breeze” phenomenon; sensu Cochrane and Laurance 2008). Therefore, forest loss and fragmentation per se may lead to different edge-interior temperature gradients, and different changes in air temperature at the landscape scale.



**Fig. 1** Illustration of the two components of forest ‘fragmentation’ as defined by Tuff et al. (2016): forest loss and forest fragmentation per se. Forest loss is the removal of forest from the landscape. Forest fragmentation per se is a change in forest configuration, entailing a larger number of smaller forest patches

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## Materials and methods

### Database

We conducted an extensive review in the Google Scholar and Web of Science™ databases on April 13 2016 for original papers containing “habitat fragmentation” or “forest fragmentation”, plus “temperature” and “forest edge” in the title, abstract, and/or keywords. We also identified additional studies cited within this primary literature (Table S1). We then selected the studies that contained the coefficient of correlation ( $r$ ) or determination ( $R^2$ ) from the relationship between mean air temperature and distance from forest edge, and that used a minimum sample size ( $n$ )  $\geq 4$ . When  $r$  or  $R^2$  were not specified, but authors presented the scatter plot of the relationship between mean air temperature and distance from forest edge, we calculated  $r$  values extracting the raw data from the figures included in the papers using the DATA THIEF III program (Tummers 2012). When authors reported  $F$  statistics as a measure of effect size, we transformed it to correlation coefficients using the formulas proposed by Rosenberg et al. (2000). From the 41 papers we reviewed, 15 studies showed useful data (see Table S1), representing 43 independent effect sizes (i.e. collected in different forest patches or in different areas within the same patch) from six broad forest types in eight countries (Table 1). We then built a database containing the coefficient of correlation for each forest type, forest edge age, time of day and duration of measurements, annual season of measurements, edge orientation and matrix composition outside forest edges (Table 1). All measures were made above ground (0.3 to 1.5-m height). The study by Didham and Ewers (2014) was the only that assessed edge-interior temperature gradients at different heights, so in this case we considered each height as a different measurement of effect size (Table 1).

### Meta-analysis

We calculated the global correlation coefficient for the relationship between mean air temperature and distance from forest edge. We fitted a random effects model because we can expect important differences among population effect sizes due to differences in samples and methods used across studies (Hedges and Vevea 1998). To avoid problems associated with publication bias, we carried out a regression asymmetry test (Egger et al. 1997), which indicated that there is no publication bias in our global meta-analysis ( $t = -0.15$ , d.f. = 41,  $P = 0.88$ ). The Cochran’s  $Q$  test showed that there is significant heterogeneity in correlation coefficients ( $Q = 52702.09$ , d.f. = 42,  $P < 0.0001$ ), indicating that we can compare correlation coefficients among samples from different forest types and surrounded by different types of anthropogenic matrices (i.e. roads, open areas,

annual crops, sand-scrub, and secondary forests; Table 1) (Gurevitch and Hedges 1999; Borenstein et al. 2009). We then compared the correlation coefficients of the association between mean air temperature and distance from forest edge among different forest types, and we also tested if correlation coefficients differed among forest types surrounded by different matrix types using a mixed-effects model meta-analysis (Viechtbauer 2010). We did not test the effect of edge orientation because most studies do not specify the orientation or show averaged data for edges with different orientations (Table 1). We also excluded forest edge age from our analyses because there was too little information available on this variable (7 effect sizes). All analyzes were performed using the *escalc*, *rma* and *regtest* functions of the *metafor* package for R version 3.2.0 (Viechtbauer 2010).

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## Results

The global correlation coefficient for the relationship between mean air temperature and forest edge distance was negative ( $r = -0.39$ ,  $P < 0.01$ , 95% CI =  $-0.57$  to  $-0.21$ ), but varied widely, from  $-0.99$  to  $0.99$ , indicating both decreasing and increasing temperature gradients (Table 1). Correlations were significantly negative in temperate forests, tropical mountain forests, and tropical rainforests (Fig. 2a), mainly when located next to a highly contrasting open matrix cover type (Fig. 2b). Gradients were also negative, but not significant, in subtropical humid forests and subtropical mountain forests, and positive (though not significant) in subtropical dry forests (Fig. 2a). Note that these three forest types were embedded in high-contrast matrices (i.e. open areas and roads; Fig. 2b; Table 1).

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## Discussion

We found support for the assumption of a negative edge-interior temperature gradient (Tuff et al. 2016), but principally for closed-canopy forests (i.e. tropical and temperate forests) surrounded by open-area matrices. Note that all the studies cited by Tuff et al. (2016) to support this gradient were in these forest types. Yet, such a gradient was not significant in three different types of subtropical forests, even when embedded in high-contrast matrices, nor in temperate forests and tropical rainforests surrounded by mid- to low-contrast matrices (i.e. sand-scrub matrix and secondary forests), most probably because there is a lower contrast in temperature between forested and non forested areas in landscapes composed of these forest types and anthropogenic matrices (Harper et al. 2005; FAO 2012). Therefore, our findings indicate that changes in mean temperature at forest edges cannot be generalized to all forest landscapes, as they depend on forest type and matrix composition.

**Table 1** Database used in meta-analysis

References	Country	R	n	Vegetation type <sup>a</sup>	Edge age (years)	Time of day <sup>b</sup>	Annual season	Edge orientation	Matrix composition <sup>d</sup>
Matlack (1993)	USA	-0.990	10	TF	5	-	-	South	Open areas
Matlack (1993)	USA	-0.240	10	TF	5	-	-	North	Open areas
Matlack (1993)	USA	0.700	10	TF	-	-	-	South	Young secondary forest
Matlack (1993)	USA	-0.570	10	TF	-	-	-	North	Old secondary forest
José et al. (1996)	India	-0.990	7	TMF	-	10–12 h	Dry season	Different orientations <sup>c</sup>	-
Cadenasso et al. (1997)	USA	-0.910	7	TF	-	-	Summer	North	Open areas
Cadenasso et al. (1997)	USA	0.200	7	TF	-	Midday	Summer	North	Open areas
Cadenasso et al. (1997)	USA	0.220	7	TF	-	-	Summer	North	Open areas
Cadenasso et al. (1997)	USA	0.520	7	TF	-	Midday	Summer	North	Open areas
Williams-Linera et al. (1998)	Mexico	-0.770	6	TRF	4	9–10, 12–13 and 15–16 h	-	Southeast and Southwest <sup>c</sup>	Open areas
Williams-Linera et al. (1998)	Mexico	-0.920	6	TRF	15	9–10, 12–13 and 15–16 h	-	Southeast and Southwest <sup>c</sup>	Open areas
Davies-Colley et al. (2000)	New Zealand	-0.810	48	SHF	90	12–15 h	Winter	North	Open areas
Lehtinen et al. (2003)	Madagascar	-0.750	12	TRF	-	11–15 h	Rainy season	-	Sand-scrub
de Siqueira et al. (2004)	Brazil	-0.840	6	TRF	-	10–14 h	-	North–South, and East–West <sup>c</sup>	Open areas
Lehman et al. (2006)	Madagascar	-0.960	10	TMF	-	9–14:30 h	-	-	Annual crops
Pohlman et al. (2007)	Australia	-0.780	6	TRF	-	-	Dry and rainy	Different orientations <sup>c</sup>	Open areas
Pohlman et al. (2007)	Australia	-0.890	6	TRF	-	-	Dry and rainy	Different orientations <sup>c</sup>	Open areas
Delgado et al. (2007)	Spain	-0.360	9	SMF	-	12–15 h	Spring–Summer	-	Road
Delgado et al. (2007)	Spain	-0.290	9	SMF	-	12–15 h	Spring–Summer	-	Road
Delgado et al. (2007)	Spain	-0.430	9	SMF	-	12–15 h	Spring–Summer	-	Road
Delgado et al. (2007)	Spain	-0.270	9	SMF	-	12–15 h	Spring–Summer	-	Road
Delgado et al. (2007)	Spain	-0.230	9	SMF	-	12–15 h	Spring–Summer	-	Road
Delgado et al. (2007)	Spain	-0.200	9	SMF	-	12–15 h	Spring–Summer	-	Road
Delgado et al. (2007)	Spain	-0.130	9	SMF	-	12–15 h	Spring–Summer	-	Road
Delgado et al. (2007)	Spain	-0.160	9	SMF	-	12–15 h	Spring–Summer	-	Road
Heithecker and Halpern (2007)	USA	-0.810	41	TF	-	Over 24 h	Summer	South and West <sup>c</sup>	Open areas
Heithecker and Halpern (2007)	USA	-0.880	41	TF	-	Over 24 h	Summer	North and East <sup>c</sup>	Open areas
Heithecker and Halpern (2007)	USA	-0.960	41	TF	-	Over 24 h	Summer	South and West <sup>c</sup>	Open areas
Heithecker and Halpern (2007)	USA	-0.590	41	TF	-	Over 24 h	Summer	North and East <sup>c</sup>	Open areas
Heithecker and Halpern (2007)	USA	-0.910	41	TF	-	Over 24 h	Summer	South and West <sup>c</sup>	Open areas
Heithecker and Halpern (2007)	USA	-0.770	41	TF	-	Over 24 h	Summer	North and East <sup>c</sup>	Open areas
Wright et al. (2010)	Australia	0.910	15	SDF	-	11–17 h	Winter	North and South <sup>c</sup>	Open areas
Wright et al. (2010)	Australia	0.000	15	SDF	-	11–17 h	Summer	North and South <sup>c</sup>	Open areas
Wright et al. (2010)	Australia	0.870	15	SDF	-	11–17 h	Winter	North and South <sup>c</sup>	Open areas

Table 1 continued

References	Country	<i>R</i>	<i>n</i>	Vegetation type <sup>a</sup>	Edge age (years)	Time of day <sup>b</sup>	Annual season	Edge orientation	Matrix composition <sup>d</sup>
Wright et al. (2010)	Australia	-0.660	15	SDF	-	11–17 h	Summer	North and South <sup>c</sup>	Open areas
Dovčiak and Brown (2014)	USA	-0.970	12	TF	4	-	Summer	North and South <sup>c</sup>	Open areas
Dovčiak and Brown (2014)	USA	0.690	12	TF	18	-	Summer	North and South <sup>c</sup>	Open areas
Didham and Ewers (2014)	New Zealand	0.990	8	SHF	-	12–16 h	Summer	North	Open areas
Didham and Ewers (2014)	New Zealand	-0.340	8	SHF	-	12–16 h	Summer	North	Open areas
Didham and Ewers (2014)	New Zealand	-0.350	8	SHF	-	12–16 h	Summer	North	Open areas
Didham and Ewers (2014)	New Zealand	-0.640	8	SHF	-	12–16 h	Summer	North	Open areas
Didham and Ewers (2014)	New Zealand	-0.190	8	SHF	-	12–16 h	Summer	North	Open areas
Magnago et al. (2015)	Brazil	-0.380	30	TRF	-	-	Summer	North	Open areas

<sup>a</sup> Following FAO's (2012) criteria, we identified five broad forest types: *TF* temperate forests, *TMF* tropical mountain forests, *SHF* subtropical humid forests, *SMF* subtropical mountain forests, *SDF* subtropical dry forests, and *TRF* tropical rainforests

<sup>b</sup> Time of day and duration of measurements

<sup>c</sup> In all these cases the authors show averaged data for transects with different orientations

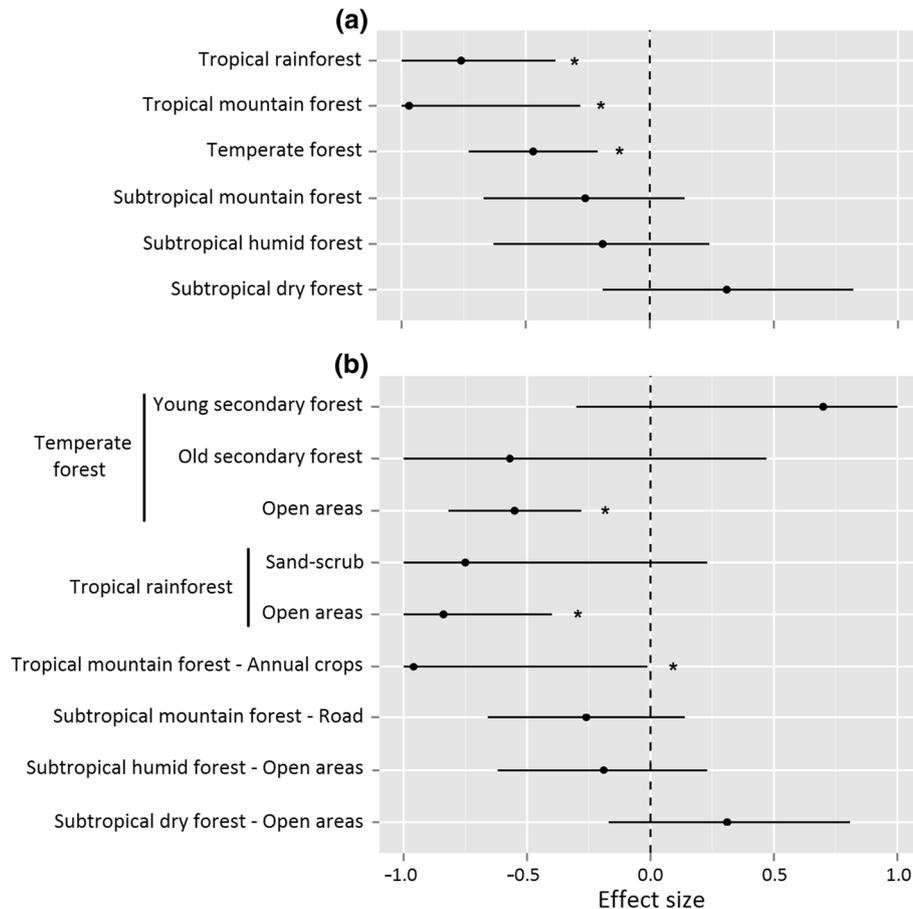
<sup>d</sup> Open areas refer to cattle pastures and abandoned fields dominated by grasses. Regarding roads, we merged data for paved and unpaved roads because these authors do not find significant differences in temperature between these two types of roads

(-) Unavailable data

We found high variability in correlations even for the same forest type next to the same matrix type (Fig. 2b). We initially thought this might be due to differences in time of day when measurements were made, as a temperature gradient may reverse at night when forests are warmer than the surrounding matrix. However, all studies but one were conducted only during the day (Table 1), so the high variability is not likely due to time of day. We also do not think that such variability is related to the differences in the season when measurements were made, as most effect sizes (63%) were measured in tropical and subtropical forests with relatively small differences in temperature throughout the year, and when measured in temperate forest, most samples (12 out of 16, 75%) were measured during the summer. We rather suggest it is more likely associated with differences among studies in edge orientation and edge age. Edges receiving direct radiation (e.g. those oriented to South in the northern hemisphere) likely show stronger gradients (Chen et al. 1993; Matlack 1993; Turton and Freiburger 1997). Also, secondary growth at forest edges ‘seals’ them in a few (< 10) years—a process called “edge evolution” (sensu Laurance et al. 2002)—reducing the likelihood of thermal gradients (Williams-Linera 1990; Matlack 1993; Didham and Lawton 1999). In fact, Williams-Linera et al. (1998) demonstrated that in a tropical rainforest landscape the trees isolated in cattle pastures and fenced for 54 months may exhibit microenvironmental conditions similar to those of forest interior areas. Therefore, thermal changes at forest edges are likely lower than generally thought (e.g. Ewers and Banks-Leite 2013), as most forest edges are relatively old (> 10 years) and at least half of such edges do not receive direct radiation, which may reduce thermal changes in fragmented landscapes.

The variability in edge-interior temperature gradients can also be related to differences among studies in the composition and configuration of the landscape surrounding each forest edge. For example, the amount of forest edge and the average distance between neighboring forest patches at the landscape scale can promote temperature differences up to 1.6 °C among study sites during winter in a heterogeneous landscape in Mid-western USA (Latimer and Zuckerman 2016). Also, the distance to nearby human settlements (e.g. cities and urban areas) can also cause contrasting edge effects, as mean air temperature decreases with increasing the distance from urban centers (i.e. urban heat island effects: Latimer and Zuckerman 2016). In fact, land surface temperature increased with decreasing the distance between neighboring residential areas in the Shanghai metropolitan region of China (Li et al. 2011, 2013). Therefore, to better understand the association between forest temperature and distance from forest edge, future studies should measure (or control for) the effects of forest edge age, edge orientation, and landscape composition and configuration surrounding the study edges.

Although we found a negative temperature gradient from forest edge to interior in closed-canopy forests in



**Fig. 2** Correlation coefficients (mean and 95% confidence intervals) of the association between mean air temperature and distance from forest edge in different forest types (a), and in different forest types surrounded by different matrix types (b). Values with *asterisk* are significant ( $P < 0.05$ )

an open matrix, it is uncertain if this local-scale gradient scales up to a landscape effect of forest fragmentation on temperature. For example, the reduction of large tracts of closed-canopy forest to smaller patches surrounded by open matrix increases both the edge to area ratio and the amount of warmer, open cover in the landscape (Fig. 1). Both of these patterns will lead to increasing average temperature in the forest at the landscape scale, at least for closed-canopy forest in the daytime. Therefore, for “fragmentation” as forest loss only, the scaling-up assumption should be valid. Supporting this idea, Li et al. (2011) reported that land surface temperature decreases in urban landscapes (i.e. open areas) covered by a higher percentage of vegetation (greenspaces).

In contrast to the effect of forest loss, the landscape-scale inference is not so clear when we consider the second aspect of fragmentation, where a given amount of forest is divided into a large number of small patches (“fragmentation per se”, sensu Fahrig 2003, 2017; Fig. 1). Fragmentation per se implies an increase in forest edge in the landscape relative to a landscape containing a smaller number of larger patches (Fig. 1). This could lead to a larger effect of (warm) matrix on closed-canopy forest edges, during daytime. However,

because of the “vegetation breeze” phenomenon (sensu Cochrane and Laurance 2008), fragmentation per se also implies a larger effect of (cool) forest core areas on matrix. In particular, the warm air over the open areas will rise throughout the day, causing low pressure at the surface and drawing cool and moist air from surrounding forest patches into the matrix (Cochrane and Laurance 2008; Tuff et al. 2016), which should feed back to reduce the temperature gradient in forest. In other words, the relatively warm air on the matrix can be cooled by the air coming from the interior of forest patches, and this mixing (and cooler) air in the matrix can therefore contribute to weaken the temperature gradient from forest edge to interior, being this “weaken effect” more pronounced when forest landscapes are more fragmented (i.e. when they are composed of a larger number of forest patches). Consistent with this idea, land surface temperature decreased with increasing the number of vegetation patches in urban landscapes (Li et al. 2011), which may contribute to explain why fragmentation per se generally has positive (not negative) effects on biodiversity (Fahrig 2017). Additional studies using adequate sampling designs and analyses (see Hadley and Betts 2016) are needed to better

understand the role of forest fragmentation per se on landscape-scale forest temperature.

### Concluding remarks

Our findings suggest caution in assuming that fragmentation increases forest temperature, as the negative temperature gradient from forest edge to interior is only clearly supported for temperate and tropical forests in an open matrix during the daytime. Also, the idea that this local-scale gradient scales up to an effect of forest fragmentation on temperature is uncertain and needs to be explicitly evaluated using a landscape approach (McGarigal and Cushman 2002; Hadley and Betts 2016). Thus, care should be taken with regional- and landscape-scale extrapolations from local-scale patterns (see e.g. Ewers and Banks-Leite 2013), as thermal changes are not evenly distributed along forest edges.

The high variability in thermal changes found in this study may be, however, useful to explain, at least partially, the multiple pathways that succession may follow in fragmented forests (Arroyo-Rodríguez et al. 2016), and the high variability in population and community dynamics along forest edges (Laurance 2002; Laurance et al. 2002). These abiotic and biotic variations along forest edges are expected to increase the taxonomic and functional differentiation (i.e. increasing beta-diversity) of biotic assemblages among forest edges (Arroyo-Rodríguez et al. 2013; Sfair et al. 2016), thereby contributing to increase species diversity at the landscape scale (gamma-diversity) (Sfair et al. 2016). These ideas are directly linked to recent hypotheses, such as the “landscape-divergence hypothesis” (Laurance et al. 2007) and the “dominance of beta diversity hypothesis” (Tscharrntke et al. 2012), so they represent novel avenues for future research. Additional studies at broader spatial scales are therefore needed to improve our understanding on the importance of temperature as a driver of population, community and ecosystem dynamics in fragmented forests, and thus design adequate conservation strategies to such emerging forests.

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