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RESEARCH ARTICLE

Does habitat fragmentation affect landscape-level temperatures? A global analysis

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Abstract
Context Habitat fragmentation per se (habitat subdivision independent of habitat loss) is a major driver of biodiversity change, potentially due to its impacts on climate. Habitat fragmentation may make landscapes hotter by increasing the amount of habitat edges, but can reduce landscape-level temperatures due to the "vegetation breeze" phenomenon. The plausibility of these two alternative hypotheses is unclear, as no study analyzed the effects of habitat fragmentation per se on temperature.
Objectives We quantify, for the first time, the impacts of habitat fragmentation on landscape-level temperature across the globe.
Methods We analyzed satellite data on forest cover and three climatic variables: mean daily temperature, albedo and evapotranspiration. The analyses were performed separately for tropical, temperate, and boreal regions. We compared the climatic variables between pairs of landscapes with similar amount of forest, but different levels of forest fragmentation (number of patches).
Results Habitat fragmentation reduced landscape-level temperature in all climatic regions. The magnitude of this cooling was stronger in the tropics and weaker in the boreal region due to different evapotranspiration rates. This landscape-scale cooling contradicts local-scale studies, which have indicated that edge effects rise local temperatures. However, habitat fragmentation may intensify vegetation breeze, resulting in final cooling at the landscape scale.
Conclusions Habitat fragmentation leads to colder landscapes. We propose a new conceptual model to unify local (edge-induced) and landscape-level effects of habitat fragmentation on temperature, advancing the understanding of the consequences of habitat fragmentation on climate globally.

Keywords Fragmentation per se · Climatic variables · Landscape · Temperature · Vegetation breeze · Edge effect

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Introduction

The combined processes of habitat loss and habitat fragmentation are considered major drivers of biodiversity change globally (Novacek and Cleland 2001). These processes have also been considered the primary causes of biodiversity loss and ecosystem degradation across the world (Wilson et al. 2016), affecting different levels of ecological organization (Robinson et al. 1992). As shown by extensive empirical evidence, habitat loss, which is simply the reduction in the amount of original habitat, has indeed clear negative effects on biodiversity (Fahrig 2003, 2017; Fahrig et al. 2019). However, the effects of fragmentation per se are less clear, and are still a source of much debate. Habitat fragmentation per se is defined as the division (breaking apart) of habitat, independent of habitat loss (Fahrig 2003, 2017; Fahrig et al. 2019). The distinction between habitat loss and habitat fragmentation is of central importance both for theoretical and applied purposes, as two landscapes with a similar amount of habitat, but different degrees of habitat fragmentation (e.g. number of patches) may support different biodiversity levels (Fahrig 2003, 2017). Although habitat fragmentation has traditionally been considered negative for biodiversity, a recent revision pointed that most of the significant responses to habitat fragmentation are actually positive (Fahrig 2017; but see Fletcher et al. 2018). Thus, despite the extensive literature on the effects of habitat fragmentation on species and communities globally, the direction and magnitude of such effects, as well as their specific underlying mechanisms, are still unclear (review in Ewers and Didham 2006).

One of the recently proposed mechanisms by which habitat fragmentation impacts biodiversity is the alteration of climatic variables in remnant patches (Tuff et al. 2016). Alterations on closely related climatic variables such as albedo, evapotranspiration (ET) and land surface temperature (LST) have already been described as a response to habitat loss (Peng et al. 2013; Zhao and Jackson 2014; Li et al. 2015, 2016; Schultz et al. 2017; Prevedello et al. 2019), but their potential responses to habitat fragmentation per se have not been evaluated yet. Therefore, it is still not clear which process, habitat loss or habitat fragmentation per se, would present a greater influence on climatic variables. The removal of tree cover frequently leads to hotter, drier, and more variable thermal conditions within remnant patches due to edge effects (Murcia 1995; Chen et al. 1999; Alkama and Cescatti 2016; Bernaschini et al. 2019). Most studies on edge effects have shown that temperatures are usually higher in the matrix or near forests edges, and decline exponentially towards forest interiors (Kapos 1989; Williams-Linera 1990; Matlack 1993; Young and Mitchell 1994; Chen et al. 1995; Didham and Lawton 1999; Saunders et al. 1999; Pohlman et al. 2007; Yan et al. 2007; Didham and Ewers 2014; Magnano et al. 2015; Latimer and Zuckerberg 2016; Hofmeister et al. 2019). However, the degree to which such effects may affect landscape-level temperature is unknown, as these studies focused solely on the local scale of habitat patches (e.g. single remnant patches) rather than landscapes (e.g. 5 $\times$ 5 km areas), while habitat fragmentation is clearly a landscape-scale process (McGarigal and Cushman 2002; Fahrig 2003, 2017).

As habitat fragmentation increases the amount of edges in a landscape (Fahrig 2003), and forest edges are usually hotter than forest interiors (see Tuff et al. 2016), it is usually assumed that habitat fragmentation increases landscape-level temperature, a hypothesis that we will refer to as the "edge-warming hypothesis" (Malcolm 1994; Ewers et al. 2010; Lafortezza et al. 2010). Nevertheless, it is still unclear whether and how edge effects scale up from individual local patches to affect temperature, as well as biodiversity, at the landscape scale (Arroyo-Rodríguez et al. 2016; Fahrig et al. 2019). The edge-warming hypothesis has been recently criticized for a number of reasons, and it has been suggested that matrix-edge forest contacts may actually result in a final cooling effect on the landscape scale (Arroyo-Rodríguez et al. 2016). The "vegetation breeze" phenomenon may explain this cooling, as it promotes atmospheric circulation that can increase rainfall and moisture over the matrix areas (Cochrane and Laurance 2008). Therefore, the cooling effects derived from vegetation breeze could surpass the local warming, resulting in final cooling at the landscape-level, a hypothesis that will be called the "vegetation breeze hypothesis". The plausibility of the vegetation breeze and the edge-warming hypotheses has not been tested yet, as landscape-scale analyses of the effects of habitat fragmentation per se on local climate have never been carried out, probably due to a lack of adequate methodological approaches and high-resolution forest cover maps until recently (Hansen et al. 2013). Landscape-scale analyses of how habitat fragmentation affects temperature across the globe are fundamental to obtain a general picture across different regions, especially considering that the relative influence of albedo and ET on LST is distinct along the latitudinal gradient (Jin and Dickinson 2010; Peng et al. 2013; Li et al. 2015, 2016; Schultz et al. 2017; Prevedello et al. 2019).

Here, we quantify for the first time the impacts of habitat fragmentation per se on landscape-level temperature across different climatic regions of the globe. We test the relative plausibility of the edge-warming and the vegetation breeze hypotheses, which predict that habitat fragmentation causes warming and cooling, respectively, at the landscape scale. To do so, we use a recently-released, high-resolution global forest cover dataset (Hansen et al. 2013), and a carefully designed analytical approach. We compared pairs of landscapes with the same amount of forest cover, but with different levels of forest fragmentation (i.e. number of forest patches), therefore testing the effects of habitat fragmentation per se on LST. Based on the results, we built a new conceptual model to integrate local- and landscape-level impacts of edge effects and habitat fragmentation on temperature, in which warming at the local (patch) scale and cooling at the landscape scale occur in a synergic way, rather than antagonistically. Our analysis advances substantially understanding of the consequences of habitat fragmentation on climate and, consequently, on biological communities and ecosystems functioning (Tuff et al. 2016; Nowakowski et al. 2018; Williams and Newbold 2020).

Materials and methods

We quantified the impacts of habitat fragmentation on LST using a six-step methodological approach: (i) compilation of global forest cover, climate and altitude datasets; (ii) preliminary treatment of all datasets, including quality control, standardization of spatial resolution and calculation of annual averages; (iii) conversion of the original global forest dataset into a presence–absence forest cover map and calculation of the degree of fragmentation, i.e. number of patches, in each landscape (5 × 5 km areas) across the globe; (iv) application of a "moving window" searching strategy to compare pairs of landscapes with similar amount of forest cover (difference < 5%), but different levels of forest fragmentation (number of forest patches); (v) calculation of the difference of each climatic variable between the cells of each pair of landscapes; (vi) application of statistical analyses to quantify causal relationships among the degree of forest fragmentation and the climatic variables (Fig. 1). We ran all analyses in R 3.4.2 (R Core Team 2017).

Forest cover, climatic variables and altitude data

We obtained high-resolution global forest cover for the year 2000 from the Global Forest Cover dataset provided by Hansen et al. (2013). The dataset is derived from the Landsat 7ETM + data and includes all global land, except for Antarctica and a number of Artic islands, in a total of 128.8 M km^2. Forest cover is characterized as all vegetation taller than 5 m in height, both natural and planted (Hansen et al. 2013). This threshold is based on the ability to distinguish tall woody vegetation in multispectral imagery, particularly those present in global-scale earth observation systems such as Landsat and MODIS (Hansen et al. 2010). Despite being criticized for not differentiating native and planted forests (Tropek et al. 2014), these high-resolution maps are suitable in capturing biophysical features that depend on forest cover across the globe (Prevedello et al. 2019). The original forest cover dataset is encoded as a percentage per pixel (30 × 30 m), in the range 0 (no forest cover) to 100% (pixel completely covered by forest). We converted the percentages into forest presence–absence data according to the "International Geosphere-Biosphere Programme" (IGBP) (Friedl et al. 2010), considering that forest was present when it covered more than 60% of a pixel.

We then upscaled the 30-m presence–absence map to a resolution of 0.05° (~ 5 km, equivalent to 400 × 400 30-m pixels) to match the climatic variables imagery resolution. We considered 5 × 5 km areas as "landscapes" because most of the world's forests are within 1 km of a forest edge (Haddad et al. 2015). Therefore, using this scale, landscapes with different degrees of forest fragmentation could be properly compared. In addition, this specific scale has been previously used to study landscape-level phenomena in forest ecosystems (Laurance et al. 1998; Wallenius et al. 2010; Chen et al. 2013), and to assess the effects of forest cover on LST (Li et al. 2015; Prevedello et al. 2019). For each 5 × 5 km pixel (hereafter, "landscape"), we calculated the percentage of forest cover, in the range 0–100%, by dividing the 30-m pixels with forest (1) by the total number of

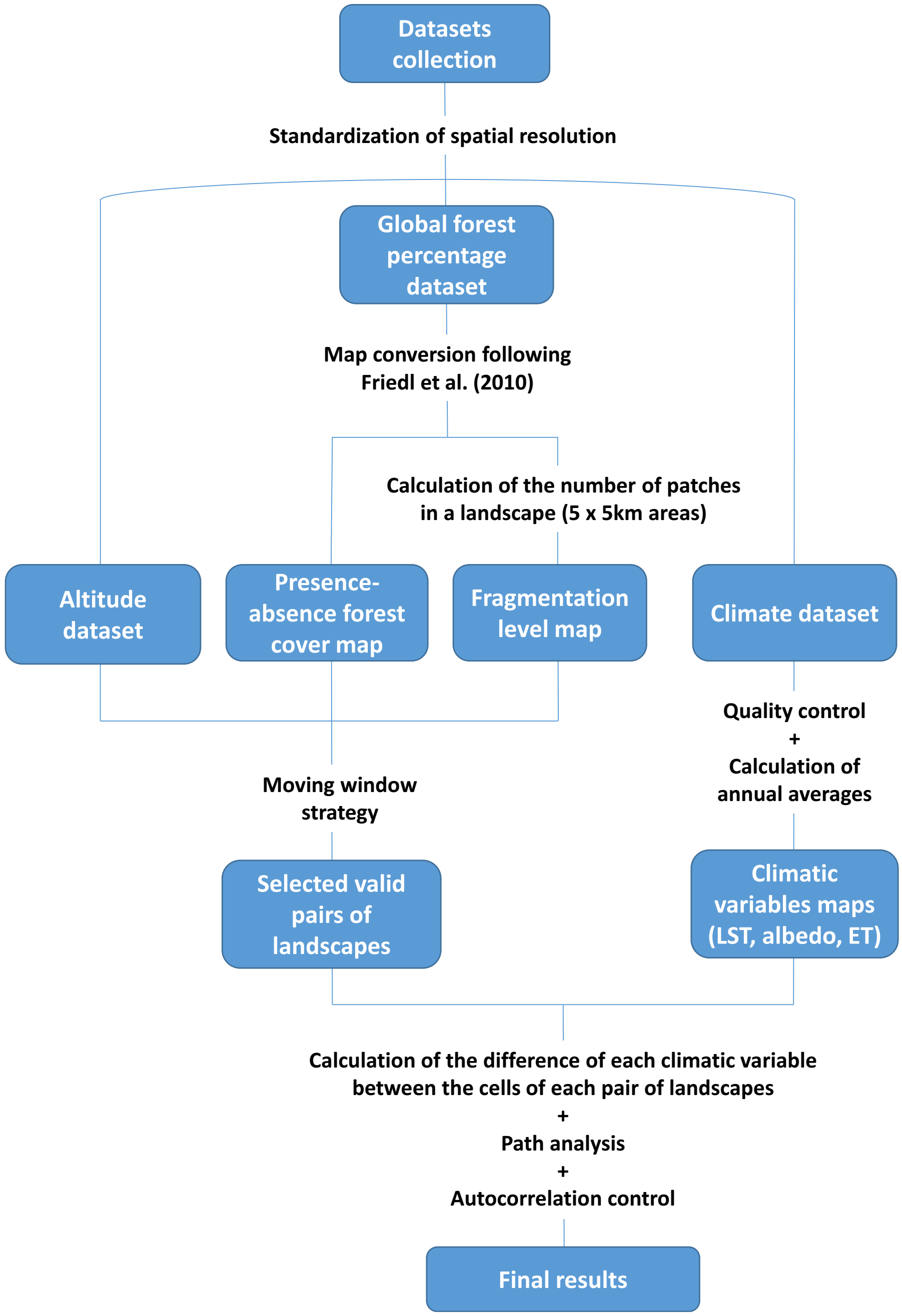

Fig. 1 Flow chart depicting data pre-processing procedures and the analytical approach used to investigate the effects of forest fragmentation on land surface temperature (LST). Standardization of spatial resolution allowed us to compare maps of climatic variables from different sources. The conversion of the global forest percentage dataset following Friedl et al. (2010) resulted in the creation of a presence–absence forest map, which allowed calculating the number of patches in each landscape (5 × 5 km cell). A moving window searching algorithm was then applied to the different datasets (including altitude) to obtain the valid pairs of landscapes (see "Moving window strategy" for further details). Finally, we analyzed the data from the valid pairs of landscapes with path analysis, controlling for spatial autocorrelation, to obtain our final results

pixels (400 $\times$ 400). We also calculated the number of forest patches within each landscape to measure the degree of habitat fragmentation. This metric is the most intuitive and frequently used fragmentation metric (Fahrig 2017), and it allows to broadly classify landscapes as more "fragmented" or more "continuous" (e.g. landscapes with more and less than 10 patches, respectively). To quantify the number of patches, we used the 30 m forest-non-forest map (1–0), according to the IGBP classification, considering as a "patch" a contiguous group of forest pixels, using the eight-neighbor rule, according to Turner et al. (2001).

We used LST, the radiative skin temperature of the land surface, as the main climatic variable to detect the direct and indirect effects of habitat fragmentation. LST is the driving force in the exchange of long-wave radiation and turbulent heat fluxes at the surface–atmosphere interface (Li et al. 2013) and has presented acceptable results in several sensible heat flux models (Zhan et al. 1996). LST closely resembles air temperature trends when analyzing the effects of forest cover on local temperature even at different latitudinal zones (Li et al. 2016). We preferred to use the LST product rather than the Climate Research Unit air temperature data, as the former contains more spatial details than the latter, which is normally gridded from a relatively sparse distribution of weather stations (Jin and Dickinson 2010; Benali et al. 2012; Li et al. 2016).

To model the indirect effects of forest fragmentation on LST, we used two climatic variables that are closely related to the variation of LST: evapotranspiration (ET) and albedo (Jin and Dickinson 2010; Peng et al. 2013; Zhao and Jackson 2014; Li et al. 2015, 2016; Schultz et al. 2017; Prevedello et al. 2019). The LST equation is determined in part by surface albedo, and the decrease in LST is partially related to evapotranspiration rates (Jin and Dickinson 2010; Zhao and Jackson 2014). Moreover, ET and albedo have been used in many current models that investigate the biophysical regulation of climate (Bonan 2008). We obtained LST and ET data from the collection-5 MODIS products (NASA EOSDIS Land Processes DAAC 2007), recorded from a satellite with overpass time at $\sim$ 10:30 AM and 22:30 PM, which have been validated (Wan 2008; Mu et al. 2011; Running et al. 2017) and used in previous publications (e.g. Peng et al. 2013; Li et al. 2015). For LST, we obtained monthly EOS-Terra-MODIS (MOD11C3) data that include monthly daytime and nighttime temperature observations (in °C) at 0.05° resolution. We then calculated the mean daily temperature by averaging daytime and nighttime LST values. We only used LST data with estimated emissivity error $\leq$ 0.02 and LST error $\leq$ 2 K (the original temperature unit for this dataset) for quality control.

For ET, we used the annual MOD16A3 product (in mm/month), originally at a 1-km resolution (ca. 0.0083°). Monthly ET is estimated with the algorithm based on the logic of Penman–Monteith equation, which uses daily meteorological reanalysis data and 8-day remotely sensed vegetation propriety dynamics from MODIS as input, such as latent heat and shortwave radiation (Mu et al. 2011; Running et al. 2017). The input data is independent of the MODIS LST product (Mu et al. 2011). We upscaled the original data to 0.05° resolution (approximately 6 $\times$ 6 original pixels) to match the LST and forest cover data. For quality control, we only used 0.05° pixels for which all the 36 original pixels (0.0083°) contained data.

For albedo, we used the albedo GLASS02B06 product (Global LAnd Surface Satellites) (Liang 2012), an 8-day based MODIS dataset from albedo GLASS collection, originally at a 1-km resolution (ca. 0.0083°). The GLASS dataset has also been validated (Q. Liu et al. 2013) and used in previous publications (e.g. Peng et al. 2013; Li et al. 2015). This dataset was generated from multisource remote sense data (e.g. MODIS albedo products) and newly developed algorithms (Q. Liu et al. 2013). The algorithms were applied to fill data gaps and smooth albedo time series (N. F. Liu et al. 2013). The commonly used MCD43C3 albedo product from the collection-5 MODIS had few valid albedo data in different global regions for the year 2001 due to unfavorable atmospheric conditions in tropical regions, such as cloud cover throughout the year, and solar zenith angles in high-latitude regions (N. F. Liu et al. 2013). Therefore, we chose to use the albedo GLASS02B06 product. This product comprises black-sky and white-sky albedo. Following Li et al. (2015), we calculated the actual albedo (blue-sky) as an average of black-sky and white-sky albedo with monthly averages, and then calculated annual averages. We considered only pixels that had good-quality information for all months in a year. The selected quality control flags for albedo were "00" and

"01", indicating uncertainty < 5 and < 10%, respectively. We also upscaled the original data to 0.05° resolution (approximately 6 × 6 original pixels).

We also obtained global altitude data from the Global 30 Arc-Second Elevation (GTOPO30), a global digital elevation model (EROS 1996), to control possible temperature differences as a response to altitudinal variation. This model returns a regular grid for the entire globe, representing Earth's relief at a 30 arc-seconds sampling interval (approximately 1 km). The GTOPO30 is based on elevation data derived from different sources, such as the Digital Elevation Terrain Data and the Digital Chart of the World (Miliaresis and Argialas 2002), and has been used in previous publications (Miliaresis and Argialas 2002; Seyler et al. 2009). We also modified the original data to 0.05° resolution to match MODIS data.

The thresholds for quality control of each climatic variable were determined according to their respective current use in the literature (e.g. Li et al. 2015, 2016; Prevedello et al. 2019). All climatic variables were quantified for the year 2001, rather than 2000, as the forest cover maps were produced as a combination of satellite imagery obtained across different months of 2000. This choice also reflected the assumption that the forest fragmentation process (cause) precedes the changes in the climatic variables (consequences), as shown in a previous study that analyzed forest loss effects (Prevedello et al. 2019). This previous study showed that similar patterns emerge when using 2000 or 2001 climate data to assess forest change (i.e. deforestation or reforestation) impacts on climatic variables, despite data from 2000 result in larger variability in the results. We did not consider the potential seasonal variation of each climatic value, focusing only on annual averages, even knowing that forest cover changes impacts may vary seasonally (Li et al. 2015), as there are no global forest cover maps for different seasons within each year. In addition, focusing on annual averages allows more direct comparison between forest fragmentation effects (our study) and forest loss and gain effects (Prevedello et al. 2019), as this previous study also used annual averages.

Moving window strategy

We applied a "moving window" strategy to quantify the relationships between forest fragmentation and climatic variables around the globe (similarly to Li et al. 2015 and Prevedello et al. 2019). This approach allowed us to compare close pairs of landscapes (< 50 km) differing in the number of forest patches, but sharing a similar regional climatic condition, thus minimizing the effects of potentially confounding variables (e.g. latitude and distance to water bodies). Each window had 9 × 5 pixels (longitude × latitude), approximately equal to 50 × 28 km, with adjacent windows partially overlapping in 4 cells in longitude and 2 cells in latitude.

To be considered valid for the analysis, the window should have at least one pair of landscapes that fitted three criteria:

(i) Difference < 5% in forest cover. This criterion ensured that the pair of landscapes had a similar habitat amount, but varying degrees of habitat fragmentation (number of forest patches);
(ii) A landscape with < 10 patches and another with > 10 patches. This allowed us to compare always a more "continuous" landscape to a more "fragmented" one. Similar results were obtained when we used 30 patches as the cutting value (Table S1);
(iii) Difference < 50 m in altitude. This measure controlled the effects of potentially confounding variables caused by temperature differences as a response to altitudinal variation.

If more than one pair within a window fitted the three criteria, we selected only the pair with the largest difference in the number of patches, to obtain samples with the greatest difference in fragmentation levels. Using only one pair of valid landscapes per window also maximized the independence of observations and reduced the possible spatial autocorrelation among them. Finally, if the same pair of selected landscapes occurred in two adjacent windows (which overlapped partly), we only used the first occurrence in the subsequent analyses.

For each selected pair of landscapes, we calculated the difference in the degree of forest fragmentation between landscapes (ΔF) as:

$$\Delta F = F_{\mathrm{f}} - F_{\mathrm{c}}$$

where F_f is the number of patches of the more "fragmented" landscape and F_c is the number of patches of the more "continuous" landscape. Subsequently, we calculated the mean differences in LST, ET and albedo (ΔLST, ΔET and Δalbedo, respectively) within each valid pair of landscapes in a similar manner. The resulting ΔLST, ΔET and Δalbedo values represent "standardized" differences, as they were calculated between landscapes with distinct habitat fragmentation levels, but with similar habitat amount and regional climatic background (as the two compared landscapes were always < 50 km apart). Therefore, by using those standardized differences in our subsequent tests, we were able to perform a robust analysis on how habitat fragmentation affects LST across the globe. For these procedures, we used the packages "raster" (Hijmans et al. 2017), "rgdal" (Bivand et al. 2018) and "reshape" (Wickham 2017a).

Data analysis

We obtained a total of 800 valid pairs of landscapes for the tropical region, 5626 valid pairs for the temperate region, and 6105 valid pairs for the boreal region (Figs. S1 and S2). We then used path analysis to explore the hierarchical inter-relationships among the mean daily ΔLST, ΔET, Δalbedo and fragmentation metrics. For comparative analysis, we also quantified daytime and nighttime ΔLST in separate path analyses (e.g. Table S1; Fig. S3). In this type of analysis, the variables may act simultaneously on each other, in presumed cause-and-effect relationships (Grace 2006). Path coefficients are prediction coefficients and may be estimated as standardized coefficients, where the predicted change in one variable due to another is measured in standard deviations units (Grace 2008).

We performed path analysis separately for each climatic region (tropical = 20° S–20° N; temperate = 20° S–50° S or 20° N–50° N, and boreal = > 50° S or > 50° N), since the relative influence of albedo and ET on LST is distinct along the latitudinal gradient (Jin and Dickinson 2010; Peng et al. 2013; Li et al. 2015, 2016; Prevedello et al. 2019). We established the most likely relationships between the variables according to the literature (Jin and Dickinson 2010; Peng et al. 2013; Zhao and Jackson 2014; Li et al. 2015, 2016; Prevedello et al. 2019), as follows (Fig. 2):

(i) ΔLST depended on ΔF, Δalbedo and ΔET;
(ii) Δalbedo depended on ΔF;
(iii) ΔET depended on ΔF and Δalbedo.

Each relationship corresponded to a sub-model; the three sub-models, combined, formed the global path model. Based on this global model, we calculated the direct, indirect (product of coefficients within each sub-model) and the total effects (sum of direct and indirect effects) of ΔF on ΔLST (see also Fig. 2).

For comparative purposes, we also calculated how a pre-defined degree of forest fragmentation would rise or cool down landscape-level LST. To do so, we multiplied the total effect of ΔF on ΔLST by the standard deviation of LST. A ΔF = 100 value (in other words, the fragmentation of a single forest patch into 100 patches in a landscape) was considered the criterion to measure the corresponding change in LST. For example, if the total effect of ΔF on mean daily ΔLST in the tropical region was estimated as − 0.34, it would indicate that an increase in one standard deviation of habitat fragmentation (standard deviation of ΔF = 103.08 patches) would reduce LST in 0.34 standard deviations, i.e. 0.48 °C (− 0.34 × 1.42 °C, 1.42 °C being the standard deviation of ΔLST). We performed all analyses with the packages "lavaan" (Rosseel et al. 2018) and "scales" (Wickham 2017b), using mean daily ΔLST values (see Supplementary Material for daytime and nighttime ΔLST results).

Spatial autocorrelation control

Spatial autocorrelation may violate the assumption of independence of observations, increasing Type I error (Legendre 1993; Diniz-Filho et al. 2003). To avoid this, we controlled for the potential spatial autocorrelation in each of the three sub-models that formed our global path model. We built six alternative versions of each sub-model; the six versions had the same explanatory variables (ΔF, Δalbedo and ΔET), but different autocorrelation structures, either none (null model), spherical (corSpher), linear (corLin), rational quadratic (corRatio), gaussian (corGaus), or exponential (corExp) (Zuur et al. 2009). The correlation structure was in the form

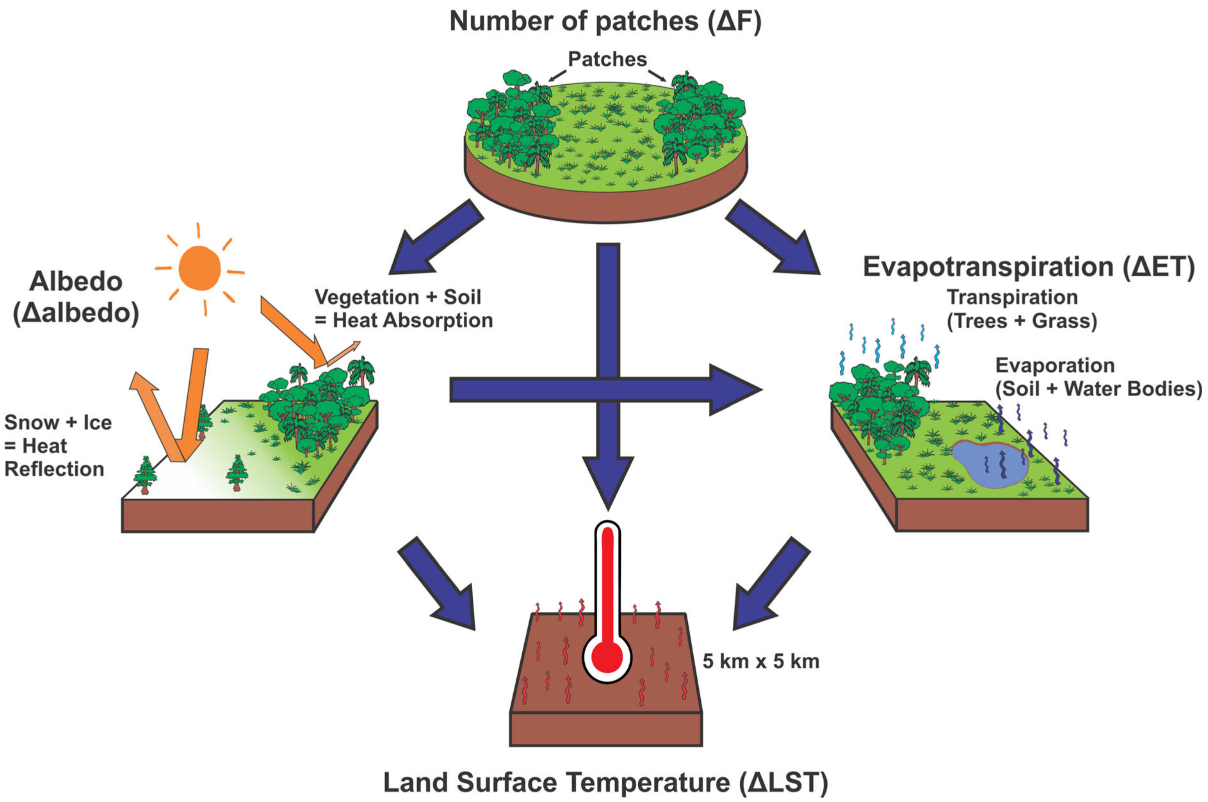

Fig. 2 Possible relationships between habitat fragmentation (number of habitat patches) and climatic variables (albedo, evapotranspiration (ET) and land surface temperature (LST)). These are the most likely relationships between all variables according to the literature. Higher albedo values, found in surfaces with snow and ice, reduce heat absorption when compared to vegetation and soil, potentially reducing LST. This reduction (cooling) may also be mediated by higher ET rates, which are estimated by the condensed water from substrate evaporation (e.g. water bodies) and vegetation transpiration

"= $\sim$ longitude + latitude", as implemented in the R package "nlme" (Pinheiro et al. 2018).

For each sub-model, we compared the fit of the six alternative versions to determine the most suitable autocorrelation structure. Model fit was compared via model selection based on AICc (Burnham and Anderson 2002), using package "MuMIn" (Barton 2018). Due to the long computational time to fit all models to the entire dataset of each region, we used a random sub-sample ($n = 800$) for each climatic region. The sub-sample size chosen (800) was the sample size of the region with fewer valid observations (tropical region). In almost all comparisons, models with some type of autocorrelation structure were always more plausible than the model with no structure (Table S2). Thus, we used the autocorrelation structure of the top-ranked model in each model selection for the final path analysis, which combined the three sub-models. In this final analysis, we used all valid pairs of landscapes of each climatic region, instead of the random sub-samples, to maximize the robustness of the analysis. The results obtained with control for spatial autocorrelation were similar to results without this control (Figs. S4 and S5; Tables S1 and S3).

Results

Both the direct and indirect effects of forest fragmentation on LST varied across climatic regions (Fig. 3). According to the path analysis, the fragmentation of a single forest patch into 100 patches in a landscape led to a reduction in mean daily LST of − 0.26 °C in tropical regions, − 0.16 °C in temperate regions and − 0.04 °C in boreal regions (for complete statistics, see Table S3). The variation in ET and LST was best explained by their respective sub-models in the

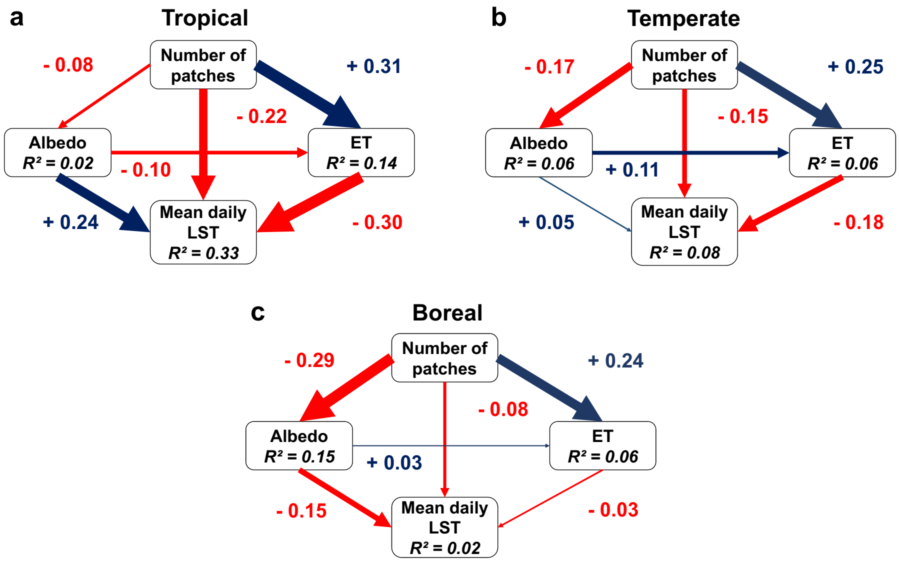

Fig. 3 Global path models depicting the direct and indirect effects of forest fragmentation per se on LST in tropical (**a**), temperate (**b**) and boreal (**c**) regions. The indirect effects of forest fragmentation (number of forest patches) are mediated by albedo and evapotranspiration (ET). Arrows are proportional to the absolute standardized path coefficients (numbers). Red and blue arrows indicate negative and positive coefficients, respectively. R^2 values indicate the coefficient of determination of the component sub-models for each response variable

tropical region, while the variation in albedo was better explained in the boreal region, as evidenced by R^2 values (Fig. 3). The direct and indirect effects of forest fragmentation on LST also varied for daytime versus nighttime LST (Fig. S3).

In all climatic regions, the direct effect of habitat fragmentation on LST was negative, with the strongest direct effect in the tropical region (vertical arrows in Fig. 3). Habitat fragmentation also had clear indirect effects on LST, mediated by changes in ET and albedo (diagonal arrows in Fig. 3). In all climatic regions, habitat fragmentation had a positive effect on ET and a negative effect on albedo (Fig. 3). The effect of habitat fragmentation on ET was strongest in the tropical region (coefficient = + 0.31), and was similar in the temperate and boreal regions (+ 0.25 and + 0.24, respectively; Fig. 3). On the other hand, the effect of habitat fragmentation on albedo was weaker in the tropical region (– 0.08; Fig. 3a) and stronger in the boreal region (– 0.29; Fig. 3c).

The increase in ET caused a reduction in LST in all climatic regions (Fig. 3). The decrease in albedo resulted in a decrease in ET in the tropical region and an increase in the temperate and boreal regions (horizontal arrows in Fig. 3). The decrease in albedo increased LST in the tropical and temperate regions, but it decreased LST it in the boreal region (Fig. 3).

Discussion

Forest fragmentation led to colder landscapes in all climatic regions across the globe, corroborating the vegetation breeze hypothesis and refuting the edge-warming hypothesis. The magnitude of this cooling varied along the latitudinal gradient, being stronger in the tropics and weaker in the boreal region. The final landscape-level cooling in all regions apparently contradicts most local-scale studies, which have indicated that edge effects tend to increase local temperatures (Tuff et al. 2016). Therefore, the results of the present study clearly show that the local warming caused by edge effects should not be scaled up from individual local patches to the landscape scale, as suggested recently (Arroyo-Rodríguez et al. 2016). In fact, similar extrapolations of local (patch-scale) effects to predict habitat fragmentation effects have already been recently criticized, as the scale up of a small-scale process (edge effects) to a large-scale pattern (habitat fragmentation) is not evidence of a pattern, but rather a prediction that should be tested at the larger scale (Arroyo-Rodríguez et al. 2016; Fahrig et al. 2019), as we did here.

The positive effect of habitat fragmentation on ET (top-right diagonal arrows in Fig. 3) may be a response to mechanisms mediated by edge effects, such as the reduction of water vapor concentration between the leaves and the atmosphere (Kerbauy 2004) and the loss of moisture by the soil due to increased solar radiation (Ranney et al. 1981; Kapos 1989). In turn, the raise in ET rates ultimately leads to lower temperatures, because of energy absorption by latent heat loss and the consequential reduction in the energy available to sensible heat loss (West et al. 2010). The cooling caused by ET has been reported in previous reviews and empirical and modelling studies, being dominant in the tropical region (Snyder et al. 2004; Jackson et al. 2008; Anderson et al. 2011; Alkama and Cescatti 2016; Duveiller et al. 2018) as also found in our study (bottom-right diagonal arrows in Fig. 3). On the other hand, the mechanisms that explain the role of albedo on final landscape cooling are yet to be explained: our results were not consistent with what was reported in the literature for the edge effects on albedo at the local scale (e.g. Baldocchi et al. 2000; Corlett 2014).

The direct reduction in LST caused by habitat fragmentation (vertical arrows in Fig. 3) may be related to moisture redistribution at the landscape scale. During daytime, the microclimatic differences between the interior of forest fragments and the surrounding non-forest matrix imply a pressure unbalance that results in the uptake of humid air from habitat fragments by the matrix, as described in the vegetation breeze phenomenon (Cochrane and Laurance 2008). This phenomenon explains why several forest edges have lower humidity rates than the interior of forest fragments (Chen et al. 1995; Didham and Lawton 1999; Hennenberg et al. 2008). The result is the cooling of warm air over the matrix by latent heat loss (West et al. 2010). During the capture of humid air, originally warm air over the matrix rises, promoting moisture condensation in clouds that precipitate over the landscape (Cochrane and Laurance 2008). This convective movement is more intense particularly in heterogeneous environments (Avissar and Liu 1996; Avissar and Schmidt 1998), which is typically the case of fragmented landscapes, composed by a mosaic of forest and non-forest patches. Thus, habitat fragmentation could cool temperatures down not only by capturing and redistributing moisture from fragment interiors, but also by increasing precipitation.

We observed a low-to-moderate explanatory power of the response variables for all global path models in the different climatic regions (Fig. 3). A number of reasons may explain this limited explanatory power, such as the non-inclusion of complex variables in the analyses (e.g. soil type, retroactive mechanisms in sea-ice interactions). Disregarding seasonal variation of climatic variables throughout the year is also another potential source of variability. Tropical forests maintain a strong cooling effect along the year due to ET effects; on the other hand, there is substantial warming in mid- and high-latitude forests because of strong albedo warming combined with weak ET cooling in cold seasons (Li et al. 2015). These effects were in fact partly detected by our analysis, as our global path models had higher explanatory power (R^2) in the tropical region, in particular the sub-models including ET (Fig. 3a). Additionally, sub-models including albedo presented a better adjustment in the boreal region (Fig. 3c), probably because of the complex albedo-vegetation relationship in higher latitudes (Bonan 2008; Li et al. 2015, 2016; Schultz et al. 2017). Despite these unaccounted factors, our analyses revealed clear direct and indirect effects of habitat fragmentation on LST, and its variation along the latitudinal gradient. Alternatively, it is possible that forest loss has stronger effects on LST than forest fragmentation (see Prevedello et al. 2019), as also suggested for biodiversity (Fahrig 2003), a possibility that may be tested in the future by including both forest loss and fragmentation in a unified explanatory model of LST.

Although refuting the edge-warming hypothesis at the landscape scale, our results do not exclude the possibility that forest edges are indeed warmer than forest interiors. To conciliate local and landscape impacts of edge effects and habitat fragmentation on temperature, we propose a new conceptual model, in which local- (patch-) scale warming and landscape-scale cooling occur synergistically, rather than antagonistically (Fig. 4). In this model, warming at the local scale, within habitat patches, occurs due to the close contact between habitat edges and the matrix, the latter presenting higher and more variable temperatures (Fetcher et al. 1985; Geiger et al. 2003). This warming effect could extend into considerable distances within

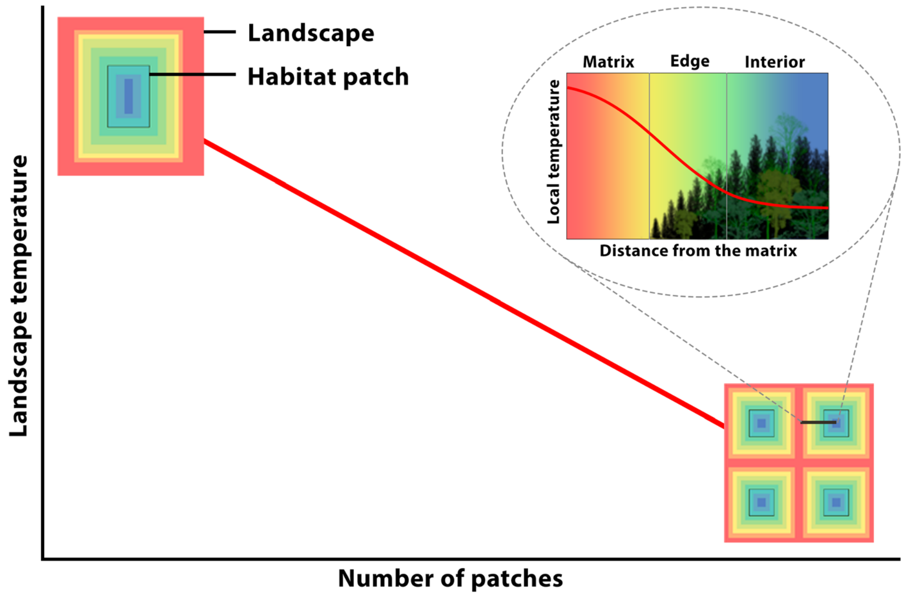

Fig. 4 A new conceptual model integrating local- (patch-) and landscape-level impacts of edge effects and habitat fragmentation on temperature. Red lines and curves represent thermal gradients. The local (patch) scale is depicted within the hatched circle on the top right. At this local scale, temperature is gradually reduced from the matrix into habitat patch interior (thermal gradient with warmer (red) and colder (blue) temperatures), as predicted by edge effects. The landscape scale, in its turn, is represented by the two illustrations on the top left and the bottom right, which depict two landscapes with a same total habitat amount, but different number of patches (1 versus 4, respectively). At this scale, the greater the number of patches in a landscape, the lower the temperature (see red thermal line), as predicted by the vegetation breeze phenomenon and higher evapotranspiration

habitat patches (Tuff et al. 2016), but would not be directly extrapolated to the landscape scale because other processes would also be important, especially vegetation breeze and evapotranspiration, which affect temperatures not only within patches, but also across the matrix. The effects from these two processes apparently surpass local, edge-induced warming within habitat patches, leading to final landscape cooling, as detected in our study.

Our analysis advances substantially understanding of the consequences of habitat fragmentation on climatic variables across the globe, and shows the importance of landscape-scale studies to this aim. The analysis brings new theoretical implications, as temperature changes induced by habitat fragmentation may affect different ecological levels and processes, from individuals to ecosystems (Tuff et al. 2016). Our study shows the need to evaluate if habitat fragmentation can contribute to weaken the temperature gradient from forest edge to interior due to vegetation breeze mediated effects, as already hypothesized in the literature (Arroyo-Rodríguez et al. 2016). This would affect the premises commonly raised by studies on thermal individual performances along edge-forest interior gradients (see Tuff et al. 2016). The study also shows the need to test which process, habitat loss or habitat fragmentation per se, has a stronger effect on landscape-level climate, as they may present opposite effects on temperature (see "Introduction"). Finally, it is necessary to consider that the drier conditions inside remnant patches due to habitat fragmentation make them more susceptible to burn more frequently (Cochrane and Laurance 2008) and may ultimately affect ecosystem carbon cycling (Molen et al. 2011). For all these reasons, we recommend considering forest fragmentation as a potentially important factor in mitigation scenarios for climate change, in search to prioritize the most effective conservation efforts.

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Compliance with ethical standards

Conflict of interest The authors declare that they have no conflict of interest.

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