Tropical forests are thermally buffered despite intensive selective logging

**Running head: Logged forests retain high thermal variation**

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# Abstract

Tropical rainforests are subject to extensive degradation by commercial selective logging. Despite pervasive changes to forest structure, selectively logged forests represent vital refugia for global biodiversity. The ability of these forests to buffer temperature-sensitive species from climate warming will be an important determinant of their future conservation value, although this topic remains largely unexplored. Thermal buffering potential is broadly determined by: (1) the difference between the ‘macroclimate’ (climate at a local scale, 101 to 103 m) and the ‘microclimate’ (climate at a fine-scale, 10-3 to 10-1 m, that is distinct from the macroclimate); and (2) the availability of microclimates to organisms. We compared these metrics in undisturbed primary forest and intensively logged forest on Borneo, using thermal images to capture cool microclimates on the surface of the forest floor, and dataloggers to capture those inside leaf litter, tree holes and deadwood. Despite major differences in forest structure 9-12 years after repeated selective logging, we found that logged forest was largely indistinguishable from primary forest in terms of macroclimate and microclimate temperature, and the overall availability of microclimates. Microclimate temperature inside deadwood warmed slightly faster in logged forests than in primary forests, but the opposite was true within leaf litter and tree holes, and the effect amounted to less than 0.1°C difference between forest types for 1°C warming in the macroclimate. We therefore conclude that selectively logged forests are similar to primary forests in their potential for thermal buffering, and subsequent ability to retain temperature-sensitive species under climate change. Selectively logged forests can play a crucial role in the long-term maintenance of global biodiversity.

**263 words (max. 300)**

# Introduction

Land-use change is a profound threat to Earth’s terrestrial biodiversity (Sala *et al.*, 2000; Maxwell *et al.*, 2016). Most of this biodiversity is found in tropical regions (Jenkins *et al.*, 2013), where rates of deforestation and forest degradation are among the highest globally (Hansen *et al.*, 2013). The detrimental impacts of deforestation on tropical biodiversity are well known (Gibson *et al.*, 2011; Barlow *et al.*, 2016); however, tropical forest degradation via commercial selective logging is 20 times more widespread than on-going conversion (Hansen *et al.*, 2008; Asner *et al.*, 2009), making it important to understand the value of these disturbed forests for biodiversity. Selectively logged forests constitute a large and effective refuge for species of conservation concern that cannot survive in deforested land (Edwards *et al.*, 2011; Gibson *et al.*, 2011; Edwards & Laurance, 2013). Protecting selectively logged forests may be a cost effective way to retain tropical biodiversity (Edwards *et al.*, 2014a), but this is heavily contingent on the assumption that these forests will maintain their current conservation value into the future.

Several factors may influence the value of selectively logged forests for biodiversity in the long-term, and a key consideration is the interaction of multiple drivers of biodiversity loss (Brook *et al.*, 2008; Mantyka-pringle *et al.*, 2012; Sirami *et al.*, 2016). The impacts of climate change are particularly important, and increasingly so as this century progresses (Sala *et al.*, 2000; Chou *et al.*, 2013; IPCC, 2013). Novel (non-analogous) climatic conditions are predicted to appear first in the tropics (Mora *et al.*, 2013), where many species have narrow thermal limits (Deutsch *et al.*, 2008; Tewksbury *et al.*, 2008; Khaliq *et al.*, 2014) and where there is limited dispersal potential owing to poor dispersal ability of many species (Van Houtan *et al.*, 2007). This vulnerability of tropical species is compounded by an absence of target habitats containing analogous climates (Colwell *et al.*, 2008), and widespread deforestation creating a hostile matrix through which dispersal must occur (Brook *et al.*, 2008; Scriven *et al.*, 2015). The ability of tropical species to withstand climate change, and so avoid extinction, is likely to be highly dependent on their ability to adapt in situ within existing forest areas. The extent to which species persistence can be facilitated within selectively logged forests will, therefore, greatly influence the conservation value of these habitats.

In primary forests and secondary forests re-growing on abandoned farmland, previous studies found that organisms – particularly ectotherms – avoid suboptimal temperatures in the wider ‘macroclimate’ (climate at a spatial scale of 101-103 m) by moving locally into ‘microclimates’ (climate at a fine-scale, 10-3 to 10-1 m, that is distinct from the macroclimate; Scheffers *et al.*, 2014a, 2014b; González del Pliego *et al.*, 2016). Climate at this fine-scale is more relevant for the majority of terrestrial biodiversity, which primarily consists of small-bodied ectotherms (Suggitt *et al.*, 2011; Potter *et al.*, 2013; Nadeau *et al.*, 2016). Indeed, the vast proportion of terrestrial species are small in size, flat in shape, or thermoregulate via contact with the ground, and so it is important to consider microclimates close to, and including, the surfaces on which these species live (Kaspari *et al.*, 2014; Scheffers *et al.*, 2016).

The most informative fine-scale temperature data are derived from highly replicated point measurements, and demonstrate that loss of vegetation cover causes local daytime warming (Senior *et al.*, in review; Ewers & Banks-Leite, 2013; Hardwick *et al.*, 2015; González del Pliego *et al.*, 2016). Selective logging affects vegetation by lowering and thinning the canopy, reducing the number of vegetation strata, and creating large forest gaps (Okuda *et al.*, 2003; Kumar & Shahabuddin, 2005). As such, the forest floor of logged forests likely receives a greater amount of solar radiation, partitioned increasingly as direct rather than diffuse radiation (Oke, 1987). The most tangible impact on the local climate would be overall warming of logged forests, increasing the necessity for thermal buffering. Simultaneously, the potential for thermal buffering may be compromised if structural changes also influence the temperature and distribution of cool microclimates, particularly if their temperature becomes more similar to that of the wider macroclimate (e.g. Caillon *et al.*, 2014), or there are simply fewer cool microclimates available overall. Previous evidence suggests that the availability of cool ‘microhabitats’ (localised environments within which cool microclimates are contained; (Scheffers *et al.*, 2014a; González del Pliego *et al.*, 2016; Shi *et al.*, 2016) can be reduced (e.g., leaf litter; Saner *et al.*, 2009) or increased (e.g., deadwood; Carlson *et al.*, 2016) by selective logging, implying that forest disturbance does alter thermal environments.

A key novel question that we address in this paper is whether vegetation change following commercial selective logging reduces the potential for thermal buffering. We focused on cool microclimates in the understorey only (climate at 10-3 to 10-1 m scale that is cooler than the macroclimate and located within 2 m of the forest floor). Microclimates on the surface of the forest floor were captured by a thermal camera, while dataloggers were used to capture microclimates within cool understorey microhabitats: leaf litter, tree holes and deadwood (Scheffers *et al.*, 2014a, 2014b; González del Pliego *et al.*, 2016). We determined thermal buffering potential according to: (1) the microclimate temperature relative to that of the macroclimate; and (2) the availability of microclimates in space. The former is roughly a measure of microclimate ‘quality’ – assuming an organism can move into the microclimate, how effectively will it be buffered from macroclimate warming? The latter captures the likelihood that organisms can locate and move into microclimates, according to their occurrence and configuration within the habitat (Caillon *et al.*, 2014). We expected that logged forests would be structurally distinct from primary forest, leading to reduced thermal buffering potential and, thus, impaired ability of temperature-sensitive species to respond in situ to excessively high temperatures in the wider macroclimate.

# Methods

## Study Area

Sampling took place in in an extensive area of contiguous forest in Sabah (Malaysian Borneo; Fig. 1a). This area represents over 10,000 km2 of lowland dipterocarp forest, comprising production forest and areas of undisturbed protected forest (Reynolds et al. 2011). In this study, we sampled sites in forest that had been commercially selectively logged twice (Ulu Segama-Malua Forest Reserve, 4°57'42.8"N, 117°56'51.7"E). The area was first logged from 1987-1991, using tractors and high-lead extraction techniques to harvest commercial trees (those in the family Dipterocarpaceae) with stems >0.6 m diameter at breast height (D.B.H.), and yielding ~113 m3 of timber per hectare (Fisher *et al.*, 2011; Edwards *et al.*, 2014b). Between 2001 and 2007, the area was re-logged and the minimum harvested tree diameter reduced to >0.4 m D.B.H., yielding an additional 31 m3/ha of timber (Fisher *et al.*, 2011). Thus, we sampled sites that had been heavily disturbed about 10 years prior to the study, at which point 67% of the forest was classified as being in ‘very poor’ condition (Reynolds *et al.*, 2011), and the area was left to recover naturally. Control sites were located in undisturbed, protected primary forest (Danum Valley Conservation Area (DVCA); 4°57'45.2"N, 117°48'10.4"E).

## Sampling design

We sampled twelve sites, six in twice-logged forest and six in primary forest, along existing transects (Edwards *et al.*, 2011, 2014b; Fig. 1b). Sites were more than 2 km apart, and at least 100 m from forest edges. Within each site, we established five 50 x 50 m plots, with plot centres spaced at 125 m intervals along the transect (Fig. 1c; 60 plots in total). Fieldwork was conducted from April to July 2015, during the severe El Niño Southern Oscillation (ENSO) event of 2015-2016 (NOAA Climate Prediction Center: http://www.cpc.noaa.gov/products/analysis\_monitoring/ensostuff/ensoyears.shtml) when maximum daily temperature was 7% higher and mean rainfall 17% lower than the 5-year average (across April to July for the years 2007 to 2011).

### Forest structure

To quantify the level of disturbance to the forest from selective logging, we used an established methodology for assessing forest structure in each plot (Hamer *et al.*, 2003; Lucey & Hill, 2012). The variables we measured were: the basal area (cm2/m2 forest) of mature trees (circumference > 0.6 m) and saplings (circumference 0.1-0.6 m), based on the distance to and circumference at breast height of the two nearest in each of four quadrants centred on the plot centre (Fig. 1d); the proportion of mature trees that were dipterocarps (indicative of mature, complex forest); percentage shade cover; and visual estimates of percentage vegetation cover at ground (1.5 m above ground), understorey (15 m above ground) and canopy (the main stratum of leaf cover > 15 m above ground) levels. For full methodological details see Supplementary Text S1.

### Quantifying surface microclimates

Fine-scale surface temperature of the forest floor is particularly relevant for small-bodied, surface-dwelling organisms, such as many insect and reptile species. We measured surface temperature within each plot using an infrared camera (FLIR Systems, model E40); macroclimate temperature was defined as the air temperature at 1.5 m above-ground, measured using a whirling hygrometer. Each site was visited on two days, and each plot within the site was sampled five times each day between 05:00 hrs to 14:30 hrs. During each sample of any given plot, the observer stood at the centre of the plot, took a single hygrometer reading and then, holding the camera at breast height and pointing 45° downwards (relative to the ground), took a photo in four orthogonal directions (Scheffers *et al.*, 2016). Each thermal image comprised 19200 distinct observations of surface temperature (one per pixel), and covered a surface area of approximately 1 m2. In total, we recorded 2400 thermal images (4 images per plot x 5 repeats x 2 site visits x 60 plots).

For all subsequent analyses, a unique data point comprised thermal information from the four photographs taken each time a plot was sampled: 76800 observations of surface temperature measurements for each plot (i.e. combining 19200 observations from the four photos taken in each orthogonal direction). The temperature of cool surface microclimates was defined as the 5th percentile (i.e. coolest) across all 76800 pixels. To identify individual ‘cool’ pixels we determined lower and upper threshold values from the 5th and 25th percentile, respectively, from each two-hour time period (05:00-07:00 hrs, 07:00-09:00 hrs, 09:00-11:00 hrs, 11:00-13:00 hrs and 13:00-15:00 hrs) across all temperatures from all photos taken in that time period (Fig. 2). This ensured that cool pixels were defined relative to all other observations taken in that time period. The area of surface microclimates was then calculated as the average number of cool pixels per m2 (the surface area encompassed in one photo), multiplied by the area of one pixel (0.5 cm2; FLIR). Spatial configuration of cool pixels was quantified using the Aggregation Index: the number of edges that cool pixels share, divided by the maximum number of edges that they could possibly share (He et al. 2000; Caillon et al. 2014). Higher values of the Aggregation Index indicate less dispersal of microclimates through space (increased clustering), which makes them more difficult for organisms to track (Sears *et al.*, 2016).

### Quantifying microclimates in leaf litter, tree holes and deadwood

Many ectotherms, such as amphibians, spend some or all of their time exploiting cool microclimates inside microhabitats, which thermal images are unable to capture. We selected three types of microhabitat known to provide cool microclimates (Scheffers *et al.*, 2014b, 2014a; González del Pliego *et al.*, 2016), and placed one temperature datalogger (HOBO pendant datalogger, Onset, model UA-001-64K or model UA-002-64K) per plot in each microhabitat type: leaf litter (1.5 m left of the plot centre), tree holes (> 2 cm at widest point of entrance hole, < 2 m above the ground) and deadwood (> 10 cm stem diameter). The hygrometer measurements of macroclimate temperature were not always synchronised with the dataloggers inside microhabitats, hence we additionally measured macroclimate temperature using a datalogger suspended 1.5 m above the ground at the centre of each plot, shielded against direct radiation and precipitation by an inverted plastic funnel (Shoo *et al.*, 2010; Scheffers *et al.*, 2014a). All dataloggers recorded temperature every 20 minutes for five consecutive days, occurring within one week of thermal image collection. We used only data from within the same diurnal time period as that during which thermal images were taken (05:00 hrs to 14:30 hrs), to facilitate qualitative comparisons of thermal buffering by microclimates at the surface and inside microhabitats.

To estimate the occurrence of microclimates inside microhabitats, we measured the volume of leaf litter, tree holes and deadwood within a 50 x 5 m subplot centred on each plot centre (60 sub-plots in total), with the long edge running parallel to the transect. For full methodological details see Supplementary Text S2. We divided microhabitat volume by the total area surveyed to generate microhabitat volume per m2 forest, for each plot.

## Statistical analyses

### Forest structure

To examine the impact of selective logging on forest structure, we assessed seven structural response variables: tree basal area sapling basal area; proportion of trees that were dipterocarps (binomial data: dipterocarp vs. non-dipterocarp); percentage shade cover (proportion data); and percentage vegetation cover at ground, understorey and canopy strata (proportion data). Forest type (categorical: primary or logged) was the only explanatory variable included.

### Macroclimate and microclimate temperature

Macroclimate temperature is the temperature at a coarse spatial scale, and was captured in this study using both a hygrometer and suspended datalogger (measuring the same variable but at different times). The macroclimate does not affect thermal buffering potential per se, but it does dictate the overall necessity for thermal buffering. We modelled hygrometer and datalogger temperature separately, including forest type as the only explanatory variable.

To assess the impact of selective logging on the ability of microclimates to buffer organisms from macroclimate warming, we modelled microclimate temperature against macroclimate temperature and its interaction with forest type. The model intercept is a measure of what Shi *et al.* (2016) refer to as the ‘thermal buffering effect’ (the difference between macroclimate and microclimate temperature), while the slope is a measure of the ‘rate of change’ (the change in microclimate temperature for every 1°C rise in macroclimate temperature). Surface microclimate temperature refers to the 5th percentile of surface temperature observations for each plot, and this was compared against macroclimate temperature as measured by the hygrometer. Microclimate temperature inside leaf litter, tree holes and deadwood refers to the raw temperature recorded by dataloggers inside microhabitats, and this was compared against macroclimate temperature as measured by a suspended datalogger. Models were run separately for surface, leaf litter, tree hole and deadwood microclimates.

### Microclimate availability

Microclimate occurrence was modelled separately for surface microclimates (i.e. the average surface area of cool pixels per m2 forest), and those inside leaf litter, tree holes and deadwood (each quantified by their average volume per m2 forest). The spatial configuration of surface microclimates refers to the Aggregation Index of cool pixels (binomial data: edges shared by cool pixels vs. edges not shared by cool pixels). For all models, forest type was the only explanatory variable.

## Statistical analyses

All data were analysed using mixed effects models in R (version 3.3.0; R Core Team 2016). To account for spatial pseudoreplication, forest structure models included ‘site’ as a random intercept term, and all other models included ‘plot’ nested in ‘site’. Temperature data were recorded at multiple time points, and so full models were visually assessed for evidence of temporal autocorrelation of residuals (function “acf” in the nlme package; Pinheiro et al. 2016), and an autoregressive correlation structure incorporated into all models with temperature as a response variable (Zuur *et al.*, 2009). Generalized linear mixed effects models (GLMMs) with a binomial error distribution, tested for overdispersion, were used for binomial data (proportion of dipterocarps and surface microclimate Aggregation Index). Diagnostic plots were assessed for all models to confirm model fit, and variables transformed to normality where necessary. For true proportion data (percentage shade cover and percentage vegetation cover), the transformation used was a modification of the empirical logit (Warton & Hui, 2011).

For all models, statistical significance was inspected using likelihood ratio tests, dropping each fixed effect in turn and comparing it to the full model (Zuur et al. 2009). The significance of main effects involved in an interaction was assessed in the same way, except reduced models were compared to a full model without the interaction term.

# Results

## Changes in forest structure after logging

Following two rounds of commercial selective logging, tree basal area was reduced by 36% compared to undisturbed primary forests (*P* = 0.00612; Fig. S1a). There was no difference between primary and logged forests in terms of sapling basal area (*P* = 0.115; Fig. S1b), the proportion of trees that were dipterocarps (*P* = 0.12; Fig. S1c), or percentage shade cover (*P* = 0.272; Fig. S1d). Percentage vegetation cover at ground level was also comparable between forest types (*P* = 0.0968; Fig. S1e), but in the understorey and canopy vegetation cover was 13.7% (*P* = 0.0215; Fig. S1f) and 14.5% (*P* = 0.00246; Fig. S1g) lower in logged than in primary forests, respectively. Thus, 9-12 years after logging there were significant differences in forest structure between logged and primary forests, especially in terms of occurrence of mature trees.

## macroclimate and microclimate temperature comparable between forest types

There was no effect of selective logging on macroclimate temperature, whether measured by the hygrometer (*P* = 0.519; Fig. 3a) or suspended datalogger (*P* = 0.27; Fig. 3b). Thus, the necessity for thermal buffering was comparable between forest types. Additionally, because the baseline macroclimate temperature is constant between forest types, we can consider the temperature of microclimates relative to that of the macroclimate as a sufficient measure of thermal buffering potential, without needing to explicitly consider the absolute temperature of microclimates.

The overall difference between macroclimate and microclimate temperature (‘thermal buffering effect’) was unaffected by selective logging, regardless of whether microclimate temperature was measured at the surface (*P* = 0. 0.701; Fig. 3c), or inside leaf litter (*P* = 0. 0.36; Fig. 3d), tree holes (*P* = 0.293; Fig. 3e) or deadwood (*P* = 0.445; Fig. 3f). There was a highly significant relationship between macroclimate and microclimate temperature (*P* < 0.0001 for all microclimates). The slope of this relationship was consistent between forest types for surface microclimates (*P* = 0.947; Fig. 3c), which warmed by 0.76°C for a 1°C rise in macroclimate temperature. In contrast, for 1°C macroclimate warming, microclimates inside leaf litter warmed less in logged forest (0.23°C) than in primary forest (0.32°C; *P* < 0.001; Fig. 3d), and the same was true of tree holes in logged forest (0.34°C) compared to primary forest (0.38°C; *P* < 0.001; Fig. 3e). The pattern was reversed in deadwood (*P* < 0.001; Fig. 3f), where 1°C macroclimate warming resulted in deadwood microclimates warming by 0.35°C in logged forest and 0.25°C in logged forest. Leaf litter and tree holes therefore had greater thermal buffering potential in logged forest than in primary forest, and the reverse was true for deadwood. At the surface, however, thermal buffering potential was equivalent between logged and primary forests.

## Microclimate availability comparable between forest types

The thermal buffering potential within a habitat depends not only on the temperature of microclimates relative to the macroclimate, but also on the overall availability of those microclimates. The occurrence of surface microclimates was not impacted by selective logging (*P* = 0.999; Fig. 4a). Per m2 forest, the area of surface microclimates was 2178 cm2 in logged forest compared to 2183 cm2 in primary forest. The occurrence of microhabitats was also constant between forest types. In 1 m2 habitat, logged and primary forests respectively contained: 3430 versus 3790 cm3 of leaf litter (*P* = 0.224; Fig. 4b); 17.5 versus 12.5 cm3 of tree holes (*P* = 0.665; Fig. 4c); and 21700 versus 22000 cm3 deadwood (*P* = 0.978; Fig. 4d). Using thermal images we were also able to quantify the spatial configuration of surface microclimates, which has a bearing on the ease with which organisms can utilise microclimates. The Aggregation Index of cool surface microclimates was 89% in both logged and primary forests (*P* = 0.903; Fig. 4e). Thus, the overall availability of microclimates, including both occurrence and configuration, was not affected by selective logging, regardless of whether microclimates were located at the surface or inside leaf litter, tree holes or deadwood.

# Discussion

Forest degradation by commercial selective logging affects huge expanses of the tropics (Asner *et al.*, 2009; Lewis *et al.*, 2015). Southeast Asia has experienced the most intensive selective logging of all tropical rainforests (Lewis *et al.*, 2015), and in our study area ~145 m3 of timber was removed per hectare. Despite a recovery time of only 9-12 years (Fisher *et al.*, 2011), and the coincidental occurrence of abnormally hot and dry conditions associated with the strongest El Niño Southern Oscillation (ENSO) event since 1998 (NOAA Climate Prediction Center: http://www.cpc.noaa.gov/products/analysis\_monitoring/ensostuff/ensoyears.shtml), intensively logged forests showed very few thermal differences compared to undisturbed primary forest. This is an important finding for tropical conservation because it suggests that the potential for thermal buffering will not limit the ability of selectively logged forests to maintain high biodiversity under climate change (Scheffers *et al.*, 2013a; González del Pliego *et al.*, 2016).

## Forest structure

At a local scale, climate is highly dependent upon vegetation (Oke, 1987; Sears *et al.*, 2011). Selective logging targets the largest and oldest trees, leading to many accompanying changes in vegetation structure (Okuda *et al.*, 2003; Kumar & Shahabuddin, 2005; Edwards *et al.*, 2014a). A clear signal of historical logging in our study area was the reduction in basal area of mature trees (Fig. S1a; Berry et al. 2008), and in percentage vegetation cover at ≥15 m above ground (Fig. S1f-g). The absence of any differences in other variables (vegetation cover at 1.5 m, shade cover, proportion of trees that were dipterocarps and sapling basal area) may be a consequence of sampling only a small area of forest understorey several years after logging operations ceased, during which time there was likely rapid growth in understorey vegetation, including regeneration of both small dipterocarps and large herbaceous pioneer species (Berry *et al.*, 2008; Edwards *et al.*, 2014a).

## Macroclimate and microclimate temperature

Local temperature is affected by multiple local factors, particularly vegetation structure. In all cases, although primary forest contained more, larger trees (Fig. S1a), the absence of any long-term effect of selective logging on the amount of shade cover (Fig. S1d) suggests that forest vegetation as a whole – regardless of how it was distributed vertically – intercepted comparable amounts of incoming solar radiation in both logged and primary forests. Alternatively, vegetation in logged forest may have intercepted less incoming radiation than in primary forest (i.e. if there was less vegetation overall), but reflected a greater proportion of that which was intercepted, owing to the higher albedo of habitats with an abundance of non-tree species (Oke, 1987; Davin & de Noblet-Ducoudré, 2010; Edwards *et al.*, 2014a). In either case, given comparable levels of solar radiation reaching the understorey of logged and primary forests, it follows that the temperature at coarse and fine scales (macroclimate and microclimate temperatures) should also be comparable (Fig. 3).

The temperature of cool microclimates relative to average conditions is what largely determines their ability to buffer macroclimate warming (Scheffers *et al.*, 2014a; González del Pliego *et al.*, 2016; Shi *et al.*, 2016). We found no overall difference in temperature buffering either at the surface (Fig. 3c) or inside microhabitats (Fig. 3d-f), although there were very slight differences between logged and primary forests in rates of microhabitat warming. For a given increase in macroclimate temperature, leaf litter and tree holes warmed more in primary forests than in logged forests, and the opposite was true for temperature inside deadwood (Fig. 3d-f). That said, these differences were extremely small in biological terms – a maximum of 0.1°C difference in microhabitat warming between logged and primary forests, relative to a 1°C increase in average air temperature. We therefore conclude that available microclimates in logged and primary forest had equal potential to buffer organisms from macroclimate temperature change.

## Microclimate availability

Even if cool microclimates are present and individually effective at buffering temperature change, overall rarity or isolation could render them functionally redundant (Sears *et al.*, 2011, 2016). We demonstrate that microclimates in logged and primary forests had a similar availability (Fig. 4), whether measured at the surface or as the volume of microhabitats. This is contrary to expectations from previous studies (Ball *et al.*, 1999; Blakely & Didham, 2008; Saner *et al.*, 2009). However, high volumes of leaf litter and deadwood could be maintained in logged forest by lower decomposition rates (Ewers *et al.*, 2015; Yeong *et al.*, 2016) and large remnant pieces of deadwood from harvest operations. In undisturbed forests, tree holes tend to be associated with larger, older trees (Lindenmayer *et al.*, 2000; Blakely & Didham, 2008). A comparable quantity of tree holes might be found on relatively small trees in logged forests because of damage from logging operations (Edwards *et al.*, 2014a) and increased wind in gaps (Chen *et al.*, 1995). Additionally, we assessed tree holes in the understorey only; differences may well manifest at higher forest strata.

The true availability of microclimates to organisms is also influenced by their distribution in space. We found that microclimates on the surface of the forest floor were generally highly clustered in space, but this was not affected by logging (Fig. 4b). Spatial configuration of microclimates is a novel facet of thermal buffering potential (but see Caillon *et al.*, 2014; Sears *et al.*, 2016), likely determined by the composition of the forest floor and the relative radiative properties of these different components (e.g. bare soil vs. leaves vs. water; Oke, 1987). We therefore suggest that these characteristics of the forest floor were also comparable between forest types, further supported by the absence of any difference in leaf litter volume.

## Caveats and future directions

The potential for thermal buffering and its general necessity are influenced by moisture levels, as well as temperature (McLaughlin *et al.*, 2017). Many ectotherms, including amphibians (Duellman & Trueb, 1986) and isopods (Hassall *et al.*, 2010), can survive in hot temperatures for longer if relative humidity is sufficiently high to prevent desiccation. Although we did not measure fine-scale vapour pressure deficit (a variable combining both temperature and relative humidity), we did find that average vapour pressure deficit measurements from the hygrometer and from hygrochron iButtons (Supplementary Text S2), showed little variation within or between forests (Fig. S2).

Relative climates in primary and logged forests could be very different above the understorey (Scheffers *et al.*, 2013b), which we were unable to capture in our study. Some ectotherms move down from the upper strata to exploit more favourable temperatures in the lower storey (Scheffers *et al.*, 2013b). Hence, if temperatures in higher strata were indeed hotter in logged forest compared to primary forest, species could utilise the favourable temperatures in the understorey of logged forest that we demonstrate here.

The ability of selectively logged tropical forests to retain current levels of biodiversity will critically depend on their ability to protect species from the impacts of increasingly severe climate change (Sala *et al.*, 2000; Mora *et al.*, 2013). As average temperatures increase over this century, so too will the intensity and frequency of extreme climatic events (IPCC, 2013), including ENSO (Cai *et al.*, 2014). Thermal buffering will likely be crucial in allowing species to move locally to avoid suboptimal climates (Scheffers *et al.*, 2014a, 2014b; González del Pliego *et al.*, 2016). We sampled in some of the most intensively logged forest in the tropics, during an ENSO event with maximum temperatures 7% higher and rainfall 16% lower than the 5-year average (across April to July, for the years 2007 to 2011); it is highly unlikely that our study would have failed to detect any appreciable thermal differences between primary and logged forests had they existed. Regardless of whether commercially selectively logged forests remain biologically or structurally distinctive from undisturbed forests, this study shows for the first time that they are functionally equivalent in the provisioning of cool microclimates, and underscores their vital role in conservation both now and under future climate warming.

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# Conflict of Interest

Authors declare no conflicts of interest.

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# Supporting information

**Text S1.** Sampling methods for forest structure.

**Text S2.** Sampling methods for microhabitat volume.

**Text S3.** Sampling methods and results for analyses of vapour pressure deficit.

**Figure S1.** Comparison between primary and logged forest for the seven forest structure measures.

**Figure S2.** Comparison between primary and logged forest for vapour pressure deficit.

# Figures

**Figure 1.** Study location in Malaysian Borneo (a), and distribution of sites (b): six sites in primary forest (blue) and six sites in logged forest (orange). Each site comprised five plots along an existing transect, with plot centres separated by 125 m (c). Tree and sapling basal area was calculated from the distance to and circumference of the nearest two trees and saplings in each of four quadrants centred on the plot centre (d; see Supplementary Text S1 for more details). Curved arrows indicate the direction of magnification, from panels a-d.

**Figure 2.** Single thermal image with temperature as a continuous variable (a) and categorised into quantiles (b). Quantile boundaries are based on percentile values calculated across all temperature observations, from all photos taken during each two-hour time period (05:00-07:00 hrs, 07:00-09:00 hrs, 09:00-11:00 hrs, 11:00-13:00 hrs and 13:00-15:00 hrs). For our analyses we focused only on ‘cool pixels’, defined as those with a value greater than the 5th percentile and less than or equal to the 25th percentile (quantile 5% - 25% in panel b).

**Figure 3.** Comparison of temperature in primary (blue; PF) and logged (orange; LF) forest. Macroclimate temperature was measured using a hygrometer (a) for comparison with surface microclimates (c), and with a suspended datalogger (b) for comparison with microclimates inside leaf litter (b), tree holes (c) and deadwood (d). The grey dashed line in panels c-f indicates zero temperature buffering, where the microclimate temperature is equal to the macroclimate temperature.

**Figure 4.** Comparison between primary (blue) and logged (orange) forest in the availability of microclimates. This includes the average area of surface microclimates, per m2 forest (a); the Aggregation Index of surface microclimates (b); and the average volume, per m2 of forest, of leaf litter (c), tree holes (d) and deadwood (e).

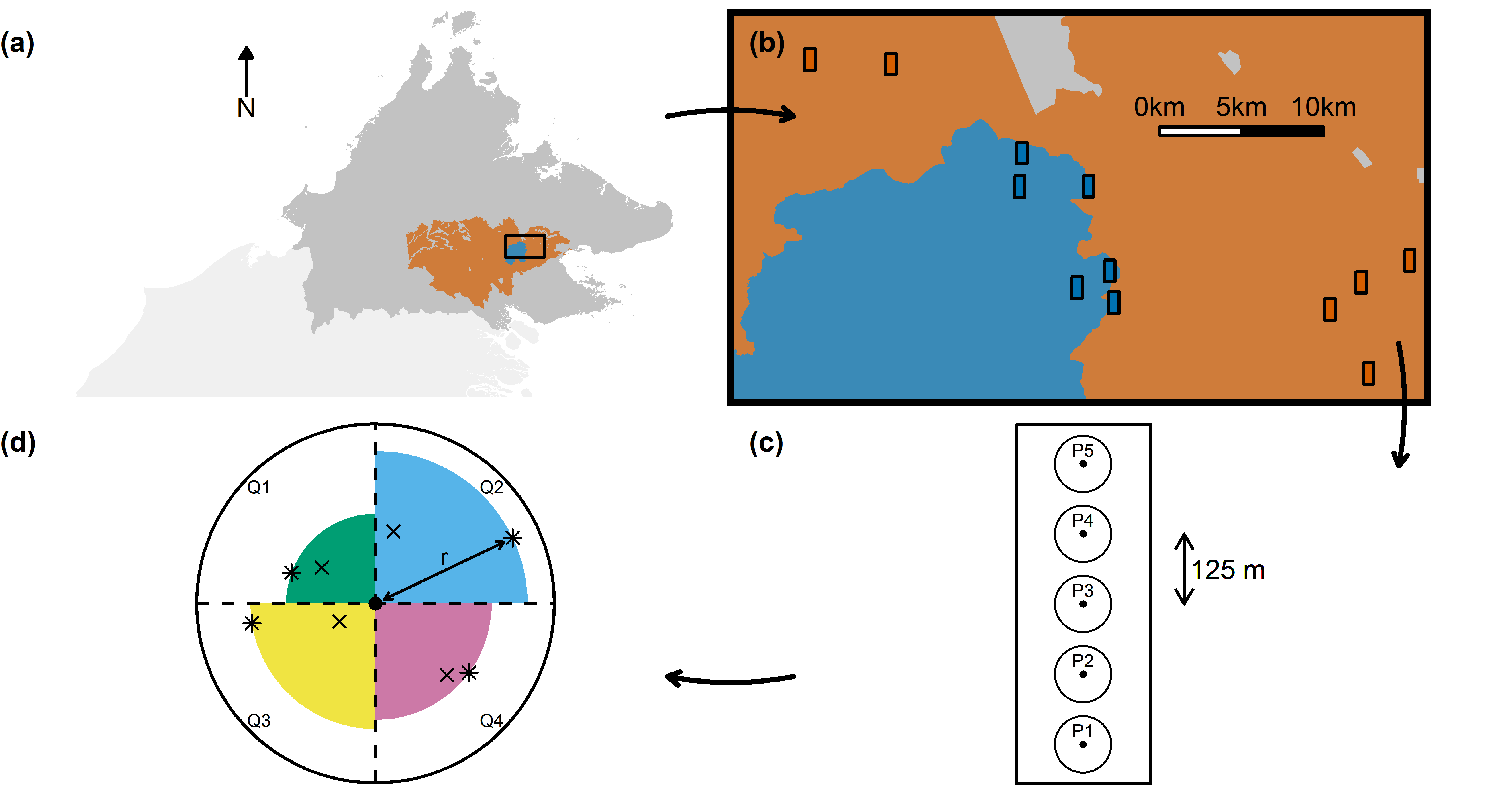
Figure 1.

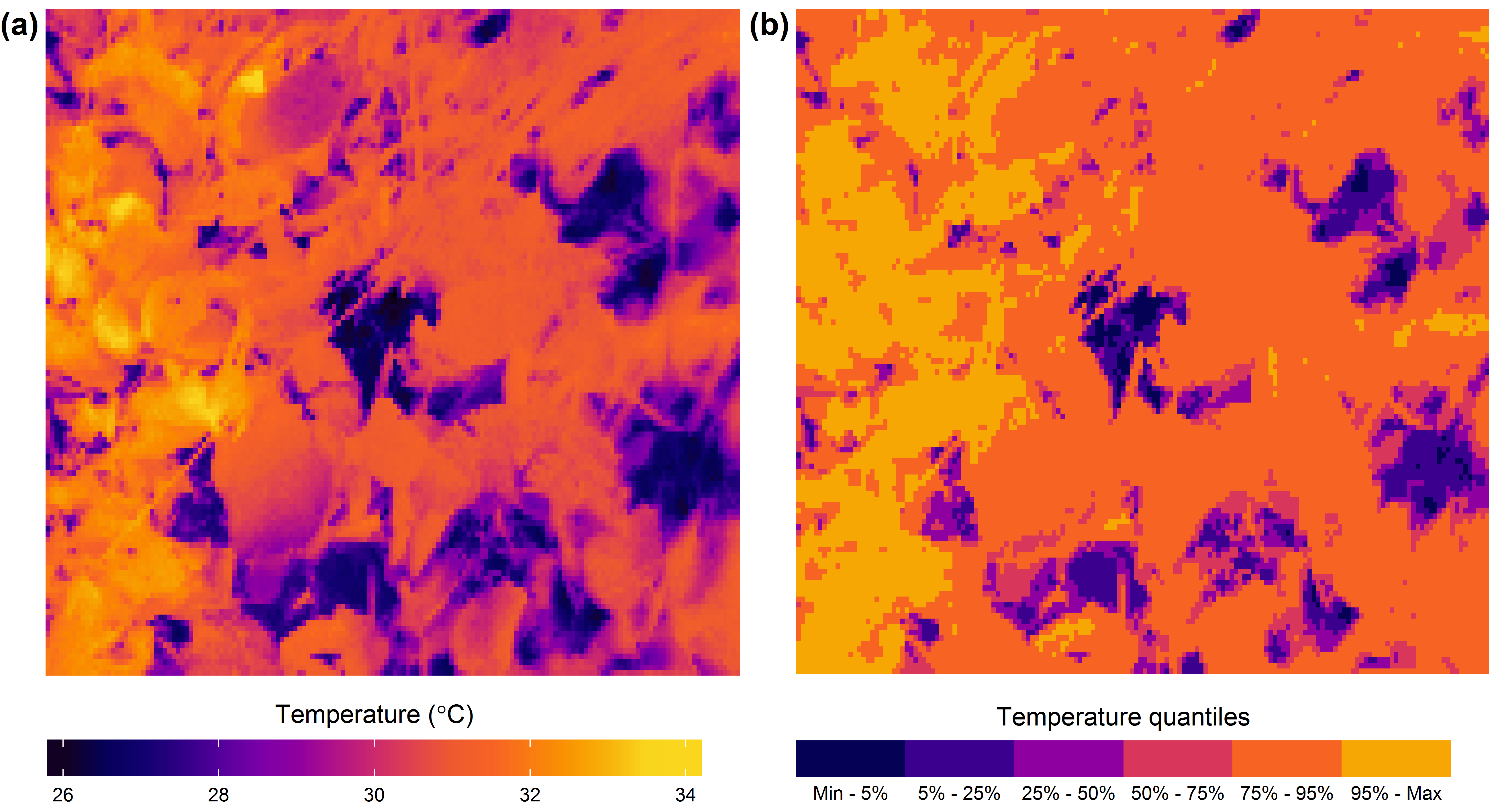
Figure 2

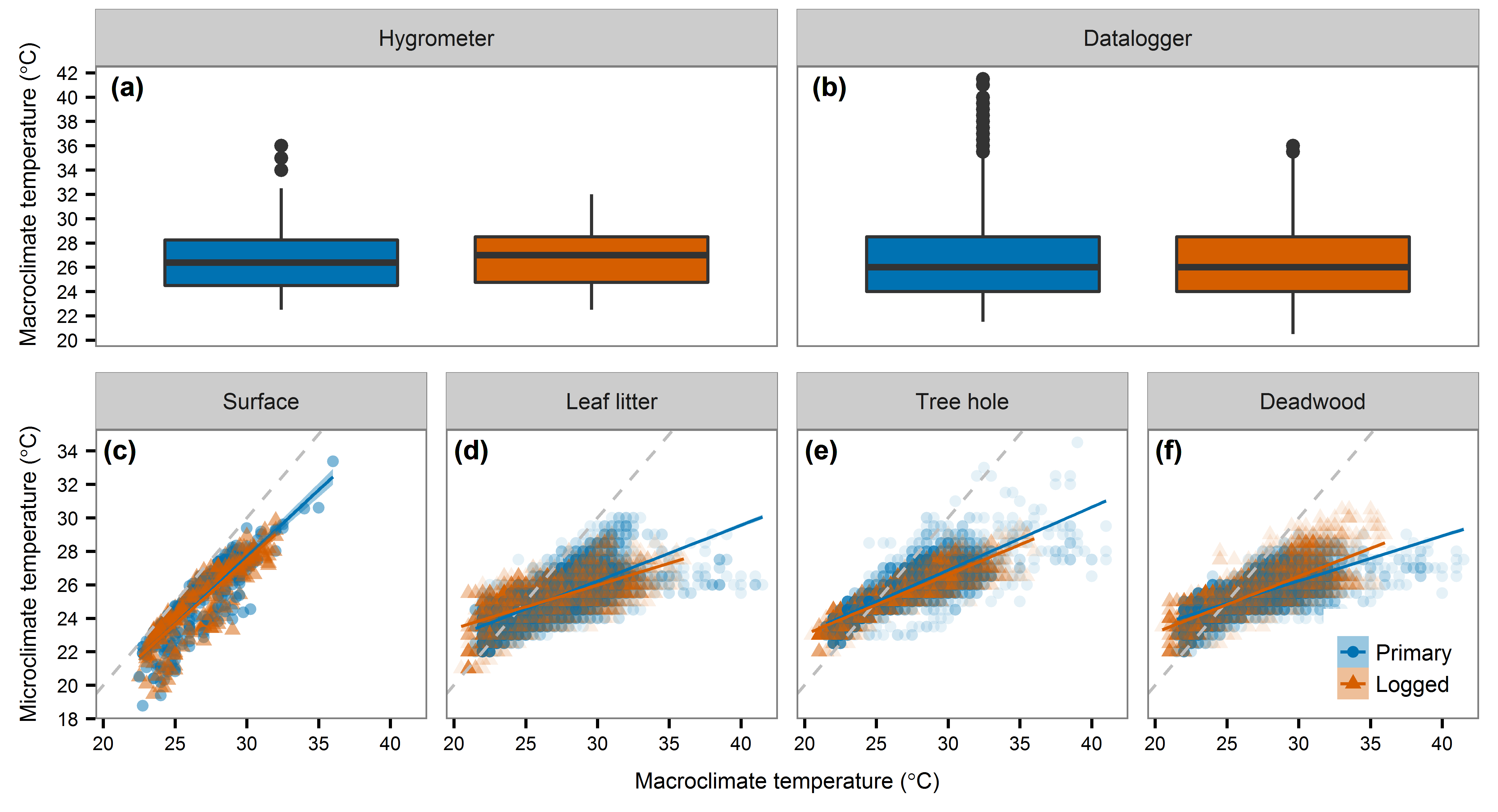
Figure 3.

Figure 4.