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The impacts of tropical forest degradation and conversion on resilience to climate change

By:

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A thesis submitted in partial fulfilment of the requirements for the degree of
Doctor of Philosophy

**The University of Sheffield
Faculty of Science
Department of Animal and Plant Sciences**

Submission Date

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Abstract

Stuff about tropical forests being important and blah blah blah.

Acknowledgements

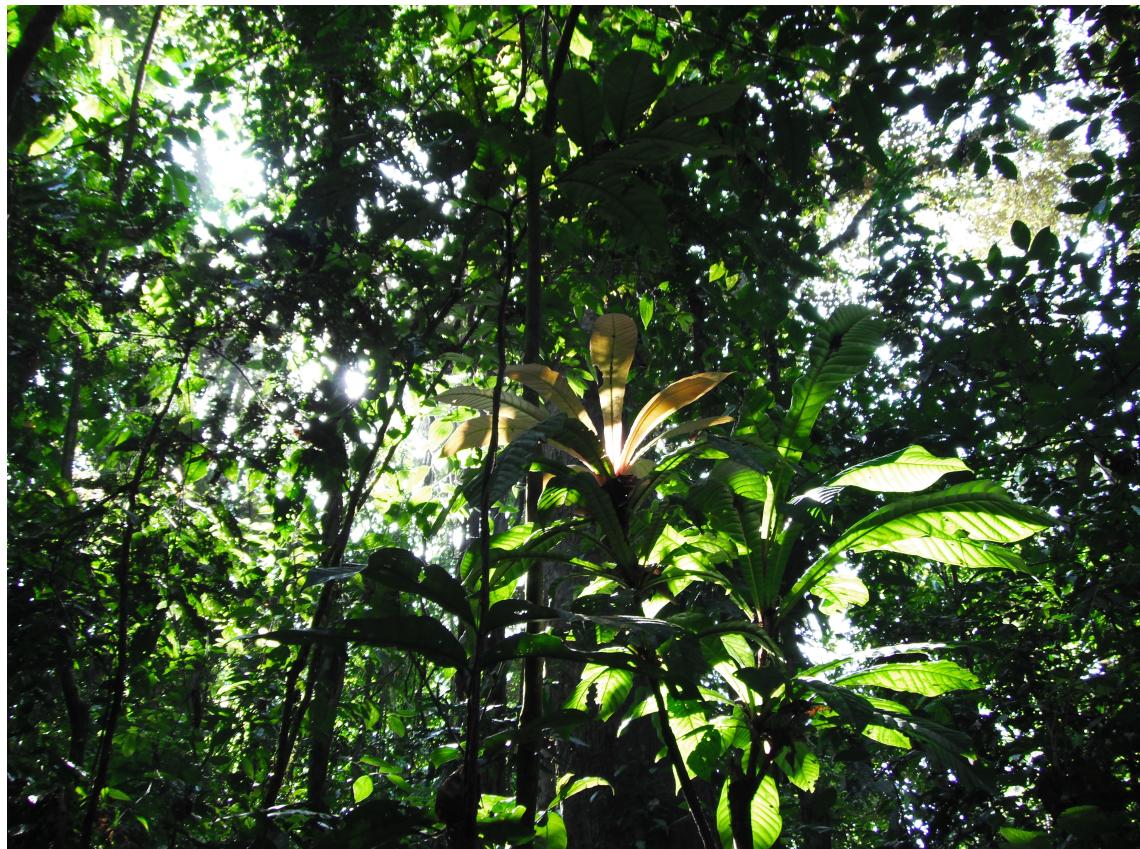
Thanks everyone for being alright.

Author's declaration

I did all this shit yo.

Chapter 1

General introduction



Sunshine through rainforest canopy in Danum Valley.

1.1 Threats to biodiversity

Throughout the Anthropocene, humans have faced crises. In 2000 the United Nations developed eight goals for 2015, known as the Millennium Development Goals, one of which was to ‘ensure environmental sustainability’ (United Nations, 2014). Amongst other things, this goal is in recognition of the current extinction crisis. Recent extinction rates far exceed their pre-human levels (Pimm et al., 1995), and are close to constituting the 6th mass extinction event (Barnosky et al., 2011).

Humans are at heart of the extinction crisis, but which of our environmental impacts is principally to blame? Five key threats are: land-use change, climate change, pollution, over-exploitation and invasive species (Hirsch and Secretariat of the Convention on Biological Diversity, 2010). Whilst the greatest overall threat to terrestrial systems is currently land-use change, climate change is forecast to become increasingly important (Sala et al., 2000).

Having diagnosed the threats for biodiversity, we cannot assuage them until we identify underlying drivers. Climate change is driven by changes in: (1) atmospheric concentrations of greenhouse gases (GHGs) and aerosols, (2) land cover and (3) solar radiation (IPCC, 2013). All of these changes occur naturally, but climate change since pre-industrial times is primarily caused by anthropogenic emissions of GHGs from the burning of fossil fuels and through land-use change (IPCC, 2013). Land-use change includes both wholesale conversion and degradation. Generally habitat is converted to create agricultural land to feed the growing human population (Foley et al., 2011; Godfray et al., 2010). Degradation of remnant, unconverted habitat may result through incipient fragmentation. Additionally, habitat degradation is caused by selective logging, hunting and fire – the key is that the overall habitat type remains the same but the quality declines.

Given the importance of the underlying drivers of climate change and land-use change for the persistence of the human population, it is unrealistic to expect these pressures to cease. One option is to mitigate change by stemming human population growth and increasing the efficiency of resource acquisition (Godfray et al., 2010).

Alternatively, the biodiversity crisis could be alleviated through a better understanding of how and why organisms respond to human impacts. In this way, we could modify our actions to minimise impact, and also facilitate organism responses that permit persistence through change. This is the step that I will address in the following review. Initially I will focus on organism responses to climate change, given the increasing importance of this pressure in the future (Sala et al., 2000). However, neither the impacts of climate change nor land-use change can be fully understood in isolation; the synergies between the two pressures are thought to be extensive, but generally poorly understood (Brodie et al., 2012; Mantyka-

pringle et al., 2012). In the tropics forest degradation is some 20 times more pervasive than deforestation (Asner et al., 2009), yet there is particularly little discussion of how habitat degradation might interact with climate change. This is the key unexplored area that I will move on to discuss, before finally outlining my PhD framework.

1.2 Responses to climate change

There are three possible outcomes for organisms experiencing environmental change: (1) they die, (2) they move to more optimal environmental conditions, or (3) they adapt in situ to the new environmental conditions. The first case results where organisms fail to adequately implement either of the latter two adaptive responses to change.

1.2.1 Extinctions due to climate change

A species is classed as extinct on the IUCN Red List if “there is no reasonable doubt that the last individual has died” (Baillie et al., 2004). Twenty-five species are classified as extinct or extinct in the wild owing partially or wholly to “climate change and severe weather” (IUCN, 2014). Between 1880 and 2012, global average temperature increased by 0.85°. This trend will continue into the future, with predictions of global average temperature for the period 2081-2100, relative to 1986-2005, ranging from an increase of 1-3.7°C, depending on the scenario used (IPCC, 2013).

Evidently the increase in global average temperature occurs on a long timescale and in concert with many other human impacts, so it can be difficult to directly attribute biodiversity loss to this change per se. The most obvious proximate cause of extinction directly due to increasing average temperature is loss of climatically-suitable habitat (Thomas et al., 2004), but examples under current climate change have yet to manifest.

Where extinctions have been attributed to climate change, this is through changes in local weather patterns. Weather is distinguished from climate as being “the state of the atmosphere at a given time and place”, whereas climate comprises “the statistics of weather conditions over a decade or more” (IPCC, 2013). Concomitant with increasing global average temperature is the increase in the frequency and intensity of extreme weather events (IPCC, 2013). This can be explained statistically, because an ‘extreme weather event’ is an event in which the climatic conditions fall towards either extreme end of the probability distribution [the 10th or 90th percentile; IPCC (2013)]. Provided the probability distribution of temperatures remains the same (or similar), an increase in average temperature corresponds to an upwards shift in the overall temperature distribution, and therefore we more commonly

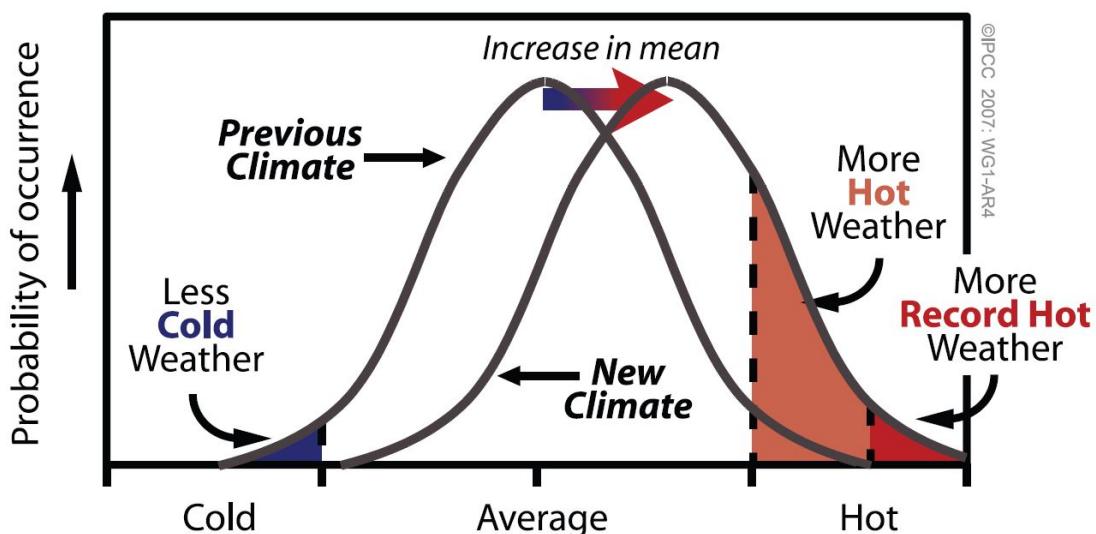


Figure 1.1: Schematic showing the increase in frequency of extreme temperatures (shaded light pink) and the magnitude of extreme temperatures (shaded dark pink), in response to increasing mean temperature for a normal distribution of temperatures. ‘extreme’ refers to events that would have been anomalous under the previous probability distribution. Figure taken directly from IPCC (2007).

see temperatures that were originally very rare, and begin to see temperatures never before recorded (Figure 1.1). It is almost certain that there will be more extremes of heat (and fewer extremes of cold) towards the late 21st Century (IPCC, 2013).

Future changes in precipitation are more difficult to predict than changes in local temperature, but precipitation events also play a significant role in species’ extinctions due to climate change. For example, extremely hot and dry years significantly contributed to the extinction of the golden toad (Pounds et al., 1999). It is likely that heavy precipitation events will increase in frequency and/or intensity over many land areas, whilst the intensity and/or duration of droughts may also increase towards the late 21st Century (IPCC, 2013).

1.2.2 Range shifts due to climate change

Species may track optimal climatic conditions by shifting their range. This commonly occurs through net population extinctions at the trailing edge, or net population colonisations at the leading edge (Parmesan et al., 1999). Dispersal by individuals may also occur in highly mobile species. Since the predominant effect of climate change is increasing temperature, many species track temperature by moving to higher latitudes — as exemplified in the Arctic, where organisms such as shrubs and red foxes have expanded polewards (Hersteinsson and MacDonald, 1992; Sturm et al., 2001). Others move to higher altitudes; both latitudinal and altitudinal shifts have been seen in birds and butterflies of temperate regions (Hill et al., 2002;

Parmesan et al., 1999; Thomas and Lennon, 1999).

Until recently, there were very few studies of range shifts due to climate change in tropical species, with some suggesting that the response should be less extreme given the slower rates of warming in the tropics (Freeman and Freeman, 2014; IPCC, 2013). It is now apparent that tropical species do shift their ranges to track climate, particularly to higher elevations (Chen et al., 2009; Pounds et al., 1999) owing to shallow temperature gradients across latitudes (Colwell et al., 2008). In fact, tropical species track climate more closely than temperate species (Freeman and Freeman, 2014). This effect could be due to: (1) greater thermal specialisation as a result of long-term thermal stability in the tropics (Freeman and Freeman, 2014); (2) slower velocity of climate change up mountains (Loarie et al., 2009) meaning it is easier for species to keep pace; or (3) fewer barriers to dispersal in the tropics, since tropical biomes have thus far retained a greater proportion of natural habitat than temperate regions. In any case, even tropical species do not track climate precisely (Chen et al., 2009).

1.2.3 In situ adaptation to climate change

In situ adaptation encompasses biochemical buffering, gene expression, phenotypic plasticity, behaviour and genetic adaptation (Peck, 2011). Adaptation is complex and largely unpredictable; hence it is rarely accounted for in models used to predict range shifts (Peck, 2011). This may be one of the reasons that species do not move as quickly as predicted.

Modifications in species' phenology represent the vast majority of documented adaptations to climate change in situ. Many of these examples come from temperate regions of the Northern hemisphere, where seasonality is the overarching determinant of species' phenology, and is itself dramatically altered by climate change (Bradshaw and Holzapfel, 2006). Specifically, spring has advanced and the growing season has lengthened. Organism responses include earlier breeding in animals such as birds and butterflies, earlier arrival of migratory birds, and earlier flowering in plants (Walther et al., 2002).

Responses such as physiological plasticity or genetic adaptation feature much less in the literature on in situ adaptation to climate change. This may signify a real scarcity of such changes in nature. The evolution of new forms that enable persistence in the same geographic range under a changing climate requires a species to become tolerant of a climatic regime to which it was previously intolerant, which seems unlikely (Parmesan, 2006). One could argue that selective pressures to evolve increased thermal tolerance would have been insufficient prior to present-day climate change. However, major evolution at the species level is not evident in the fossil record during the Pleistocene glaciation event, even though this comprised climate change of 5-10 times the magnitude of 20th Century warming (Parmesan, 2006).

While evidence for evolutionary responses to climate change is limited, this is not to say that evolution has no role to play. Where examples of such responses do exist, they underlie aforementioned ecological changes in phenology or dispersal (Parmesan, 2006). For example, Dutch great tits that display greater plasticity in their timing of reproduction are better able to match egg-laying to food availability – the peak of which has advanced as a result of climate change – and thus achieve greater fitness (Nussey et al., 2005). There are also practical explanations for the lack of documented evolutionary responses, since these adaptations are less intuitive and harder to document than ecological responses (O'Connor et al., 2012).

The literature discussed above fails to mention one additional and very significant tool that animals can employ to adapt to climate change – behaviour. All organisms ordinarily experience a range of temperatures, and so possess thermoregulatory behaviours that can also be deployed to mitigate the impacts of climate change. Chamois, for example, move to higher altitudes and reduce activity when temperature increases (Mason et al., 2014).

Habitats present a considerable degree of variation in microclimates, because of variation in microhabitat features (Scheffers et al., 2014b), slope and aspect (Suggitt et al., 2011). Behavioural plasticity allows animals to move into these microclimates (Scheffers et al., 2014b) and so track their optimal climate on a local scale. These so-called “microrefugia” are utilised by a variety of taxa around the world. In boreal forests of Finland, moose seek out the cooler microclimates of forests with higher and denser canopies, in response to high daytime temperatures (Melin et al., 2014). Similarly, in the tropics, possums choose the coolest tree hollows in which to den (Isaac et al., 2008), and herpetofauna of Singapore occupy microrefugia that not only largely avoid their critical thermal maxima (CT_{max}) – which is often exceeded in the wider macroclimate – but their microrefugia also heat less quickly than the macroclimate (Scheffers et al., 2014b).

1.3 Influence of land-use change

The most well-known interaction between climate change and land-use change is probably that the latter can cause the former, on a global scale, through the release of GHGs (IPCC, 2013). Deforestation marginally reduces the net radiative forcing that leads to global climate warming through decreases in surface albedo (IPCC, 2013). Climate change could also cause land-use change, such as through shifting the areas which are most climatically suited for agriculture (Opdam and Wascher, 2004).

In this review, however, I have focused on how organisms can adaptively respond to change. The question then becomes: how does land-use change influence an organism’s capacity to respond to climate change? On a regional scale under wholesale conversion, the answer

is relatively well-discussed. Namely, regional habitat loss creates barriers to climate-driven range shifts (Thomas et al., 2012). Recall that in response to climate change that has already happened, organisms have not moved as quickly as expected (Chen et al., 2009), and barriers to dispersal may contribute to this.

In situ adaptation may allow organisms to persist in habitats from which they are unable to move, or it may remove the need to move altogether; in either case, the influence of land-use change on in situ adaptation to climate change has not been elucidated. Given that many barriers to dispersal have already been introduced, and this will likely continue into the future, it is vital to facilitate adaptation to future climate change within the areas that species already occupy.

Most obviously, wholesale conversion of natural or semi-natural habitat appears to increase local daytime mean temperature (e.g. Wickham et al., 2012). Largely, this is caused by an increase in daily maximum temperature as a result of decreased interception by overhead vegetation of direct solar radiation (Xu et al., 2004). The effect is reversed at night when outgoing long-wave radiation is lost because of reduced interception by vegetation (Xu et al., 2004). An increase in mean temperature may exceed an organism's preferred body temperature, and so potentially lead to sublethal effects (du Plessis et al., 2012), but increasing maximum temperature generally poses the greater threat to organisms. Organisms can often acclimate to moderate increases in average temperatures (Peck et al., 2009), but if their critical thermal maximum is exceeded – even for a very short amount of time – this will cause death. Thus, species remaining in habitat after it has been converted are already likely to be under some amount of thermal stress, and future climate change may push temperatures beyond the range that they can tolerate through physiological plasticity.

Any increase in ambient temperature will ultimately increase the temperature of microclimates, and so potentially decrease their efficacy as thermal microrefugia for thermally stressed individuals. The extent to which microclimate utility is compromised depends upon the rate at which they warm alongside macroclimate warming. There is evidence from the tropics that this relationship is non-uniform, with microhabitat temperatures increasing only 0.11–0.66°C for every 1°C in the macroenvironment (Scheffers et al., 2014b). Asymmetry in warming rates will be influenced by factors that act to create the microclimate, such as the microhabitat (Scheffers et al., 2014b), slope, aspect or elevation (Suggitt et al., 2011). It is possible that microclimates could be entirely removed as a consequence of microhabitat removal (e.g. loss of some bird's nest fern species upon conversion of forest to oil palm plantation; Fayle et al., 2009) or extreme macroclimate warming (Caillon et al., 2014).

Wholesale conversion is very likely to impede the ability of persisting organisms to adapt to future climate change, but then few of the original species do persist through conversion (e.g.

Gibson et al., 2011; Katovai et al., 2012; Murphy and Romanuk, 2014) and — at least in the tropics — habitat degradation is far more pervasive. In particular, some 20% of the humid tropical biome experienced selective logging from 2000-2005 (Asner et al., 2009), whilst deforestation affected only 1.4% in the same period (Hansen et al., 2008). Although the habitat type broadly remains as ‘forest’, selective logging can be extremely disruptive. Indeed the term ‘selective’ is somewhat of a misnomer, meaning that particular species and stems (usually above a minimum trunk diameter) are targeted (Edwards et al., 2014b). These targets are typically the largest, oldest trees, the removal of which reduces canopy height and canopy density (Kumar and Shahabuddin, 2005; Okuda et al., 2003), and also fragments the forest canopy and opens up large gaps (Edwards et al., 2014b) that are often invaded by non-tree species, such as climbers and bamboo. Commercial selective logging also causes collateral damage, particularly where trees are connected by climbers (Schnitzer et al., 2004), as well as requiring roads and skid trails that bring further challenges for wildlife (Brodie et al., 2015; Laurance et al., 2014), and heavy machinery that result in soil compaction (Putz et al., 2008).

Since selective logging reduces canopy cover, just as deforestation does, so it is likely that the thermal regimes of degraded forest will be similarly altered. Moreover, there is already some indication that previously identified tropical microrefugia (in this case, leaf litter and soil; Scheffers et al., 2014b), are reduced by logging (Saner et al., 2009). Conversely, ground vegetation — another microrefugium (Scheffers et al., 2014b) — may be favoured by the release of pioneer species upon the creation of treefall gaps.

The impact of habitat degradation on species’ ability to persist under climate change is likely to be less profound than under wholesale conversion, simply because the amount of habitat change is less. However, a greater proportion of species found in undisturbed habitat remain in degraded habitat than in converted habitat (Edwards et al., 2011), and it is these species that are of primary conservation concern. Furthermore, degraded forests now represent a significant proportion of the humid tropical biome, and are therefore home to a significant proportion of all tropical forest species on Earth. The potential for these species to track climate change through dispersal is limited – there are barriers, such as hostile land-use types, as well as a shallow latitudinal temperature gradient (Colwell et al., 2008) and a potential lack of connected, higher elevation habitat (Scriven et al., 2015). Many tropical species will need to adapt to climate change within degraded forest, if they are to persist into the future. Therefore, although we do not yet fully understand the impact of any land-use change on the ability of tropical species to adapt *in situ* to climate change, I argue that we should first explore the impacts of habitat degradation, as a priority.

1.4 Thesis aims and rationale

1.4.1 Definitions

'Microhabitats' are fine-scale (mm to cm) features within a habitat, including leaf litter, dead-wood, tree holes and epiphytes within rainforest habitats. Each of these features will have its own 'microclimate' which may be different from the macroclimate that acts at the level of the whole habitat (m to ha). When microhabitat features offer a more desirable microclimate than the macroclimate, the features can be referred to as 'thermal microrefugia' ('microrefugia' henceforth).

1.4.2 Chapter 2 – A pantropical analysis of the impacts of forest degradation and conversion on local temperature

SUMMARY

1.4.3 Chapter 3 – A framework for quantifying fine-scale thermal heterogeneity in the field

SUMMARY

1.4.4 Chapter 4 – Tropical forests are thermally buffered despite intensive selective logging

SUMMARY

1.4.5 Chapter 5 – The impact of recent forest cover change on climate connectivity in the tropics

SUMMARY

Chapter 2

A pantropical analysis of the impacts of forest degradation and conversion on local temperature



Bornean horned frog (*Megophrys nasuta*).

2.1 Abstract

Temperature is a core component of a species' fundamental niche. At the fine scale over which most organisms experience climate (mm to ha), temperature depends upon the amount of radiation reaching the Earth's surface, which is principally governed by vegetation. Tropical regions have undergone widespread and extreme changes to vegetation, particularly through the degradation and conversion of rainforests. Since most terrestrial biodiversity is in the tropics, and many of these species possess narrow thermal limits, it is important to identify local thermal impacts of rainforest degradation and conversion. We collected pantropical, site-level (< 1 ha) temperature data from the literature to quantify impacts of land-use change on local temperatures, and to examine whether this relationship differed above-ground relative to below-ground and between wet and dry seasons. We found that local temperature in our sample sites was higher than primary forest in all human-impacted land-use types ($N = 113,894$ day-time temperature measurements from 25 studies). Warming was pronounced following conversion of forest to agricultural land (minimum +1.6°C, maximum +13.6°C), but minimal and non-significant when compared to forest degradation (e.g. by selective logging; minimum +1°C, maximum +1.1°C). The effect was buffered below-ground (minimum buffering 0°C, maximum buffering 11.4°C), whereas seasonality had minimal impact (maximum buffering 1.9°C). We conclude that forest-dependent species that persist following conversion of rainforest have experienced substantial local warming. Deforestation pushes these species closer to their thermal limits, making it more likely that compounding effects of future perturbations, such as severe droughts and global warming, will exceed species' tolerances. By contrast, degraded forests and below-ground habitats may provide important refugia for thermally-restricted species in landscapes dominated by agricultural land.

2.2 Introduction

It is well established that temperature is important in ecology, for everything from biochemistry, to physiology, to biogeography (Thomas et al., 2004; Kearney et al., 2009; Kingsolver, 2009; Puurtinen et al., 2015). Temperature is a key explanatory variable in species distribution models that predict the likely impacts of projected global climate change on biodiversity (e.g. Thomas et al., 2004). However, the majority of organisms experience temperature at much finer spatial scale (Gillingham, 2010; Suggitt et al., 2011) than assumed in species distribution models (often $> 100 \text{ km}^2$), and at local scales temperature is more dependent on local factors (Suggitt et al., 2011) than on regional or global atmospheric circulation (Oke, 1987; Davin and de Noblet-Ducoudré, 2010; Wiens and Bachelet, 2010; Pielke et al., 2011). One

such local factor is vegetation cover, which influences temperature through direct absorption and reflection of incident solar radiation (Oke, 1987; Murcia, 1995; Snyder et al., 2004) and through evapotranspiration, by determining the amount of thermal energy dissipated through the evaporation of water as opposed to a change in temperature (Oke, 1987; Findell et al., 2007; Lawrence and Vandecar, 2015).

Land-use change can profoundly influence vegetation cover. Current and future land-use change is concentrated in the tropics, where > 150 million hectares of forest was converted between 1980 and 2012 (Gibbs et al., 2010; Hansen et al., 2013) and 20% of the humid tropical biome was selectively logged from 2000 to 2005 (Asner et al., 2009). Previous studies, from a range of disciplines, demonstrate that land-use change in the tropics tends to increase temperature (Findell et al., 2007; Loarie et al., 2009; Davin and de Noblet-Ducoudré, 2010; Luskin and Potts, 2011; Pielke et al., 2011; Ramdani et al., 2014; Lawrence and Vandecar, 2015). This suggests severe consequences for global terrestrial biodiversity, most of which is found in tropical rainforests (Myers et al., 2000) and is thought to be especially sensitive to temperature change, owing to narrow thermal limits (Deutsch et al., 2008; Tewksbury et al., 2008; Kingsolver, 2009).

Additionally, while absolute warming from global climate change will be highest at the poles (IPCC, 2013), it is the tropics where relative warming will be greatest, with historically unprecedented temperatures occurring by 2050 (Mora et al., 2013). It is frequently stated that habitat fragmentation from land-use change will make it increasingly difficult for tropical species to track climate (Brook et al., 2008; Scriven et al., 2015), hampered by the poor dispersal ability of many tropical species (Van Houtan et al., 2007) and shallow latitudinal temperature gradients (Colwell et al., 2008). However, it is less commonly discussed that the baseline temperature onto which global climate predictions are projected might itself be dramatically higher in altered land-use types (Foster et al., 2011; Tuff et al., 2016).

To understand current and future consequences for tropical biodiversity from land-use change and climate change it is vital to understand thermal change at the scale at which temperature is experienced by organisms (Wiens and Bachelet, 2010; Gillingham, 2010; Suggitt et al., 2011). Prior evidence for local warming in the tropics as a result of land-use change originates from global General Circulation Models (Findell et al., 2007; Davin and de Noblet-Ducoudré, 2010; Pielke et al., 2011) and observational studies focused on particular locations, such as Brazil (Loarie et al., 2009), Malaysia (Luskin and Potts, 2011) and Indonesia (Ramdani et al., 2014). While General Circulation Models are limited in biological relevance by their coarse spatial resolution, observational studies are limited in generality by the site-specificity required to achieve their fine spatial resolution (Li et al., 2015). Any studies that utilise meteorological station data have limited biological relevance because stations are specifically positioned to minimise the influence of the very same local

characteristics that are important to local biota, such as vegetation cover, slope and aspect (Frenne and Verheyen, 2016).

There are several conditions under which local warming due to land-use change might be ameliorated, which have yet to be explicitly tested. We hypothesise that low intensity forest degradation, including commercial selective logging, fragmentation and forest regrowth (Lewis et al., 2015), will correspond to relatively little net change in vegetation, and hence a smaller difference in temperature. Any warming effects of land-use change are likely reversed at night, as habitats with relatively low vegetation cover will radiate heat back to the atmosphere more freely (Oke, 1987; Chen et al., 1995). Water availability is fundamental in determining how much thermal energy can be dissipated through evaporation, and so we also expect that warming would be less during the wet season given the high water availability (and more cloudy weather) relative to dry season, and below-ground relative to above-ground. In the latter case, even when water availability is very low, soil buffers external temperature change (Scheffers et al., 2014a) because soil has a higher specific heat capacity than air, and thus requires a greater change in thermal energy to achieve the same change in temperature (Oke, 1987).

In the present study, we carry out analyses of published data to test the effect of land-use change on local temperature across the tropics. We collected local, in situ temperature data from the literature for paired sites (< 1ha) that differed in land-use type. Categories of land use we studied were primary forest, degraded forest, plantation, pasture and cropland (Table 2.1; modified from Extended Data Table 1 in Newbold et al., 2015). We examine how land-use change affects day-time temperature at fine-scale spatial resolution, and we quantify the effects of: (1) forest conversion compared with forest degradation; (2) below-ground compared to above-ground; and (3) wet season conditions compared to the dry season. We focus on day-time temperatures because few studies collected night-time temperature, although we also separately test how the latter is impacted by land-use change for the subset of studies able to provide these data. Recent studies also highlight the importance of climatic extremes for species' survival (e.g. Deutsch et al., 2008; Christidis et al., 2013), hence we conduct additional analyses for those studies that provide these data.

2.3 Methods

2.3.1 Literature search

We collated temperature data from peer-reviewed literature using ISI Web of Knowledge. The search terms were: “tropic*” AND (“temperature” OR “local climate”) AND (“land use”

Land-use type	Definition
Primary forest	Forest where any disturbances identified are very minor (e.g. a trail or path) or very limited in the scope of their effect (e.g. hunting of a particular species of limited ecological importance).
Degraded forest	Forest with one or more disturbances ranging from moderate intensity/breadth of impact (e.g. selective logging and bushmeat extraction), to severe intensity/breadth of impact (e.g. regrowth after clear-felling).
Plantation	Extensively managed or mixed timber, fruit/coffee, oil-palm or rubber plantations.
Cropland	Farming for herbaceous crops, without presence of livestock.
Pasture	Farming of livestock.

Table 2.1: Land use classification definitions (modified from Extended Data Table 1 in Newbold et al. (2015)).

OR landuse OR “land cover” OR landcover OR urban* OR city OR cities OR agri* OR arable OR built* OR metropol* OR deforest* OR forest) AND (*change OR expansion OR growth OR encroach OR modif* OR conversion OR convert**). We refined the search output by including only the following research areas: “environmental sciences ecology”, “remote sensing”, “agriculture”, “biodiversity conservation”, “forestry”, “urban studies”; this returned 1,372 published studies. Excluding book chapters (21) and articles that were deemed irrelevant based on the title (298) or abstract (484) reduced the total to 525 articles. We reviewed each of these articles manually. Additional unpublished data (two studies) were also provided by co-authors (P.G., L.K.G.).

2.3.2 Selection criteria

All data originated from studies with at least two different sites in at least two different land-use types. Sites were located between 23.44° North and South, and the natural vegetation type was defined by authors as forest. Sites were fully contained within the land-use type of interest and positioned beneath the canopy (where applicable). Within a single study, sampling methodology was consistent across all sites and land-use types. Differences between studies, such as soil depth or the use of radiation shields for dataloggers, were accounted for by the analytical approach (see ‘Statistical analysis’). All sites within a single study differed in elevation by no more than 150 m.

Data collected through remote sensing or from meteorological stations were excluded, because they are inherently unrepresentative of local climatic conditions in forested areas. Meteorological stations are established to strategically avoid the very same local conditions in which we are primarily interested (Frenne and Verheyen, 2016). Acceptable methods of tem-

perature measurement were those taken in situ, using a thermometer, temperature probe or temperature dataloggers. We included temperature data reported as an average across multiple spatial replicates for each land-use type within a study, provided that (1) the area over which data were averaged and (2) the number of spatial replicates within this area was consistent across different land-use types within the study. We set the maximum area over which data could be averaged as 1 ha, to ensure our study focused on temperature changes at a fine spatial scale. Aggregated spatial replicates of measurements within 1 ha were considered as a single site. Where raw data were provided, a single site comprised the individual point at which measurements were taken.

We included data reported as an average across multiple temporal replicates within a study site, provided that (1) the period of time over which data were averaged and (2) the number of temporal replicates within this period was within either day or night and was consistent across different sites within the study. We set the maximum time period over which data could be averaged as 183 days (half a year), provided this time period was entirely within either the dry season or the wet season, as defined by the authors. Aggregated temporal replicates within a study site were recorded as a single observation. Where raw data provided more than one measurement per day, we calculated a daily mean for each study site (between sunrise and sunset only), each of which represented a distinct observation. If night-time data were available, we applied the same approach for observations measured between sunset and sunrise. For those studies providing more than one temperature observation per day or night, we also calculated temperature minima and maxima for the time period(s) available (day or night).

2.3.3 Data collation

Where possible, temperature data were extracted from text, tables or graphs in the publication. Data in graphs were extracted using Digitizelit (www.digitizeit.de; Scheffers et al., 2014b). We also extracted: site coordinates and elevation; site descriptions of sufficient detail to enable categorisation into land-use types; season (dry or wet); time of measurements (day or night); and whether temperature was recorded above- or below-ground. In many cases, temperature data or methodological information were reported inadequately or not at all, in which case authors were contacted directly for information.

In some cases we were unable to retrieve all the required methodological information, and made estimates. We estimated coordinates from Google Earth, based on detailed descriptions in the text, and we estimated elevation from coordinates using a global digital elevation map at 3-arc second resolution (NASA, 2017). Unless authors had explicitly stated that data were collected during day or night, we determined this by comparing the time of

data collection to the time of sunrise and sunset, estimated from the date of collection and the site coordinates using solar calculations developed by the National Oceanic and Atmospheric Administration (NOAA, nd), and implemented in R using custom functions (<https://github.com/rasenior/SolarCalc>). Our main analyses use day-time temperature only because very few studies considered night-time temperature, though we retained night-time temperature data where they were available for an additional, simplified analysis.

We assigned categories of land use based on Extended Data Table 1 in Newbold et al. (2015), which comprise ‘primary forest’, ‘degraded forest’ (renamed from ‘secondary’), ‘plantation’, ‘pasture’ and ‘cropland’ (Table 2.1). ‘Urban’ could not be included due to insufficient data.

2.3.4 Statistical analysis

Each data point in our main analysis comprised an observation of day-time temperature in a particular land-use type. We modelled each temperature observation against land-use type using a linear mixed effects model, implemented in the `lme4` package (Bates et al., 2015) in R (R Core Team, 2017). Studies differed substantially in methodology and location, hence the identity of the study from which data were taken was included as a random intercept term. Exploratory plots suggested that the slope of the relationship between land-use type and temperature, as well as the intercept, varied by study. The decision to include a random slope of land-use type, with respect to study identity, was determined using AIC with the full fixed effects structure (Zuur, 2009). Fixed effects were then selected using backward stepwise model simplification (Zuur, 2009), with the following categorical variables: land-use type (five levels); position relative to ground level (above- or below-ground); and season (dry or wet season), as well as pairwise interactions between land-use type and the latter two variables. We tested interactions using likelihood ratio tests, and then removed interactions to test main effects independently. For a subset of studies with suitable data, we used an analogous approach with only land-use type included as a fixed effect, to model nocturnal temperature and also temperature minima and maxima (for day-time and night-time separately).

Model estimates of local temperature are presented relative to the model estimate for primary forest (above-ground and in the dry season). Both the position relative to ground level and seasonality interacted with land-use change to influence local temperature, but for clarity we discuss each explanatory variable separately. As such, temperature differences between primary forest and altered land-use types are averages across all combinations of position and season. The influence of position on these thermal differences is presented as an average across seasons, and the influence of seasonality is an average across positions.

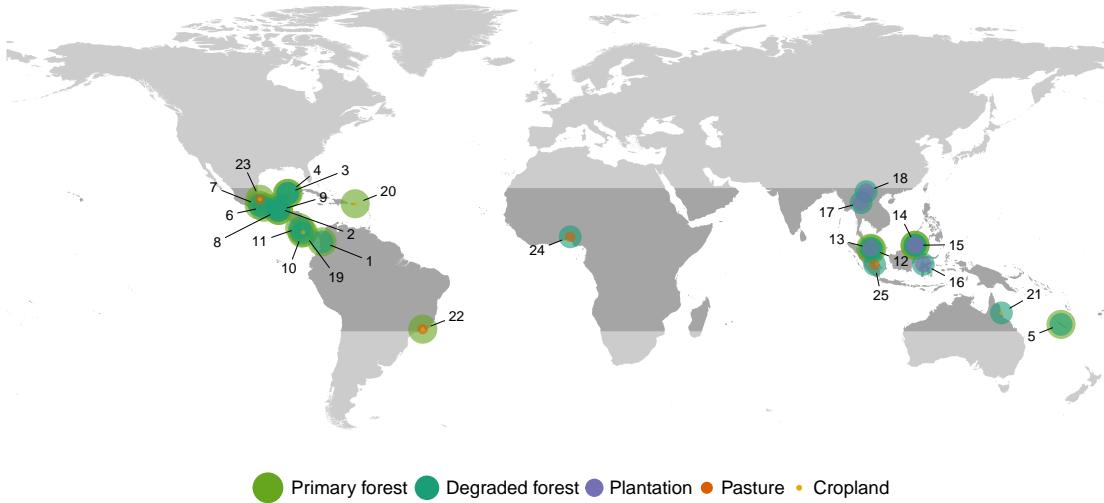


Figure 2.1: Locations of the 25 studies contributing data to the analyses. Point labels correspond to the study number in Table 1. The shading and size of concentric points corresponds to different land-use types, to indicate the data provided by each study.

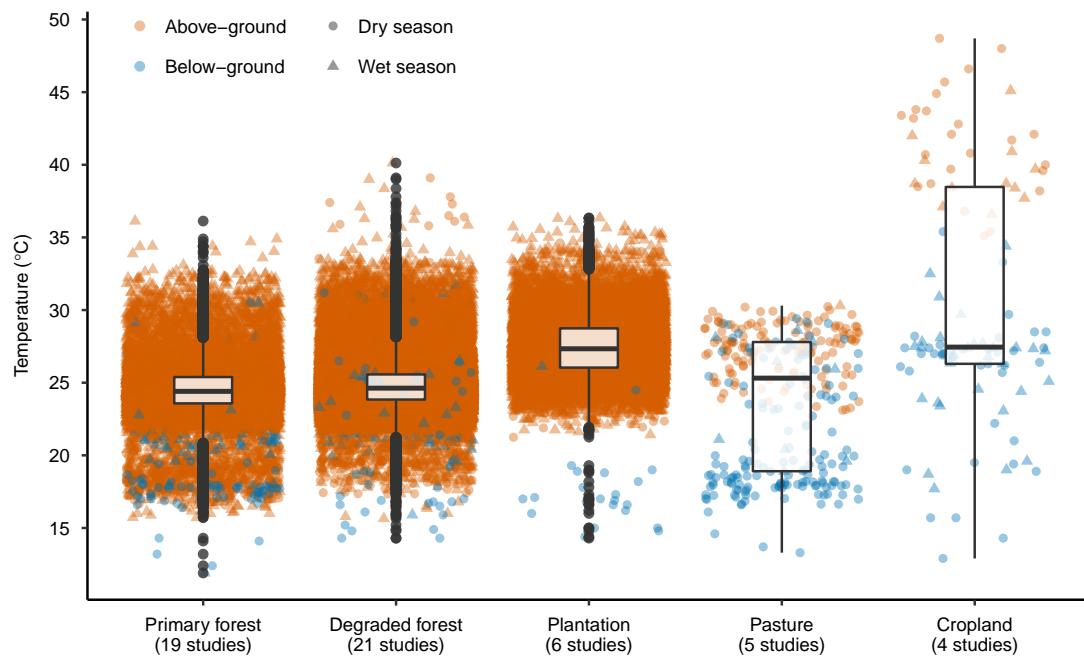


Figure 2.2: Raw day-time temperature against land-use type, across all studies contributing data to the analyses (plotted by study in Figure A.1). Point shading indicates temperatures measured above-ground (orange) or below-ground (blue), and different symbols indicate temperatures measured during the dry season (circles) or wet season (triangles).

2.4 Results

In total, 25 studies met the criteria for inclusion (Table 2.2). Studies spanned 12 countries, across every continent within the tropics (Figure 2.1), and provided 113,894 observations of day-time temperature (Figure 2.2 and Figure A.1). Most observations represented either a single temperature observation within, or mean temperature across, a single day at the point location where measurements were taken. Six studies reported temperature at a coarser temporal resolution (mean = 107 days; minimum = 14 days; maximum = 183 days), and six studies reported temperature at a coarser spatial resolution (mean = 527 m²; minimum = 64 m²; maximum = 1,000 m²). The maximum elevational difference between sites within a single study ranged from 0 to 141 m (mean = 33 m), and site elevation was random with respect to land-use type (LMM, $X^2 = 19.33$, df = 14, P > 0.05; Figure A.2). We were also able to obtain 113,459 night-time temperature observations (including temperature extremes) from 10 studies, plus 113,230 observations of day-time temperature extremes from 11 studies; but none of these data were collected in cropland or pasture.

In all cases, the final model included a random slope for land-use type ('LUT') and random intercept with respect to the identity of the study ('studyID') from which data originated. The final model of day-time temperature ('temp_day') included land-use type, position relative to ground level ('position') and season, as well as pairwise interactions between land-use type and the latter two fixed effects:

```
lmer(temp_day ~ LUT*position + LUT*season + (LUT|studyID))
```

The final models of (1) night-time temperature, and temperature extremes (minimum and maximum) (2) during the day and (3) during the night, all had the same model structure, with land-use type as the only fixed effect:

```
lmer(temp ~ LUT + (LUT|studyID))
```

2.4.1 Effect of land-use change

Altered land-use types were substantially hotter than primary forest (LMM, $X^2 = 29.49$, df = 4, P < 0.001; Table 2.3; Figure 2.3), and the magnitude of the warming broadly matched the intensity of vegetation change associated with each land-use type. Thus, degraded forests in our sample were the most similar to primary forest with an average difference of only +1.1°C, which was not statistically significant based on 95% confidence intervals (Figure 2.3). By contrast, converted habitats in our dataset – plantation, pasture and cropland – were, on average, hotter than primary forest by 2.7°C, 6.2°C and 7.6°C, respectively. Results were

Study	Country	Land-use type				Position	Season
		Primary forest	Degraded forest	Plantation	Pasture		
1. González del Pliego (Unpublished data)	Colombia	X	X			X	X
2. González-Dí Pierro et al. (2011)	Mexico	X	X			X	X
3. Goode (Unpublished data)	Mexico	X	X			X	X
4. Goode and Allen (2009)	Mexico	X	X			X	X
5. Ibanez et al. (2013)	New Caledonia	X	X			X	X
6. Lebravia-Trejos et al. (2011)	Mexico	X	X			X	X
7. Negrete-Yankelevich et al. (2007)	Mexico	X	X			X	X
8. Santos (2011)	Mexico	X	X			X	X
9. Santos and Benítez-Malvido (2012)	Mexico	X	X			X	X
10. Sonnleitner et al. (2009)	Costa Rica	X	X			X	X
11. Wood and Lawrence (2008)	Costa Rica	X	X			X	X
12. Yashiro et al. (2008)	Malaysia	X	X			X	X
13. Adachi et al. (2006)	Malaysia	X	X			X	X
14. Hardwick and Orme (2016)	Malaysia	X	X			X	X
15. Hardwick et al. (2015)	Malaysia	X	X			X	X
16. Klein et al. (2002)	Indonesia	X	X			X	X
17. Wanglu et al. (2013)	Thailand	X	X			X	X
18. Werner et al. (2006)	China	X	X			X	X
19. Holl (1999)	Costa Rica	X				X	X
20. Liu and Zou (2002)	Puerto Rico	X				X	X
21. King et al. (1998)	Australia	X				X	X
22. Badejo et al. (2004)	Brazil	X				X	X
23. Campos (2006)	Mexico	X				X	X
24. Badejo (1990)	Nigeria	X				X	X
25. Furukawa et al. (2005)	Indonesia	X				X	X

Table 2.2: Summary of the 25 studies contributing data to analyses. Study number corresponds to point labels in Figure 2.1. Crosses indicate the land-use types, position(s) relative to ground level and season(s) considered by each study.

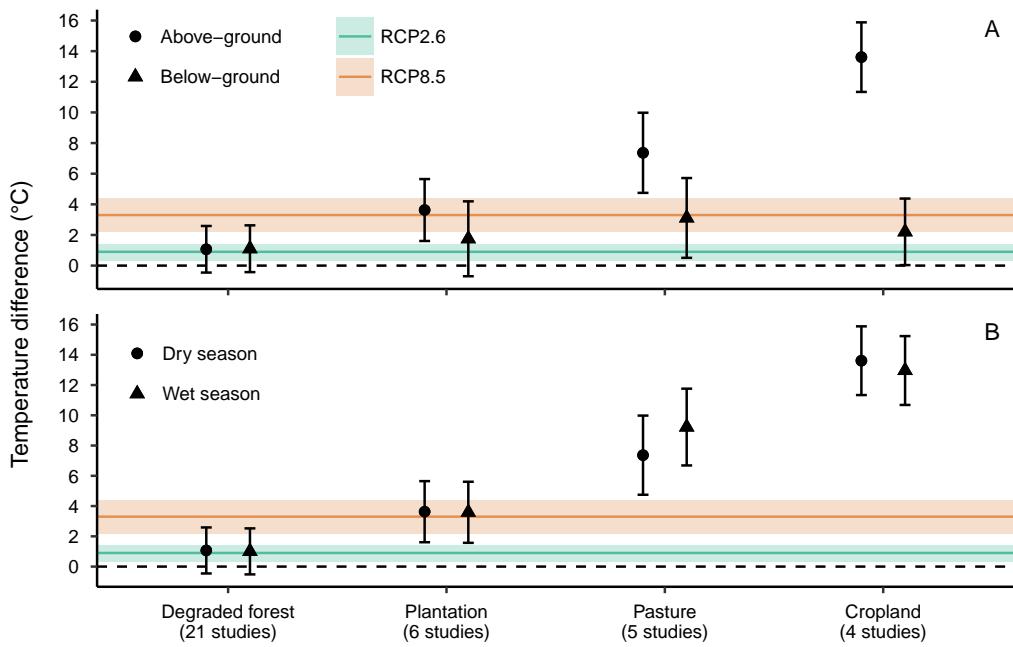


Figure 2.3: Model estimates of local day-time temperature in altered land-use types relative to primary forest (depicted by the black dashed line). In Panel A, different symbols denote position relative to the ground (above-or below-ground), and the season is held at the reference level (dry season). In Panel B, different symbols denote the season (dry or wet), and the position relative to the ground is held at the reference level (above-ground). Error bars are 95% confidence intervals. Solid lines indicate projected warming in the tropics for the period 2081–2100 compared to the period 1986–2005, as a result of global climate change (IPCC, 2013). Shaded bands indicate 5%–95% ranges from the distribution of the climate model ensemble. Colors represent the lowest and highest warming scenarios (RCP2.6 and RCP8.5, respectively).

robust to resampling from studies that provided disproportionate numbers of observations (section A.1; Figure B.3).

Night-time temperature, and day-time and night-time temperature extremes, showed varying results relative to primary forest in the two altered land-use types for which data were available: degraded forest and plantation. In all cases, sample sizes were very limited and confidence intervals were large, hence results should be interpreted with caution. Night-time temperature in degraded forest and plantation did not differ from that of primary forest (LMM, $\chi^2 = 2.09$, $\text{df} = 2$, $P > 0.05$; Figure A.4), and neither did night-time minimum temperature (LMM, $\chi^2 = 2.31$, $\text{df} = 2$, $P > 0.05$; Figure A.5D). Maximum night-time temperature was slightly higher overall in degraded forest and plantation compared to primary forest (LMM, $\chi^2 = 6.35$, $\text{df} = 2$, $P < 0.05$; Figure A.5C), although pairwise differences were not statistically significant according to 95% confidence intervals. There was no difference between primary forest and degraded forest and plantation in terms of day-time maximum temperature (LMM, $\chi^2 = 4.87$, $\text{df} = 2$, $P > 0.05$; Figure A.5A), or day-time minimum temperature (LMM, $\chi^2 = 4.60$, $\text{df} = 2$, $P > 0.05$; Figure A.5B).

2.4.2 Above- versus below-ground

The warming effect of land-use change was much stronger above-ground than below-ground (LMM, $X^2 = 1115$, df = 4, P < 0.001; Table 2.3; Figure 2.3A). The average difference between the local temperature of altered land-use types and primary forest was greater if measured above-ground rather than below-ground, by 1.9°C in plantation, 4.3°C in pasture, and 11.4°C in cropland. In degraded forest, the temperature relative to primary forest was very similar above- (+1°C) and below-ground (+1.1°C). Notably, the buffering effect below ground was so great that any difference between primary forest and impacted land uses was effectively negated in all land-use types but pasture (based on 95% confidence intervals; Figure 2.3A).

2.4.3 Dry versus wet season

Seasonality had some influence on the relationship between land-use change and temperature (LMM, $X^2 = 14.91$, df = 4, P < 0.01; Table 2.3; Figure 2.3B), but the direction of the interaction varied by land-use type, and in all cases the effect size was very small. In degraded forest and plantation, seasonality had no appreciable effect on temperature relative to primary forest (dry vs. wet season: +0.1°C in both degraded forest and plantation). In contrast, the temperature difference between pasture and primary forest was 1.9°C greater in the wet versus dry season, while in cropland the differential was 0.6°C greater in the dry versus wet season.

2.5 Discussion

Our results show that land-use change increases local temperature in the tropics (Figure 2.3). In all conditions where this relationship was evident, the temperature rise due to land-use change exceeded that predicted for the tropics by the end of the 21st Century under the minimum climate warming scenario (+0.9°C in RCP2.6; IPCC, 2013), and frequently also exceeded the maximum warming scenario (+3.3°C in RCP8.5; IPCC, 2013). Previous studies show that land-use change tends to increase local temperature (e.g. Findell et al., 2007; Loarie et al., 2009; Davin and de Noblet-Ducoudré, 2010; Luskin and Potts, 2011; Ramdani et al., 2014; Tuff et al., 2016) but this is the first study, to our knowledge, that demonstrates this effect across many locations in the tropics at a site-level resolution (< 1 ha), considering multiple modes of land-use change concurrently, and comparing the relationship above- and below-ground and between wet and dry seasons.

Land-use type	Position	Season	Temp. vs. PF	Lower CI	Upper CI	LUT mean	Position mean	Position effect (AG-BG)	Season mean	Season effect (dry-wet)
Degraded forest	AG	Dry	1.1	-0.5	2.6	AG	1		Dry	1.1
		Wet	1	-0.5	2.5	1.1	BG	1.1	0.1	Wet
	BG	Dry	1.1	-0.4	2.6					
		Wet	1	-0.5	2.6					
Plantation	AG	Dry	3.6	1.6	5.6	AG	3.6		Dry	2.7
		Wet	3.6	1.6	5.6	2.7	BG	1.7	1.9	Wet
	BG	Dry	1.8	-0.7	4.2					
		Wet	1.7	-0.7	4.2					
Pasture	AG	Dry	7.4	4.7	10	AG	8.3		Dry	5.2
		Wet	9.2	6.7	11.8	6.2	BG	4	4.3	Wet
	BG	Dry	3.1	0.5	5.7					
		Wet	5	2.4	7.5					
Cropland	AG	Dry	13.6	11.3	15.9	AG	13.3		Dry	7.9
		Wet	13	10.7	15.2	7.6	BG	1.9	11.4	Wet
	BG	Dry	2.2	0	4.4					
		Wet	1.6	-0.6	3.7					

Table 2.3: Model estimates (with 95% confidence intervals) of local day-time temperature in altered land-use types relative to primary forest (PF), with respect to position relative to ground level and season. 'Position effect' refers to the difference between temperature measured above-ground (AG) versus below-ground (BG), averaged across seasons. 'Season effect' refers to the difference between temperature measured in the dry season versus the wet season, averaged across positions. All figures are quoted in °C.

2.5.1 Thermal differences between land-use types

Human-impacted land-use types are likely hotter than intact primary forest because of changes in evapotranspiration and the amount of solar radiation reaching the Earth's surface (Oke, 1987; Findell et al., 2007; Davin and de Noblet-Ducoudré, 2010). Degradation and deforestation cause a lowering and thinning of the canopy, and reduction in rooting depth, leaf area index and surface roughness, all of which reduce evapotranspiration (Okuda et al., 2003; Snyder et al., 2004; Kumar and Shahabuddin, 2005; Findell et al., 2007; Davin and de Noblet-Ducoudré, 2010; Hardwick et al., 2015), and thereby increase temperature (Oke, 1987; Foley et al., 2005). Changes to canopy architecture and a reduction in the number of sub-canopy vegetation strata also cause warming by increasing the amount of solar radiation reaching the ground (Oke, 1987; Murcia, 1995). Our land use categories encompass a spectrum of vegetation change, from relatively little change in degraded forests (where some trees and a closed canopy are maintained) to maximal change in pasture and cropland (where trees are replaced with herbaceous plants). Accordingly, degradation had the smallest average effect (+1.1°C), followed by plantation (+2.7°C), and then pasture (+6.2°C) and cropland (+7.6°C). We expected that the same mechanisms underlying the warming effect of land-use change would also result in increased day-time temperature extremes and decreased night-time temperatures in altered land-use types, relative to primary forest (Oke, 1987; Chen et al., 1995). Unfortunately, the data available were very limited, including only three of the five land-use types (primary forest, degraded forest and plantation), and resulting in extremely large confidence intervals (Figure B.3 and S4). We urge caution when interpreting our results, which suggested either no effect or an extremely weak effect of land-use change on temperature extremes and night-time temperature; clearly more data are needed to reliably test these relationships.

2.5.2 Interaction with position relative to ground level and seasonality

We found that local warming effects of tropical land-use change are negated below-ground, despite the strength of the relationship above-ground (Table 2.3; Figure 2.3A). This can largely be attributed to the higher specific heat capacity of soil compared to air (Oke, 1987). Greater availability of water may also play a role, permitting thermal energy to be dissipated through the evaporation of water rather than increasing temperature (Oke, 1987; Davin and de Noblet-Ducoudré, 2010; Christidis et al., 2013). We expected the latter effect to result in increased buffering during the wet season (cf. Findell et al., 2007; Davin and de Noblet-Ducoudré, 2010), but instead we found that seasonality had a very limited influence on temperature relative to primary forest (Table 2.3; Figure 2.3B). The strongest influence was in pasture, where the effect of land-use change was greater in the wet season.

Potentially longer grass in pasture in the wet season could decrease albedo compared to pale exposed soil in the dry season, while the same pattern could be avoided in cropland through dry season irrigation. That said, pasture and cropland had the least data of all land-use types, and we advise that these results be interpreted with caution.

2.5.3 Implications for biodiversity

For tropical biodiversity, there are several key implications of our findings. Firstly, forest species persisting through forest conversion have already experienced thermal change similar, if not greater, in magnitude to that predicted by global climate change (IPCC, 2013). Historically the tropics have experienced relatively stable climatic conditions (Mora et al., 2013) and tropical species possess narrow thermal niches, with many already occupying the upper bounds of that niche (Deutsch et al., 2008; Tewksbury et al., 2008; Freeman and Freeman, 2014; Sunday et al., 2014). Dispersal towards more favourable climatic conditions is limited by low dispersal ability (Van Houtan et al., 2007), a scarcity of suitable destinations (Colwell et al., 2008), and the necessity to pass through an increasingly hostile land-use matrix to reach target habitat (Thomas et al., 2004; Brook et al., 2008; Scriven et al., 2015). There is already some evidence that higher temperatures in the tropics are associated with lower species abundance (e.g. for arthropods: Foster et al., 2011), and there are also fitness costs associated with long-term persistence in suboptimal climatic conditions (du Plessis et al., 2012; Gunderson and Leal, 2016). Without any further temperature change some species persisting in converted environments may already be committed to extinction, particularly species that are unable to utilise microhabitats with favourable microclimates (Scheffers et al., 2014a; González del Pliego et al., 2016). Under predicted climate change, increasing average temperature and the increasing frequency and intensity of droughts (Chou and Lan, 2012; IPCC, 2013) will likely push many species beyond their upper thermal limits, especially in heavily degraded or converted habitats.

That said, we find several circumstances where warming through land-use change is mitigated. Degraded forests were not significantly hotter than primary forests (according to 95% confidence intervals; Figure 2.3). This is encouraging because degraded forests are likely to become the most widespread land-use type in future (Hurtt et al., 2011), and many studies have demonstrated their capacity to retain species of conservation concern (Edwards et al., 2011; Gibson et al., 2011; Putz et al., 2012; Edwards et al., 2014b). For all altered land-use types, the warming effect was limited below-ground, highlighting a crucial thermal refuge for species that are able to occupy the soil, and suggesting that above-ground microhabitats, such as deadwood and epiphytes, might fulfil a similar role (Scheffers et al., 2014a; González del Pliego et al., 2016). Thermal refugia may not be a permanent solution for avoiding climate change, and sensitive species may find that even relatively cold microhabitats are

still too hot (e.g. below-ground in pasture was 4°C warmer than primary forest; Table 2.3; Figure 2.3), but refugia could at least provide species with more time to respond to suboptimal climatic conditions (Hannah et al., 2014).

2.5.4 Caveats and knowledge gaps

By collating site-level data reported from the literature, we were able to achieve high geographical coverage and fine spatial resolution that is lacking in previous studies, but this technique is biased by the availability of data towards particular regions and land-use types (Figure 2.1), and relies heavily on substituting space for time, which can misrepresent anthropogenic impacts (França et al., 2016). In particular, there was only one study located in Africa, and Southeast Asian studies provided all of the plantation data and no cropland data. Future research should seek to explicitly consider how tropical land-use change affects: vegetation structure (e.g. using Leaf Area Index cf. Hardwick et al., 2015), relative humidity (Luskin and Potts, 2011; Ewers and Banks-Leite, 2013), nocturnal climatic conditions (Chen et al., 1995; Dubreuil et al., 2011), extremes of temperature (Christidis et al., 2013), and rates of temperature change (Scheffers et al., 2014a); preferably at a range of spatiotemporal scales (Wiens and Bachelet, 2010) and with a standardised methodology to simplify comparisons across studies.

2.5.5 Conclusions

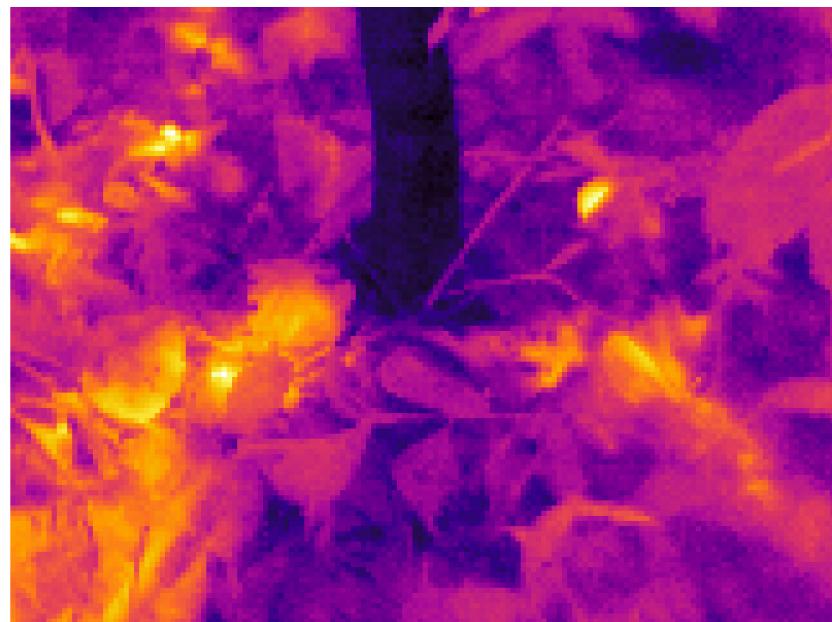
Our study confirms that tropical land-use change leads to warming at a local scale (< 1 ha) across the tropics, of a magnitude comparable to that predicted from global climate change. We find pantropical evidence that the effects of land-use change on temperature are ameliorated below-ground, and absent in degraded forests. Many studies collect site-level climate data, and through sharing of these data and collaboration between scientific disciplines, there is much that can be done to integrate theoretical and empirical understanding of the processes that govern climate at different scales. This will greatly advance our knowledge of potential synergies between two of the greatest drivers of biodiversity loss – land-use change and climate change – and highlight mitigating factors, such as thermal microrefugia, which could be a pragmatic focus for conservation management.

2.6 Data and R code

The collated dataset can be found on Dryad (<https://doi.org/10.5061/dryad.g4000>). Note that in many cases these data were aggregated for analyses. For finer resolution data please refer to the original data sources. R functions used to estimate time of sunset and sunrise can be downloaded from GitHub (<https://github.com/rasenior/SolarCalc>).

Chapter 3

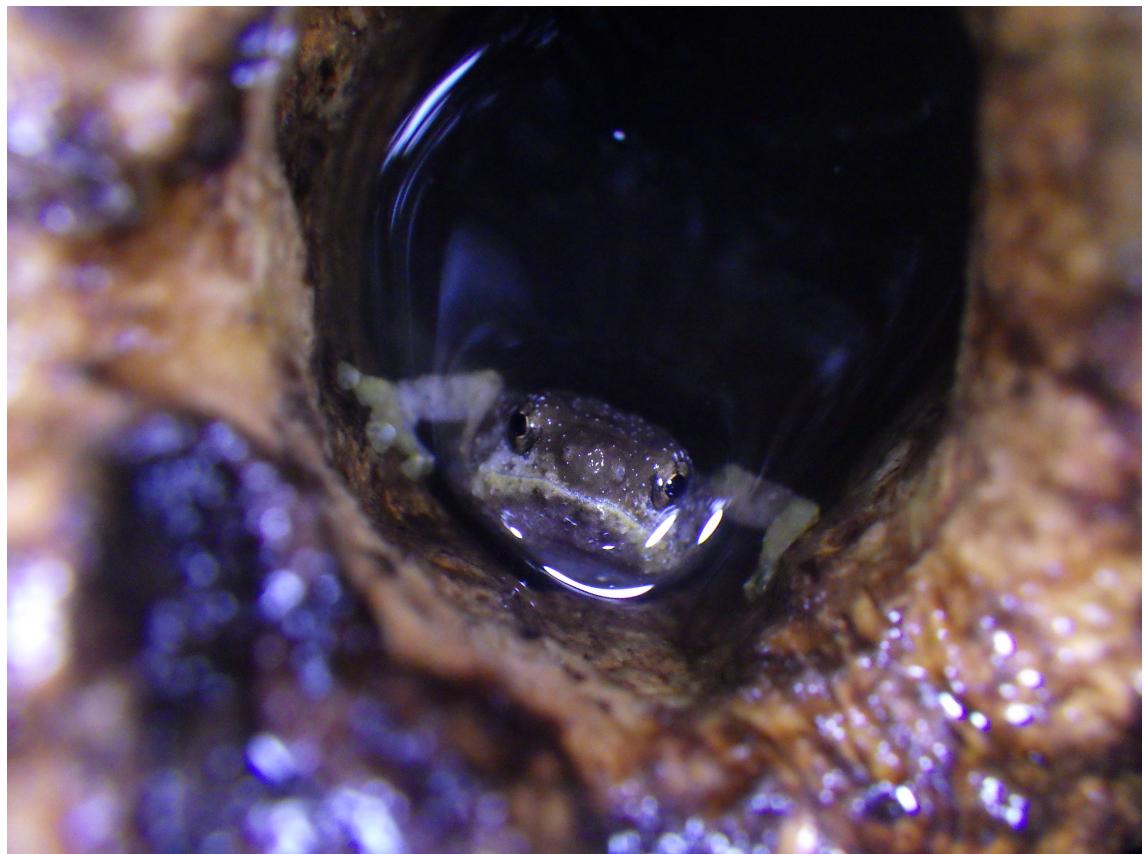
A framework for quantifying fine-scale thermal heterogeneity in the field



Thermal image of rainforest floor.

Chapter 4

**Tropical forests are thermally buffered
despite intensive selective logging**



Bornean tree hole frog (*Metaphrynellla sundana*).

4.1 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, m to ha) and the ‘microclimate’ (climate at a fine-scale, mm to m, that is distinct from the macroclimate); (2) thermal stability of microclimates (e.g. variation in daily temperatures); and (3) 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 information from dataloggers placed inside deadwood, tree holes and leaf litter. Although major differences in forest structure remained 9–12 years after repeated selective logging, we found that logging activity had very little effect on thermal buffering, in terms of macroclimate and microclimate temperatures, and the overall availability of microclimates. For 1°C warming in the macroclimate, temperature inside deadwood, tree holes and leaf litter warmed slightly more in primary forest than in logged forest, but the effect amounted to less than 0.1°C difference between forest types. 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.

4.2 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 and Laurance, 2013). Protecting selectively logged forests may be a cost effective way to retain tropical biodiversity (Edwards et al., 2014b), 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., 2017). 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; Khalil 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 m to ha) by moving locally into ‘microclimates’: climate at a fine-scale, mm to m, that is distinct from the macroclimate (Scheffers et al., 2014a,b; 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., 2017). Indeed, the vast proportion of terrestrial species are small in size, flat in shape, or thermoregulate via contact with vegetation, and so it is important to consider microclimates close to, and including, the surfaces on which these species live (Kaspari et al., 2015; Scheffers et al., 2017).

The most informative fine-scale temperature data are derived from point measurements that are highly replicated in both space and time, and demonstrate that loss of vegetation cover causes local daytime warming (Senior et al., 2017; Ewers and Banks-Leite, 2013; Hardwick et al., 2015; González del Pliego et al., 2016). Selective logging affects vegetation by lowering and thinning the canopy, reducing leaf area index (Hardwick et al., 2015; Ewers et al., 2015) and the number of vegetation strata, and creating large forest gaps (Okuda et al., 2003; Kumar and Shahabuddin, 2005). As such, the understorey of logged forests likely receives a greater amount of solar radiation, partitioned increasingly as direct rather than diffuse radiation (Oke, 1987), although these impacts diminish rapidly as selectively logged forests recover (Asner et al., 2004). The most tangible impact on the local climate could be an over-

all increase in the day-time temperature of logged forests, increasing the necessity for thermal buffering. Simultaneously, the potential for thermal buffering may be compromised if forest 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. Conversely, enhanced air-mixing in more open logged forests might create cooler and less variable microclimates. 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., 2017) by selective logging, implying that forest quality alters thermal environments.

A key novel question that we address in this paper is whether vegetation changes following commercial selective logging reduce the potential for thermal buffering. We focused on cool microclimates in the understorey only (climate at mm to 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,b; González del Pliego et al., 2016). We determined thermal buffering potential according to: (1) the microclimate temperature relative to that of the macroclimate; (2) the daily variation in microclimate temperature; and (3) the availability of microclimates in space. The first two are roughly measures of microclimate ‘quality’ – they examine how effectively an organism will be buffered from macroclimate warming, assuming it moves into the microclimate. The third captures the likelihood that organisms can locate and move into suitable microclimates, according to the occurrence, distribution and thermal diversity of microclimates within the habitat (Sears et al., 2011; Caillon et al., 2014). We predicted that logged forests would be structurally distinct from primary forest, and we tested the hypothesis that this would lead to reduced thermal buffering potential and, subsequently, impaired ability of temperature-sensitive species to respond *in situ* to excessively high temperatures in the wider macroclimate.

4.3 Materials and Methods

4.3.1 Study area

Sampling took place 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

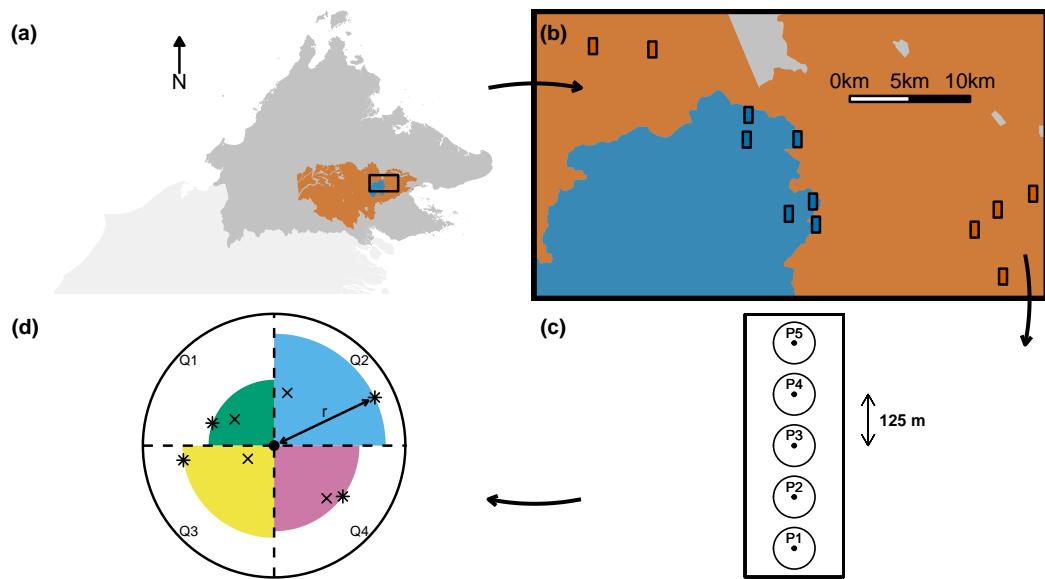


Figure 4.1: Study location in Malaysian Borneo (a), and distribution of sites (b): six sites in primary forest (blue) and six sites in logged forest (orange). Each site comprised five plots along an existing transect, with plot centres separated by 125 m (c). Tree and sapling stand basal area was calculated 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.

study, we sampled sites in forest that had been commercially selectively logged twice (Ulu Segama-Malua Forest Reserve, $4^{\circ}57'42.8''N$, $117^{\circ}56'51.7''E$). 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 m 3 of timber per hectare (Fisher et al., 2011; Edwards et al., 2014a). 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 m 3 /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 had an average density of < 10 trees per hectare with a D.B.H. greater than 40 cm (Reynolds et al., 2011). The area has been recovering naturally since logging operations ceased. Control sites were located in undisturbed, protected primary forest (Danum Valley Conservation Area; $4^{\circ}57'45.2''N$, $117^{\circ}48'10.4''E$).

4.3.2 Sampling design

We sampled twelve sites, six in twice-logged forest and six in primary forest, along existing transects (Fig. 1b; Edwards et al., 2011, 2014a). Sites were more than 2 km apart, and at least 100 m from forest edges. Within each site, we established five plots 50 m in diameter, 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, 2015) when mean daily temperature was 2.26°C higher and mean daily rainfall was 2.09 mm lower than the 5-year average (across April to July for the years 2007 to 2011; data from weather station at Danum Valley Field Centre).

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 and Hill, 2012). The variables we measured were: the stand basal area (m^2/ha) 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 trees and saplings in each of four quadrants centred on the plot centre (Fig. 1d); the coefficient of variation for the basal area of trees and of saplings; the proportion of mature trees that were dipterocarps (indicative of mature, complex forest); percentage canopy 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) height. 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., 2017). Each thermal image comprised 19200 distinct observations of surface temperature (one per pixel), and covered a surface area of approximately 1 m^2 . 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 ph-

tos taken in each orthogonal direction). For details of thermal image data extraction and processing see Supplementary Text S2. The temperature of cool surface microclimates was defined as the 5th percentile (i.e. coolest) across all 76800 pixels. For some organisms, the efficacy of thermal buffering also depends on the thermal stability of microclimates (Shi et al., 2016). We calculated daily variation in surface microclimate temperature as the difference between the minimum and maximum microclimate temperature, for each day and for each plot.

To identify spatially-explicit patches of warm and cool pixels (Fig. 2) we calculated the Getis-Ord local statistic for each pixel within the neighbourhood of the nearest eight pixels, using the function ‘localG’ in the spdep package in R (Bivand and Piras, 2015; R Core Team, 2017). Pixels with a Z-value of ≥ 3.886 were defined as being within warm patches, and those with a Z-value of ≤ -3.886 within cool patches (Getis and Ord, 1996). Thermal diversity was defined as the difference between the median temperature of the warmest warm patch minus the median temperature of the coolest cool patch (hereafter: ‘patch temperature range’). The average surface area of cool patches was calculated as the total number of pixels within cool patches, multiplied by the surface area of one pixel (0.516 cm^2), and divided by the total number of cool patches across the four photos. Finally, spatial configuration of cool patches was quantified using the Aggregation Index: the number of edges that cool patches 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 increased clustering of microclimates in space, 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,a; 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: deadwood ($> 10 \text{ cm}$ stem diameter), tree holes ($> 2 \text{ cm}$ at widest point of entrance hole, $< 2 \text{ m}$ above the ground) and leaf litter (1.5 m left of the plot centre). 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).

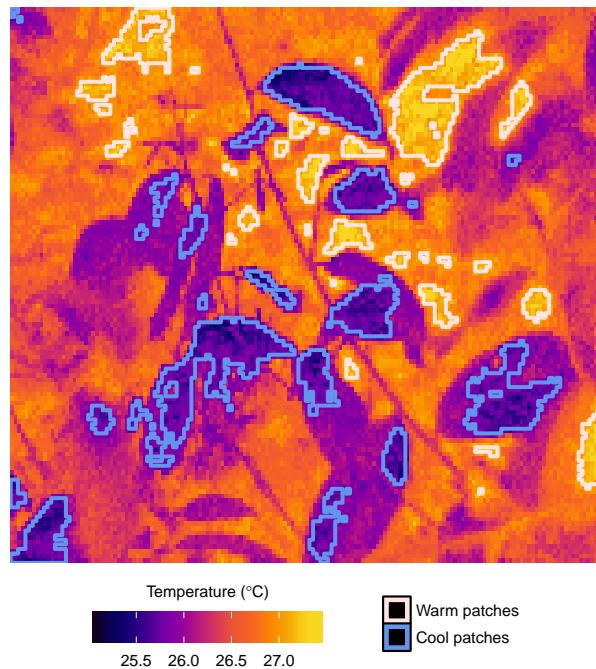


Figure 4.2: Example thermal image. Pixels are shaded from cold (purple) to hot (yellow). Warm patches (outlined in pink) and cool patches (outlined in blue) were identified using the Getis-Ord local statistic of each pixel.

All dataloggers recorded temperature every 20 minutes for six consecutive days, occurring within one week of thermal image collection. For qualitative comparison with thermal images and to lessen the degree of temporal autocorrelation, microclimate temperatures for each of the three microhabitats in each plot were calculated as the median of six daily measures, computed for each two-hour interval during the same time period as when thermal images were collected (i.e. 04:40 to 14:40 hrs). Our analyses focused on day-time thermal buffering, but we also ran analogous models for the full 24 hours to explore night-time thermal buffering (see Supplementary Text S5). In the main text, we only present data for day-time measurements because this is most relevant to organisms seeking to avoid extremes of heat, and because findings were qualitatively similar. Variation in temperature for microclimates inside microhabitats was defined as the daily range (95th percentile minus 5th percentile) of raw temperatures for each day, in each plot.

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 S3. We divided microhabitat volume by the total area surveyed to generate microhabitat volume per m² forest, for each plot.

4.3.3 Variables analysed

Forest structure

We examined the impact of selective logging on forest structure using linear mixed effects models to compare nine structural response variables between logged and primary forests: stand basal area of trees and of saplings; the coefficient of variation across individual basal areas of trees and of saplings; proportion of trees that were dipterocarps (binomial data: dipterocarp versus non-dipterocarp); percentage canopy cover (proportion data); and percentage vegetation cover at ground, understorey and canopy strata (proportion data). We found that tree stand basal area (m^2/ha) was a good measure of changes in forest structure from logging activity ($\text{LR} = 8.102, P < 0.01$; Fig. S1a; see Results for full details), hence we use this variable as a continuous measure of disturbance (henceforth: forest quality) in all our analyses exploring the thermal buffering potential of logged and unlogged forests.

Macroclimate and microclimate temperature

Macroclimate temperature is the temperature at a relatively 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 (logged or primary forest) and forest quality as explanatory variables (see Supplementary Text S4).

To assess the impact of selective logging on the ability of microclimates to buffer organisms from macroclimate warming, we modelled microclimate temperature against forest quality, forest type and macroclimate temperature, including an interaction term between the latter two variables. The slope of the relationship between microclimate and macroclimate temperature is a measure of the rate of change. Surface microclimate temperature refers to the 5th percentile of surface temperature observations (i.e. coolest) 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 two-hourly median temperature recorded by dataloggers inside microhabitats, and this was compared against macroclimate temperature as measured by a suspended datalogger.

To capture the impact of logging on the thermal stability of microclimates, we modelled microclimate temperature range against forest type and forest quality. For surface microclimates, the range was the daily range of surface temperature observations (the 5th percentiles, i.e. coolest surface temperatures). For microclimates inside microhabitats, the

range was the daily range (95th percentile minus 5th percentile) of the raw temperature observations. All 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 patches), and those inside leaf litter, tree holes and deadwood (each quantified by their average volume per m² forest). The thermal diversity of surface microclimates was captured by the temperature range between the warmest warm patch and the coolest cool patch. The spatial configuration of surface microclimates refers to the Aggregation Index of cool patches (binomial data: edges shared by cool patches versus edges not shared by cool patches). For all models, the fixed effects were forest type (logged or primary forest) and forest quality (i.e. tree stand basal area).

4.3.4 Statistical analyses

All data were analysed using mixed effects models in R (version 3.3.0; R Core Team, 2017). To account for spatial pseudoreplication, forest structure models included ‘site’ as a random intercept term, and all other models included ‘plot’ nested within ‘site’. Temperature data were recorded at multiple time points, hence the full models were visually assessed for evidence of temporal autocorrelation of residuals (function ‘acf’ in the nlme package; Pinheiro et al., 2017), and a correlation structure for both date and time was incorporated where necessary (the specific structure was chosen using AIC; Zuur, 2009). For binomial data (proportion of dipterocarps and surface microclimate Aggregation Index) we used generalized linear mixed effects models (GLMMs) with a binomial error distribution, fitted using the package lme4 (Bates et al., 2015) and tested for overdispersion. Diagnostic plots were assessed for all models to confirm model fit and, where necessary, we modified the variance structure of the residuals (Zuur, 2009) and transformed variables to normality. For true proportion data (percentage canopy cover and percentage vegetation cover), the transformation used was a modification of the empirical logit (Warton and 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, 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. The basic structure for most response variables (RV) was:

```
RV ~ forest_type + forest_quality + (1|transect/plot) + cor(~  
date_time|transect/plot)
```

4.4 Results

4.4.1 Changes in forest structure after logging

Following two rounds of commercial selective logging, tree stand basal area – our measure of forest quality – was $23.4 \text{ m}^2/\text{ha}$ in logged forest, compared to $39.5 \text{ m}^2/\text{ha}$ in primary forest ($\text{LR} = 8.102, P < 0.01$; Fig. S1a). Logged forests thus contained far fewer large trees than did primary forests. There were also more large saplings in logged forest ($9.55 \text{ m}^2/\text{ha}$) than in primary forests ($6.77 \text{ m}^2/\text{ha}$; $\text{LR} = 4.239, P < 0.05$; Fig. S1b), and trees were less variable in size ($\text{LR} = 13.038, P < 0.001$; Fig. S1c). There was no difference between forest types in terms of the variability of size among saplings ($\text{LR} = 0.114, P = 0.736$; Fig. S1d).

Changes to forest structure from selective logging were also evident in the overall amount of vegetation cover. Although there was no observed difference between logged forest and primary forest in percentage vegetation at ground level ($\text{LR} = 2.758, P = 0.097$; Fig. S1g), the proportion of trees that were dipterocarps ($X^2 = 2.42, P = 0.12$; Fig. S1e) or the percentage canopy cover ($\text{LR} = 0.874, P = 0.35$; Fig. S1f), we did find that percentage vegetation cover was higher in primary forest than in logged forest in both the understorey (primary = 68.2%; logged = 54.4%; $\text{LR} = 5.288, P < 0.05$; Fig. S1h), and in the canopy (primary = 23.1%; logged = 8.6%; $\text{LR} = 9.174, P < 0.01$; Fig. S1i). Thus, 9-12 years after logging there were significant differences in forest structure between logged and primary forests. This was especially true for the components of forest structure that typically indicate the presence of large, mature trees and high structural complexity, and which might be expected to influence microclimates and the availability of microhabitats.

4.4.2 Macroclimate and microclimate temperature in logged and primary forest

Despite differences in forest structure, we found no difference in macroclimate temperature of logged and primary forests, whether measured by the hygrometer ($\text{LR} = 0.081, P = 0.776$; Fig. S2a) or suspended datalogger ($\text{LR} = 0, P = 0.983$; Fig. S2b). Macroclimate temperature was also consistent across varying levels of forest quality, for temperature measured via the hygrometer ($\text{LR} = 0.022, P = 0.883$; Fig. S2a) and suspended datalogger ($\text{LR} = 0.527, P = 0.468$;

Fig. S2b). Thus, the necessity for thermal buffering was comparable between the two forest types.

Absolute microclimate temperature was comparable between forest types for all of the microclimates considered: surface ($LR = 0.447, P = 0.504$; Figure 4.3e), deadwood ($LR = 0.206, P = 0.65$; Fig. 3f), tree holes ($LR = 2.759, P = 0.097$; Fig. 3g) and leaf litter ($LR = 1.616, P = 0.204$; Fig. 3h). We found that the relationship between microclimate temperature and macroclimate temperature was slightly steeper in primary forest compared to logged forest for deadwood ($LR = 7.268, P < 0.01$; Fig. 3b), tree holes ($LR = 13.657, P < 0.001$; Fig. 3c) and leaf litter ($LR = 28.914, P < 0.001$; Fig. 3d). However, for 1°C macroclimate warming (from the median value) the maximum difference in microclimate warming between forest types was $< 0.1^{\circ}\text{C}$, and no such interaction was apparent for surface microclimates ($LR = 1.197, P = 0.274$; Fig. 3a). Similarly, for a $1 \text{ m}^2/\text{ha}$ increase in forest quality (i.e. tree stand basal area), tree hole temperature was slightly warmer ($LR = 4.661, P < 0.05$; Fig. 3g), but the size of this effect was negligible ($+0.00194^{\circ}\text{C}$), and not evident for other microclimates ($P > 0.05$; Fig. 3e-h). Thus we conclude that effects of logging on microclimate temperature were generally not evident, or minimal.

The final facet of microclimate temperature that we considered was daily temperature variation. This too was comparable between logged and primary forests for microclimates at the surface ($LR = 0.437, P = 0.508$; Fig. 4a), as well as those inside deadwood ($LR = 0.02, P = 0.889$; Fig. 4b), tree holes ($LR = 3.242, P = 0.072$; Fig. 4c) and leaf litter ($LR = 2.449, P = 0.118$; Fig. 4d). Microclimate temperature variation was also consistent across different levels of forest quality ($P > 0.05$; Fig. 4).

In summary, selective logging had little observed impact on absolute microclimate temperature or its daily variation. There was some evidence that thermal buffering potential was slightly enhanced for deadwood, tree holes and leaf litter inside logged forest, but the effects were extremely small and not evident for microclimates at the surface.

4.4.3 Microclimate availability in logged and primary forest

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 and thermal diversity of those microclimates. The occurrence of surface microclimates was not impacted by forest type ($LR = 0.872, P = 0.35$; Fig. 5b), and the average volume of microhabitats (per m^2 forest) was similar in logged and primary forest for deadwood ($LR = 0.263, P = 0.608$; Fig. 5d), tree holes ($LR = 3.053, P = 0.081$; Fig. 5e) and leaf litter ($LR = 0.162, P = 0.687$; Fig. 5f). There was no observed impact of forest quality on the occurrence of surface microclimates

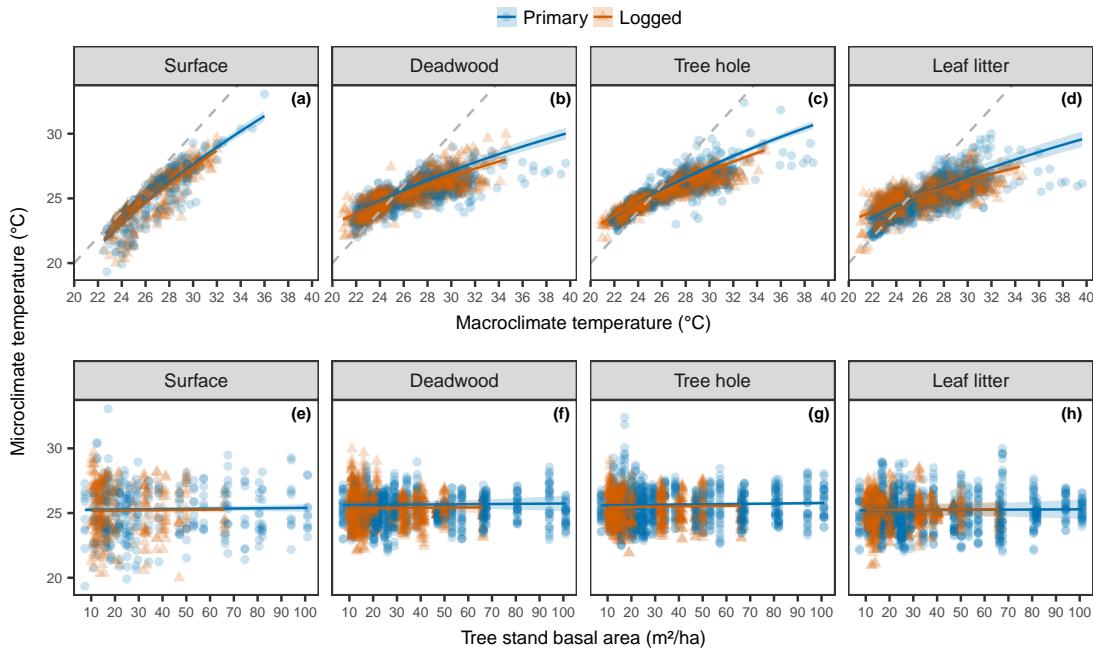


Figure 4.3: Comparison between primary forest (blue) and logged forest (orange) in terms of: (a-d) the relationship between microclimate temperature and macroclimate temperature; and (e-h) absolute microclimate temperature across varying levels of forest quality (measured as tree stand basal area). Microclimates were measured at the surface (a, e), and inside deadwood (b, f), tree holes (c, g) and leaf litter (d, h). The grey dashed lines in panels a-d indicate zero temperature buffering, where the microclimate temperature is equal to the macroclimate temperature. In all panels, shaded bands are 95% confidence intervals.

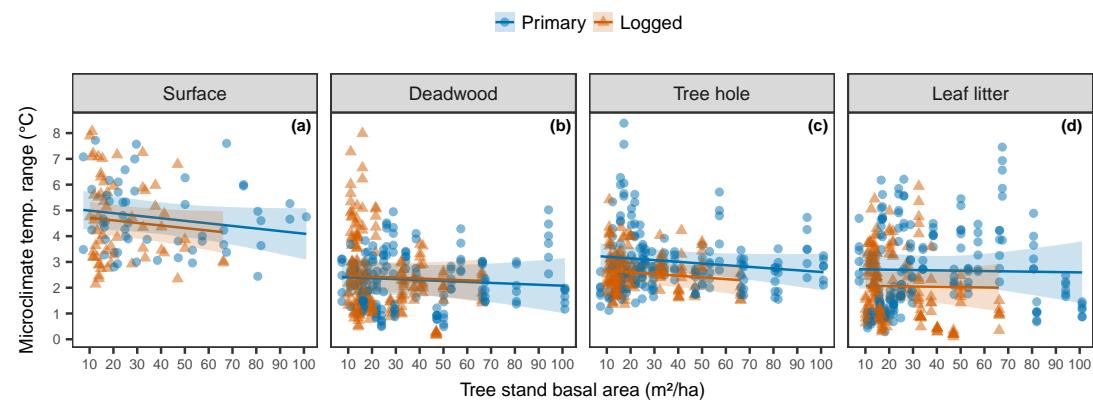
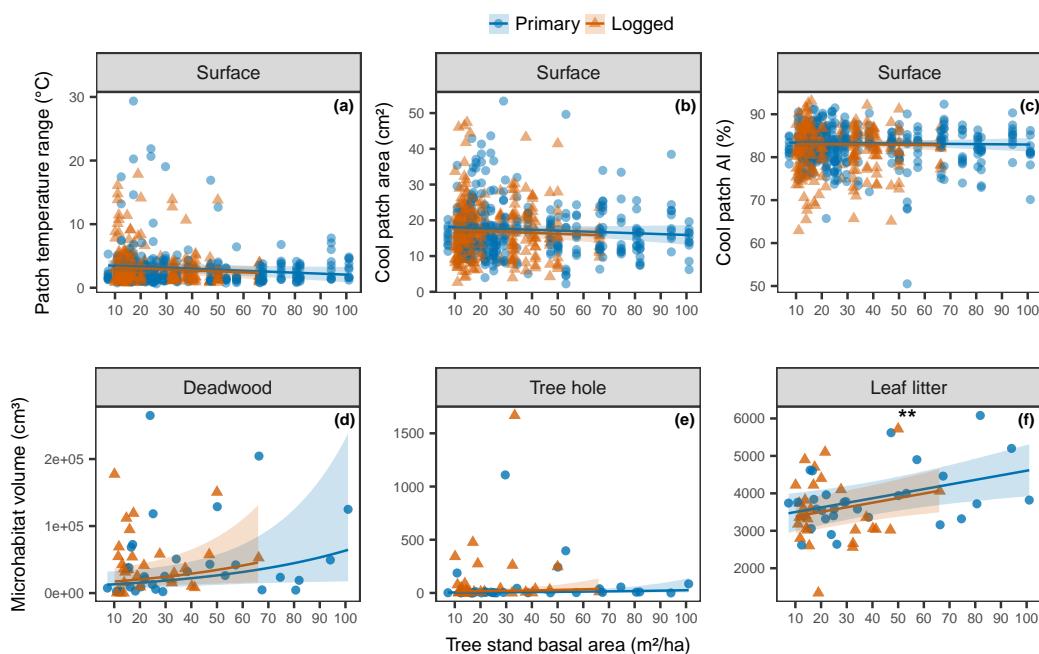


Figure 4.4: The influence of forest type (primary or logged) and forest quality (measured as tree stand basal area) on microclimate temperature range. Daily range for surface microclimates (a) was calculated as the difference between the maximum and the minimum microclimate temperature (itself calculated as the 5th percentile temperature across four photos taken at each visit to each plot). For microclimates inside deadwood (b), tree holes (c) and leaf litter (d), the daily range was the difference between the 95th percentile and 5th percentile of raw temperature measurements. Primary forest data points are depicted as blue circles and logged forest as orange triangles. Shaded bands represent 95% confidence intervals.

(LR = 1.324, $P = 0.25$; Fig. 5b) or the volume of deadwood (LR = 3.78, $P = 0.052$; Fig. 5d) and tree holes (LR = 2.172, $P = 0.141$; Fig. 5e). In contrast, we found that leaf litter volume increased by $12.3 \text{ cm}^3/\text{m}^2$ for a $1 \text{ m}^2/\text{ha}$ increase in forest quality (i.e. tree stand basal area; LR = 7.056, $P < 0.01$; Fig. 5f).

Using thermal images we were able to quantify the thermal diversity and spatial configuration of surface microclimates. Thermal diversity has a bearing on the diversity of organisms that are able to find microclimates meeting their thermal requirements (which vary according to species, age, time of day, seasonality, etc.). Spatial configuration influences the ease with which organisms can utilise microclimates. We found that the temperature range spanned by surface microclimates (both warm and cool patches) was comparable between logged and primary forests (LR = 0.276, $P = 0.599$; Fig. 5a) and with varying forest quality (LR = 3.552, $P = 0.059$; Fig. 5a). The same was true for the Aggregation Index of cool surface patches, both between logged and primary forest ($\chi^2 = 0.312$, $P = 0.576$; Fig. 5c) and with different levels of forest quality ($\chi^2 = 0.183$, $P = 0.669$; Fig. 5c).

Overall, the availability of microclimates was minimally affected by selective logging, regardless of whether microclimates were located at the surface or inside microhabitats. This was true for various different components of microclimate availability, including their occurrence, thermal diversity and spatial configuration.



The influence of forest type (primary or logged forest) and forest quality (measured as tree stand basal area) on microclimate availability. Results for surface microclimates (top row) include: the temperature range from the warmest warm patch to the coolest cool patch (a); the average surface area of cool patches (b); and the Aggregation Index of cool patches (c).

The volume (per m² forest) of microhabitats typically associated with microclimates (bottom row) is shown for deadwood (d), tree holes (e) and leaf litter (f). Primary forest data points are depicted as blue circles and logged forest as orange triangles. Shaded bands represent 95% confidence intervals. Asterisks in panel f denote a statistically significant difference at $0.001 < P < 0.01$ (**).

4.5 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 these forests having only a maximum of 12 years post-logging recovery (Fisher et al., 2011), and the coincidental occurrence during data collection of abnormally hot and dry conditions associated with the strongest El Niño-Southern Oscillation (ENSO) event since 1998 (NOAA Climate Prediction Center, 2015), we found very few thermal differences associated with selective logging. 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.

4.5.1 Forest structure

At a local scale (m to ha), climate is highly dependent upon vegetation (Oke, 1987; Sears et al., 2011). Selective logging operations generally target larger and older trees, leading to many associated changes in vegetation structure (Okuda et al., 2003; Kumar and Shahabuddin, 2005; Edwards et al., 2014b). A clear signal of historical logging in our study area was a reduction in stand basal area of mature trees by 40.8% (Fig. S1a; Berry et al., 2008), accompanied by reduced variation in tree basal area (Fig. S1c), and reduced vegetation cover at ≥ 15 m height (Fig. S1h,i). The increase in stand basal area of saplings by 41.1% (Fig. S1b) is evidence that there has been substantial natural regeneration in the intervening years.

4.5.2 Macroclimate and microclimate temperature

Although primary forest contained more large trees (Fig. S1a), the absence of any long-term effect of selective logging on percentage canopy cover (Fig. S1f) 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. This finding is in

keeping with previous studies observing rapid horizontal canopy growth following selective logging (e.g. Asner et al., 2004). 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 what was intercepted, owing to the higher albedo of habitats with an abundance of non-tree species (Oke, 1987; Davin and de Noblet-Ducoudré, 2010; Edwards et al., 2014b). In either case (or in combination), given comparable levels of solar radiation reaching the forest floor 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 and Fig. S2).

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). Given that selective logging did not affect absolute temperature of the macroclimate (Fig. S2) or microclimates (Fig. 3), we can infer that there was no overall effect of selective logging on the difference between micro- and macroclimate temperature. There was also no evidence that selective logging impacted overall daily variation in microclimate temperature (Fig. 4). There were some impacts of logging on the relationship between microclimate and macroclimate temperature for microclimates inside deadwood, tree holes and leaf litter (Fig. 3), but the effect sizes for these interactions were extremely small. The maximum difference in microclimate warming between logged and primary forests was $< 0.1^{\circ}\text{C}$ for 1°C of macroclimate warming. As such, we conclude that even when selective logging had a statistically significant influence on thermal buffering potential, the effect was small and of limited biological relevance.

4.5.3 Microclimate availability

Even if microclimates are present and effective at buffering temperature change, overall rarity or isolation could render them functionally redundant to some species (Sears et al., 2011, 2016). We demonstrate that lower forest quality was associated with less leaf litter (Fig. 5; cf. Saner et al., 2009), but forest quality and forest type had little effect on the occurrence of microclimates at the surface or inside deadwood and tree holes. This is contrary to expectations from previous studies (Ball et al., 1999; Blakely and Didham, 2008). However, high volumes of deadwood could be maintained in logged forest by lower decomposition rates (Ewers et al., 2015; Yeong et al., 2016; but see Héault et al., 2010), and large remnant pieces from harvest operations. In undisturbed forests, tree holes tend to be associated with larger, older trees (Lindenmayer et al., 2000; Blakely and Didham, 2008). A comparable quantity of tree holes might be found in logged forests because of damage from logging operations (Edwards et al., 2014b), increased wind in gaps (Chen et al., 1995) and remnant large trees that were specifically avoided by logging companies because of hollow boles. Additionally,

we assessed tree holes in the understorey only, and differences may well manifest at higher forest strata.

The availability of microclimates to organisms is also influenced by their thermal diversity and distribution in space. We found that patches of warm and cool microclimates on the surface of the forest floor spanned a temperature range of about 3°C, regardless of logging activity (Fig. 5a). Cool patches were generally highly clustered in space (Aggregation Index of 83.3%), but this was not affected by logging (Fig. 5c). Thermal diversity and spatial configuration of microclimates are relatively novel facets of thermal buffering potential (but see: Caillon et al., 2014; Sears et al., 2016; Faye et al., 2016); they are likely determined by the composition of the forest floor and the relative radiative properties of these different components (e.g. bare soil versus leaves versus water; Oke, 1987; Snyder et al., 2004). We therefore suggest that these characteristics of the forest floor were comparable between forests despite the large differences in forest structure that were evident after logging.

4.5.4 Caveats and future research 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 and 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 coarse-scale vapour pressure deficit measurements from the hygrometer and from hygrochron iButtons (Supplementary Text S4) showed little variation within or between forests (Fig. S2).

Relative climates in primary and logged forests could be very different above the understorey, which we were unable to capture in our study. Some ectotherms move down from the upper strata to exploit more favourable temperatures lower down (Scheffers et al., 2013). Hence, if temperatures in higher strata are in fact hotter in logged forest compared to primary forest, it is possible that species could move to utilise the favourable temperatures of the understorey of logged forest that we demonstrate here, potentially resulting in a ‘flattening’ of species’ vertical distributions.

While thermal cameras are an important addition to the toolbox of microclimate research (Faye et al., 2016), it is also important to remember that they are just one element. Thermal cameras are well-suited to capturing temperature at a very fine-scale and with inherent spatial information, but differences in 3D topography of a surface could affect results (e.g. the real distance between neighbouring pixels can be more than is apparent in the 2D image).

Additionally, although thermal cameras are ideal for measuring surface temperatures, they have a limited capacity to capture sub-surface temperatures, and hence we have used thermal imagery in combination with dataloggers.

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. As average temperatures increase over this century, so too will the intensity and frequency of extreme climatic events. Thermal buffering will likely be crucial in allowing species to move locally to avoid suboptimal climates. We sampled in some of the most intensively logged forest in the tropics, during abnormally hot and dry conditions of a severe ENSO event; 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.

4.6 Acknowledgements

Thanks to staff at Danum Valley Field Centre for logistical support; and Azlin Bin Sailim, Jessica Olid and Chloe Walker-Trivett for field assistance. R.A.S. was funded by a NERC studentship through the ACCE (Adapting to the Challenges of a Changing Environment) Doctoral Training Partnership (Grant No. NE/L002450/1).

4.7 Data availability

Data available from the University of Sheffield Online Research Data repository (<https://doi.org/10.15131/shef.data.5414629>).

Chapter 5

The impact of recent forest cover change on climate connectivity in the tropics



Mixed use tropical landscape in Bali.

Chapter 6

Discussion



Frilled tree frog (*Kurixalus appendiculatus*).

Appendix A

Supporting information for Chapter 2

A.1 Impact of unbalanced sampling

A.1.1 Methods

Some studies contributed substantially more temperature observations than others. To test whether these studies were unduly influencing our results, we established a threshold over which a given land-use type, in a given study, was deemed to have a disproportionate number of associated temperature observations. The threshold used — 2,071 observations — was the mean number of observations across all unique combinations of land-use type and study identity (55 in total). The same number of observations (2,071) was then randomly resampled from each of the land-use type and study combinations that exceeded the threshold. With this reduced and more balanced dataset we repeated the main analysis (see ‘Statistical analysis’ in main text for more details), modelling local day-time temperature (‘temp_day’) against land-use type (‘LUT’), position relative to ground-level (‘position’) and season. The final model structure was unchanged, and included a random slope for land-use type and random intercept with respect to the identity of the study (‘studyID’) from which data originated:

```
lmer(temp_day ~ LUT*position + LUT*season + (LUT|studyID))
```

A.1.2 Results

All results were qualitatively unchanged from those derived using the full dataset. Local day-time temperature was warmer in altered land-use types, compared to primary forest (LMM,

$\chi^2 = 32.19$, df = 4, P < 0.001; Figure B.3). Averaged across above- and below-ground, and across seasons, the temperature differential was greatest in cropland (7.7°C), followed by pasture (6.4°C), plantation (3.2°C) and degraded forest (0.9°C). The relationship between land-use type and temperature interacted with both position relative to ground level (LMM, $\chi^2 = 681$, df = 4, P < 0.001; Figure B.3A) and season (LMM, $\chi^2 = 105.63$, df = 4, P < 0.001; Figure B.3B). Specifically, the difference between altered land-use types and primary forest was greater above-ground than below-ground (Figure B.3A), and variable between seasons according to the land-use type (Figure B.3B).

A.2 Supplementary figures

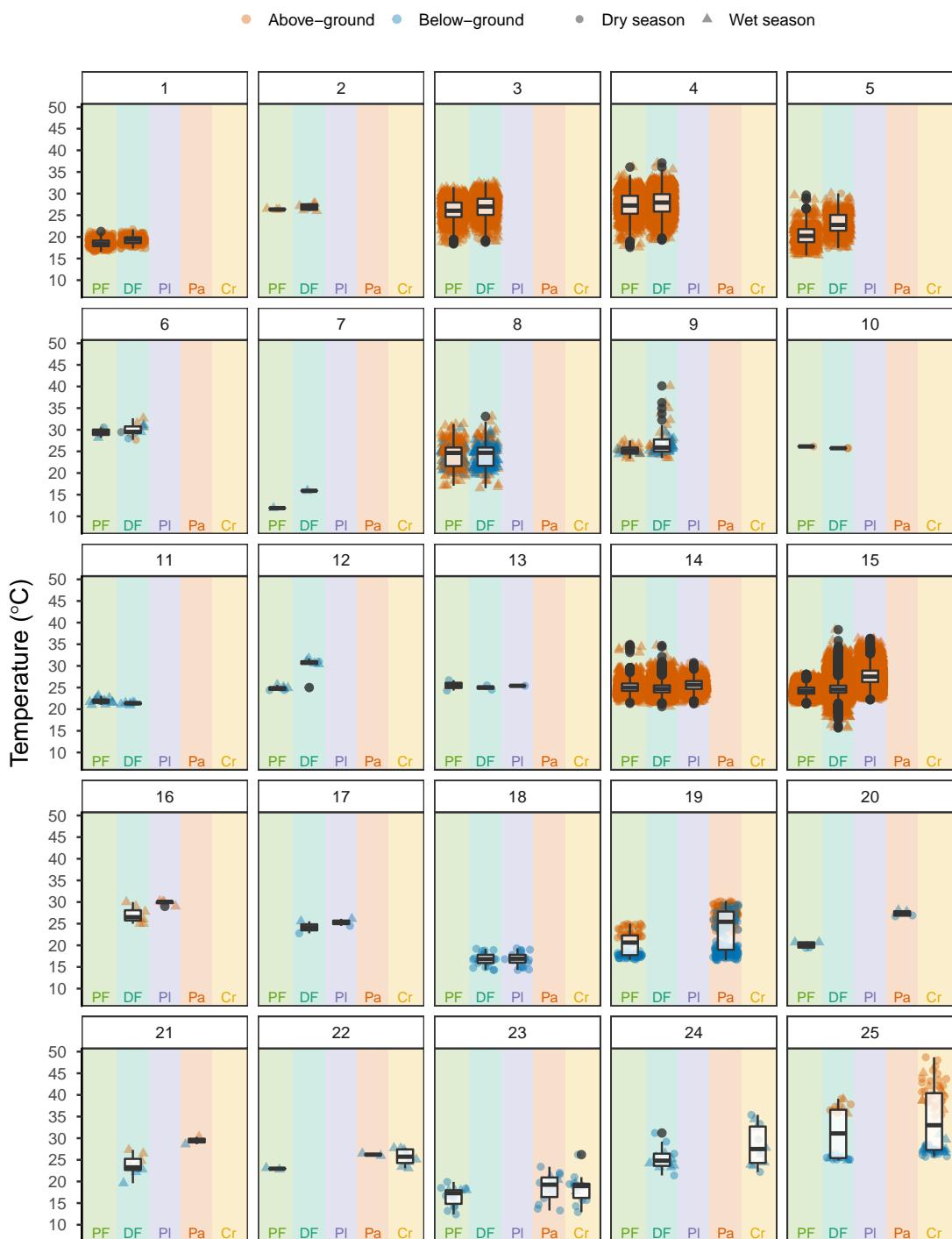


Figure A.1: Day-time temperature against land-use type for each study contributing data to the analyses. Panel numbers refer to the study number in the reference list below. Land-use types are: primary forest (PF), degraded forest (DF), plantation (PI), pasture (Pa) and cropland (Cr). Panels are ordered by the combination of land-use types for which data was available: (1-12) PF + DF; (13-15) PF + DF + PI; (16-18) DF + PI; (19-20) PF + Pa; (21) DF + Pa; (22-23) PF + Pa + Cr; and (24-25) DF + Cr. Shading of points indicates temperatures measured above-ground (orange) or below-ground (blue), and point symbol indicates temperatures measured during the dry season (circles) or wet season (triangles).

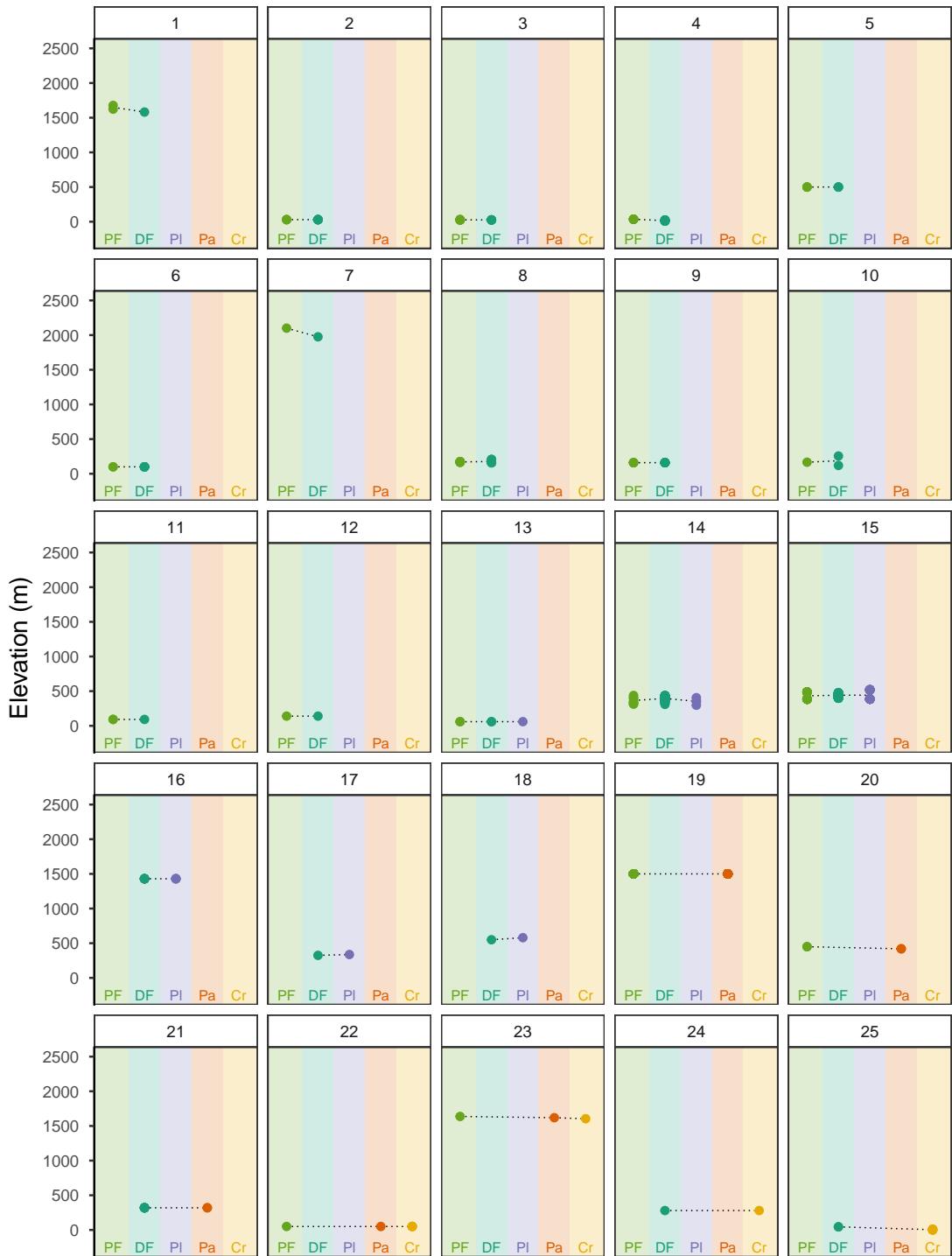


Figure A.2: Site elevation against land-use type for each study contributing data to the analyses. Panel numbers refer to the study number in the reference list below. Land-use types are: primary forest (PF), degraded forest (DF), plantation (PI), pasture (Pa) and cropland (Cr). Panels are ordered by the combination of land-use types for which data was available: (1-12) PF + DF; (13-15) PF + DF + PI; (16-18) DF + PI; (19-20) PF + Pa; (21) DF + Pa; (22-23) PF + Pa + Cr; and (24-25) DF + Cr. Dotted black lines connect the mean elevation of all the sites within each land-use type.

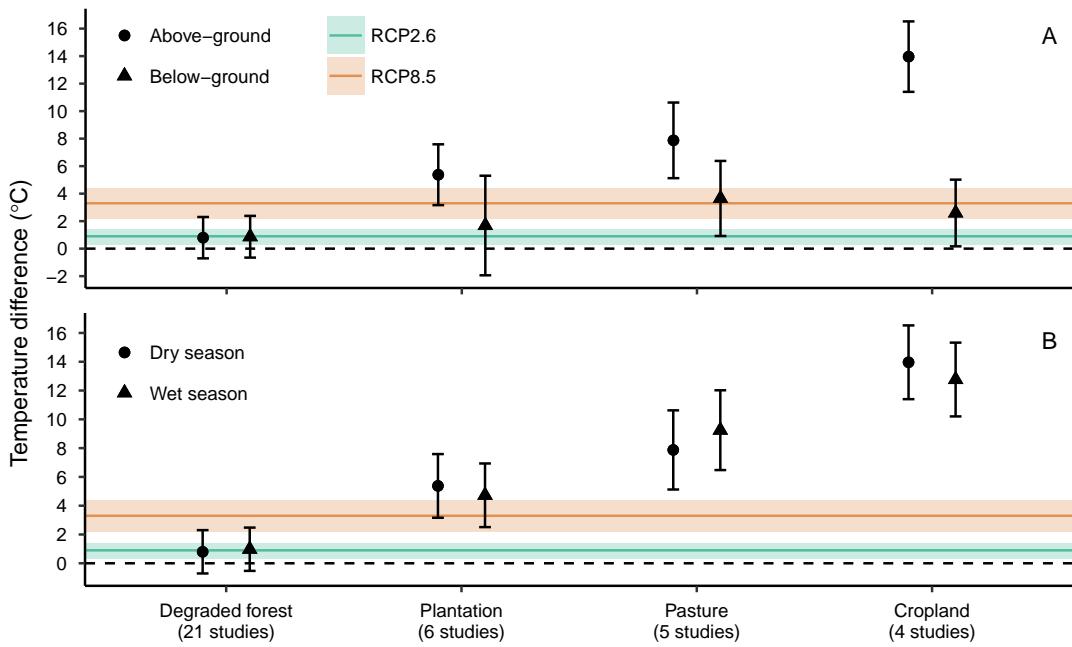


Figure A.3: Model estimates of the temperature difference between altered land-use types and primary forest, using a reduced dataset to balance sample sizes between the different studies that contributed data. Parameter estimates are standardised against the estimate for primary forest, which is represented by the dashed line. Error bars are 95% confidence intervals. Solid lines indicate projected warming in the tropics for the period 2081–2100 compared to the period 1986–2005, as a result of global climate change (?). Shaded bands indicate 5%–95% ranges from the distribution of the climate model ensemble. Colours represent the lowest and highest warming scenarios (RCP2.6 and RCP8.5, respectively).

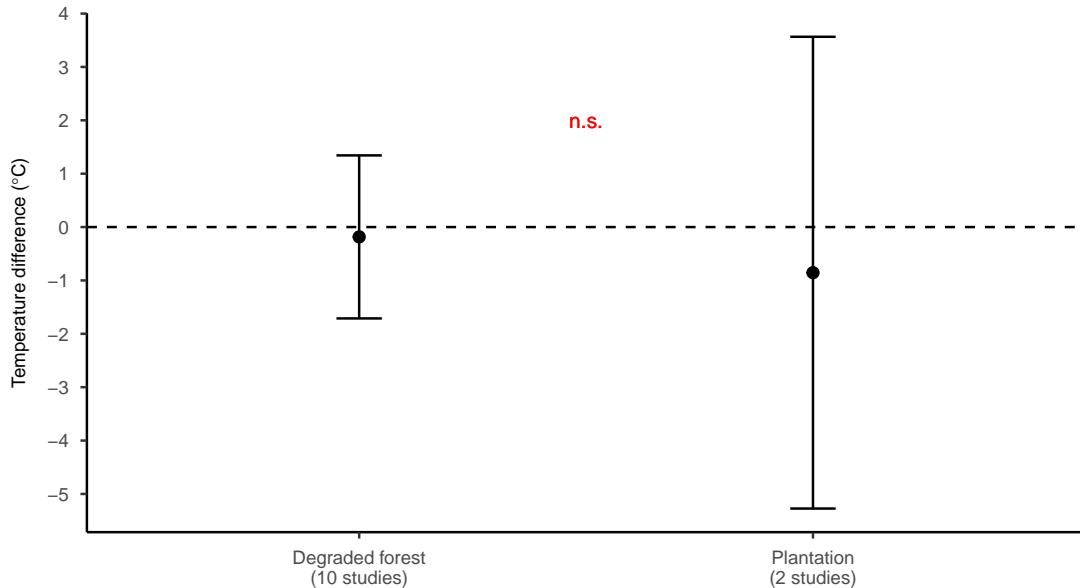


Figure A.4: Model estimates of the nocturnal temperature difference between altered land-use types and primary forest. Note that cropland and pasture are missing from this analysis because nocturnal temperature data for these land-use types were not available. Parameter estimates are standardised against the estimate for primary forest, which is represented by the dotted line. Error bars are 95% confidence intervals.

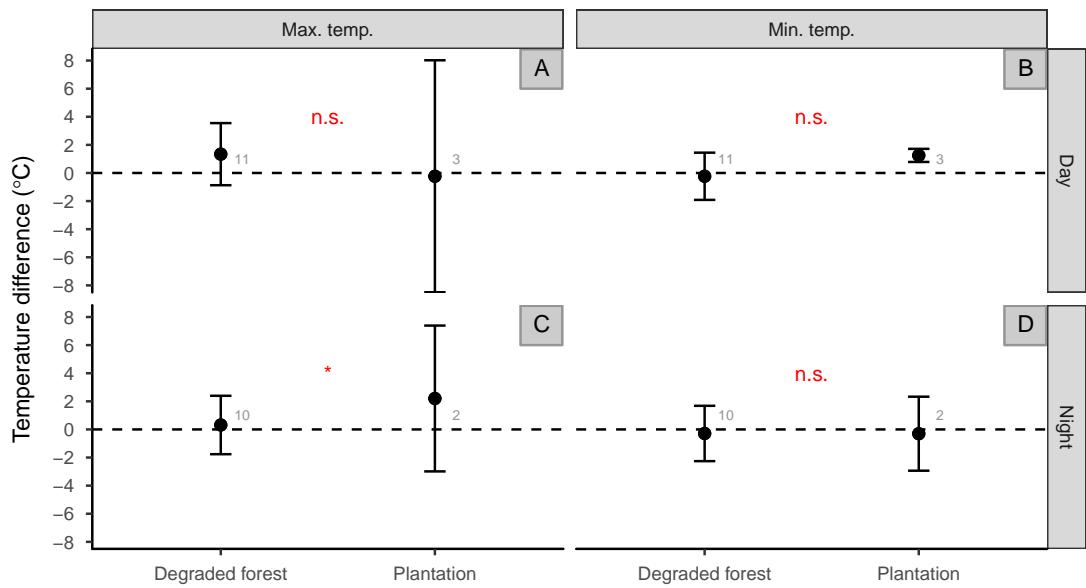


Figure A.5: Model estimates of the difference between altered land-use types and primary forest in terms of temperature extremes. Day-time results are depicted in panels A and B, and night-time results in panels C and D. Panels A and C indicate the effect of land-use change on maximum temperature, and panels B and D indicate the same for minimum temperature. Note that data for cropland and pasture are absent from this analysis because data for these land-use types were not available. Parameter estimates are standardised against the estimate for primary forest, which is represented by the dotted line. Error bars are 95% confidence intervals. The grey numbers next to points represent the number of studies providing the underlying data.

Appendix B

Supporting information for Chapter 4

B.1 Impact of unbalanced sampling

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```
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```

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B.2 Supplementary figures

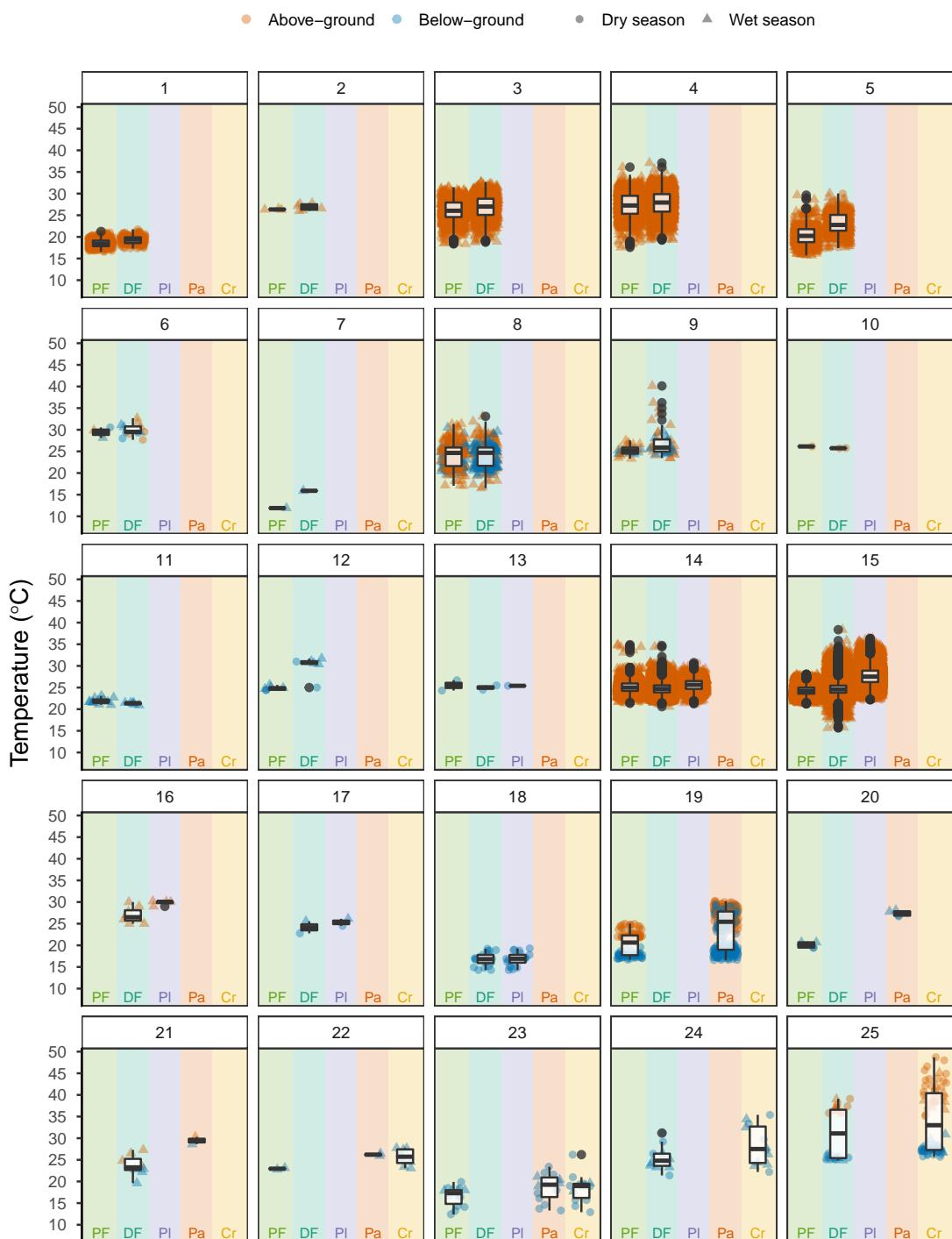


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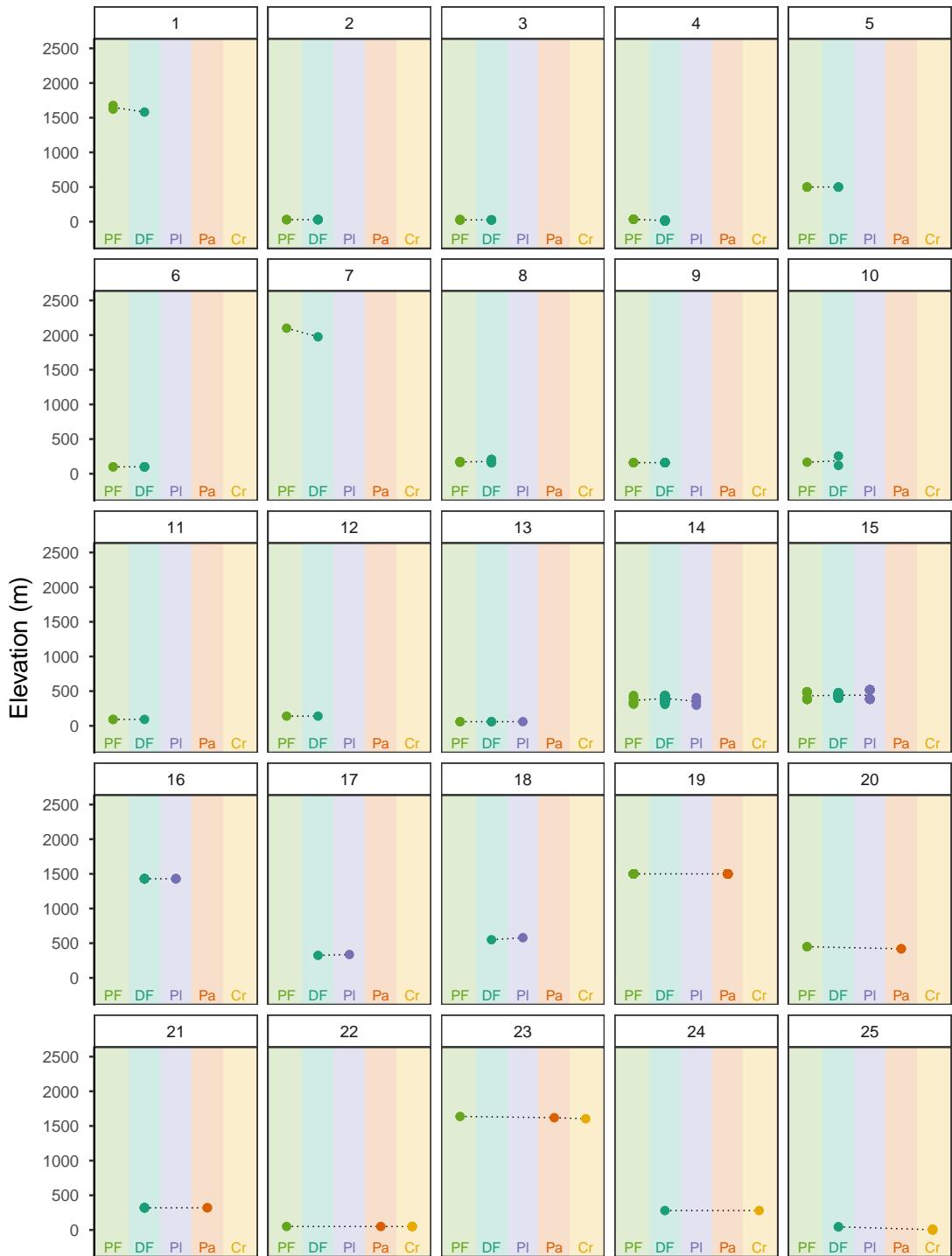


Figure B.2: Site elevation against land-use type for each study contributing data to the analyses. Panel numbers refer to the study number in the reference list below. Land-use types are: primary forest (PF), degraded forest (DF), plantation (PI), pasture (Pa) and cropland (Cr). Panels are ordered by the combination of land-use types for which data was available: (1-12) PF + DF; (13-15) PF + DF + PI; (16-18) DF + PI; (19-20) PF + Pa; (21) DF + Pa; (22-23) PF + Pa + Cr; and (24-25) DF + Cr. Dotted black lines connect the mean elevation of all the sites within each land-use type.

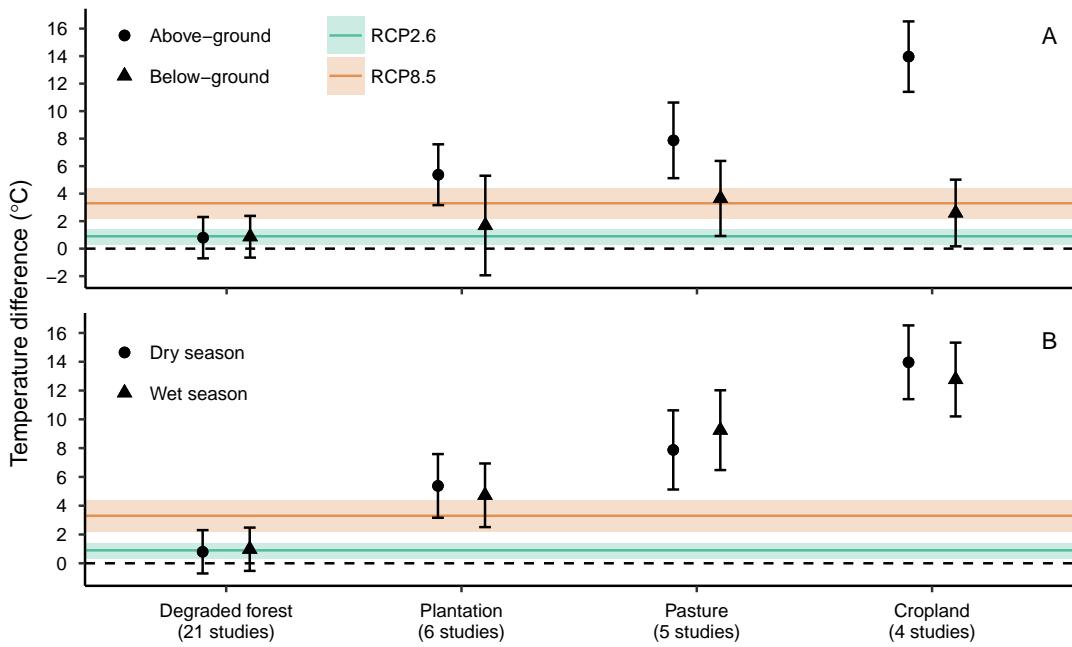


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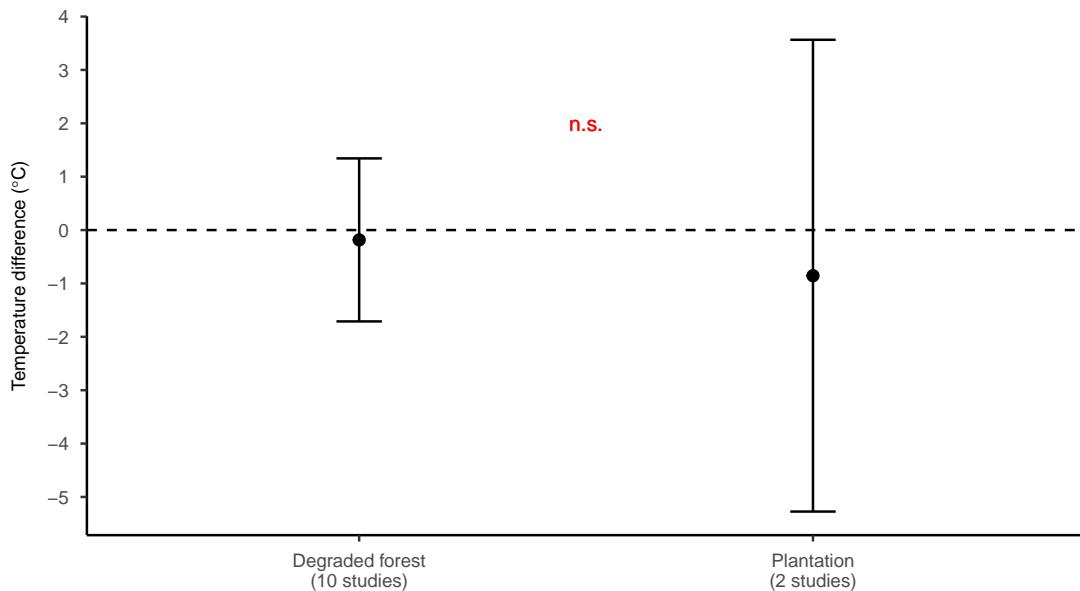


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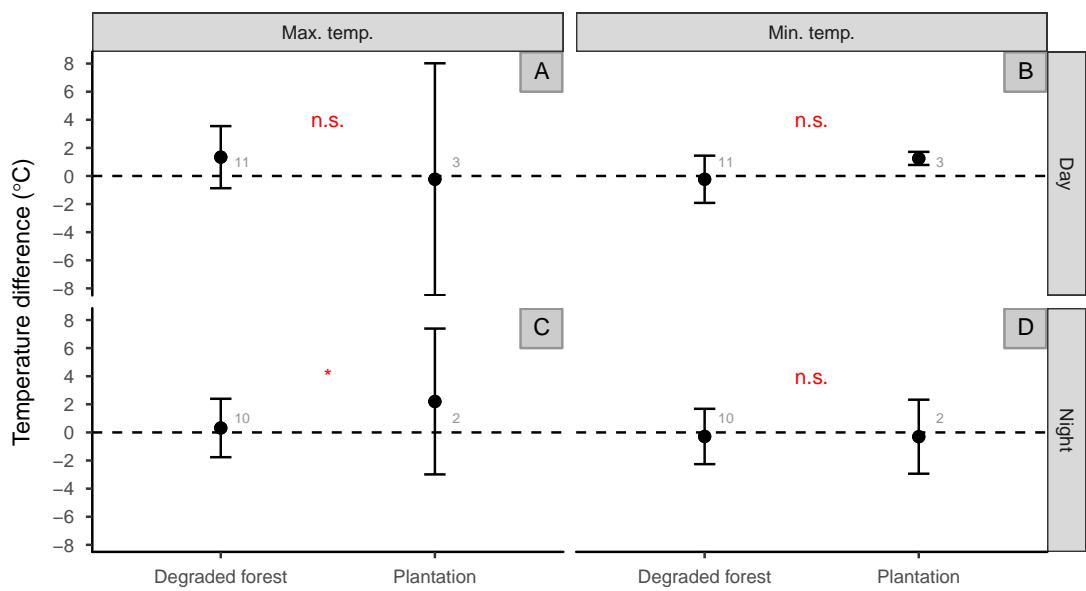


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