



The
University
Of
Sheffield.

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

By:

Rebecca Anne Senior

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

Contents

Abstract	viii
Acknowledgements	ix
Author's declaration	x
1 General introduction	1
1.1 Threats to biodiversity	1
1.2 Responses to climate change	2
1.3 Influence of land-use change	5
1.4 Thesis aims and rationale	8
2 A pantropical analysis of the impacts of forest degradation and conversion on local temperature	9
2.1 Abstract	9
2.2 Introduction	10
2.3 Methods	12
2.4 Results	15
2.5 Discussion	19
2.6 Data and R code	23
Appendices	24
A Supporting information for Chapter 2	24
A.1 Impact of unbalanced sampling	24
A.2 Supplementary figures	26
B Supporting information for Chapter 4	31
B.1 Impact of unbalanced sampling	31
B.2 Supplementary figures	33

List of Tables

2.1	Land use classification definitions (modified from Extended Data Table 1 in Newbold et al. (2015).	12
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.	17
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.	20

List of Figures

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).	3
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.	15
2.2 Raw day-time temperature against land-use type, across all studies contributing data to the analyses (plotted by study in Figure A1.1). 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).	16
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, 2013b). 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).	18

A1.1 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 (Pl), 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 + Pl; (16-18) DF + Pl; (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).	27
A1.2 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 (Pl), 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 + Pl; (16-18) DF + Pl; (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.	28
A1.3 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 (IPCC, 2013b). 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).	29
A1.4 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.	29

A1.5 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 crop-land 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.	30
A1.1 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 (Pl), 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 + Pl; (16-18) DF + Pl; (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).	34
A1.2 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 (Pl), 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 + Pl; (16-18) DF + Pl; (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.	35
A1.3 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 (IPCC, 2013b). 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).	36

A1.4 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.	36
A1.5 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.	37

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

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, 2013a). 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, 2013a). 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, 2013a).

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, 2013a). Concomitant with increasing global average temperature is the increase in the frequency and intensity of extreme weather events (IPCC, 2013a). 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 (2013a)]. 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 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, 2013a).

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, 2013a).

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, 2013a). It is now appar-

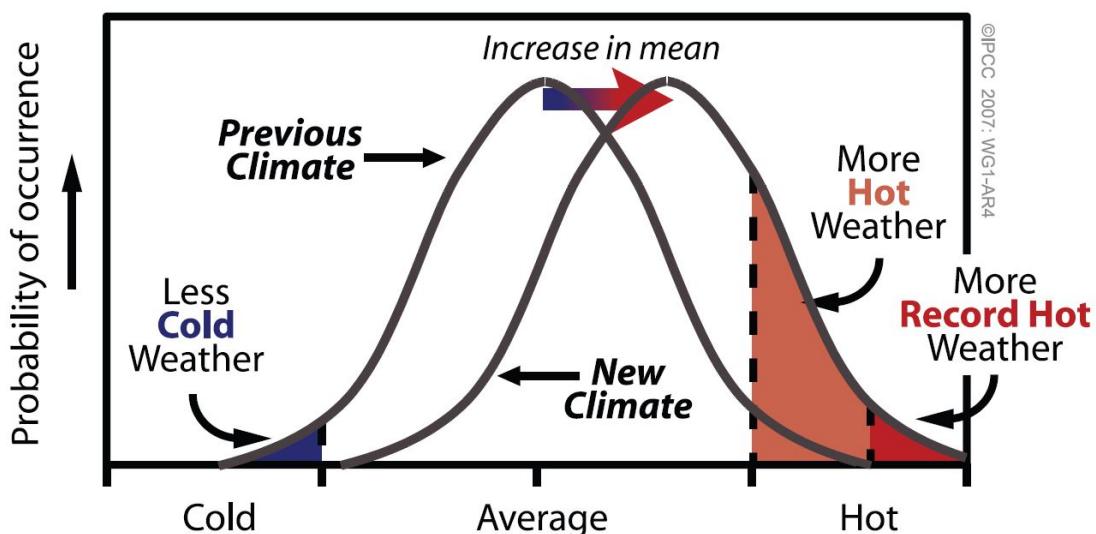


Figure 1.1: Schematic showing the increase in frequency of extreme temperatures (shaded light pink) and the magnitude of extreme temperatures (shaded dark pink), in response to increasing mean temperature for a normal distribution of temperatures. ‘extreme’ refers to events that would have been anomalous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

ent 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). Specif-

ically, 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, 2013a). Deforestation marginally reduces the net radiative forcing that leads to global climate warming through decreases in surface albedo (IPCC, 2013a). 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., 2014). 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., 2014) 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., 2014; 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

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, 2013b), 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 (Ta-

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)).

ble 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” 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 temperature 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) avail-

able (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 Digitizelt (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

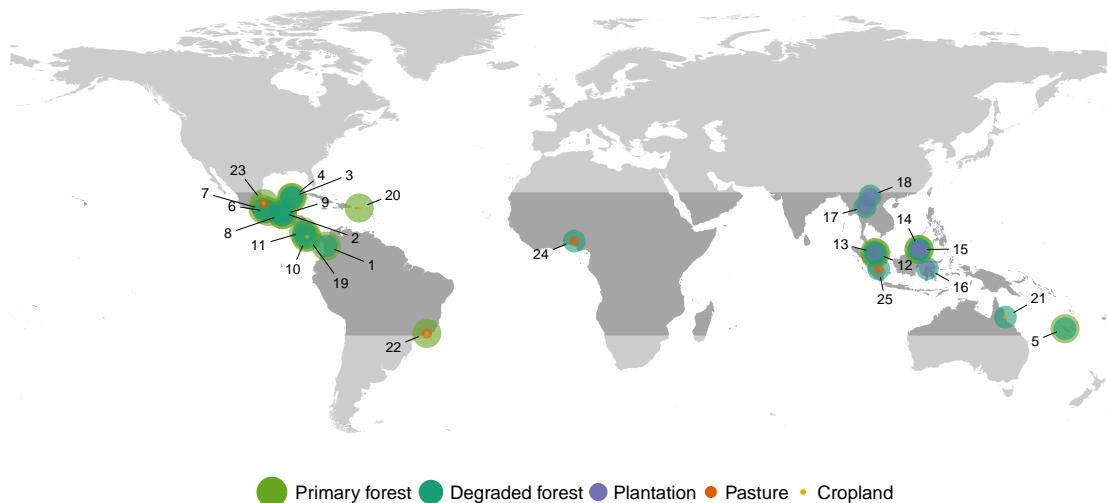


Figure 2.1: Locations of the 25 studies contributing data to the analyses. Point labels correspond to the study number in Table 1. The shading and size of concentric points corresponds to different land-use types, to indicate the data provided by each study.

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.

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 A1.1). Most observations represented either a single temperature observation within, or mean temperature across, a single day at the point

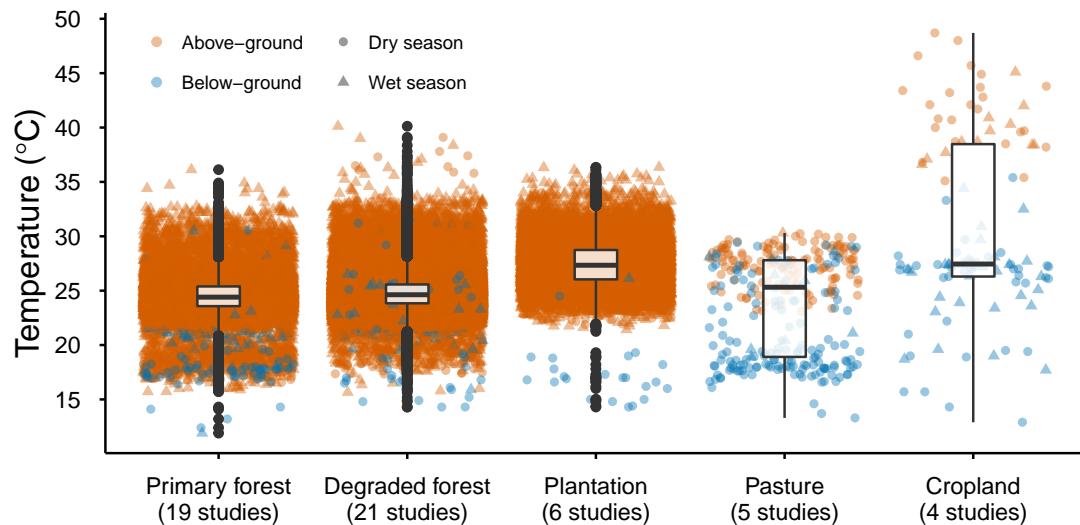


Figure 2.2: Raw day-time temperature against land-use type, across all studies contributing data to the analyses (plotted by study in Figure A1.1). Point shading indicates temperatures measured above-ground (orange) or below-ground (blue), and different symbols indicate temperatures measured during the dry season (circles) or wet season (triangles).

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 A1.2). 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))
```

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

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 robust to resampling from studies that provided disproportionate numbers of observations (section A.1; Figure A1.3).

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, $X^2 = 2.09$, df = 2, P > 0.05; Figure A1.4), and neither did night-time minimum temperature (LMM, $X^2 = 2.31$, df = 2, P > 0.05; Figure A1.5D). Maximum night-time temperature was slightly higher overall in degraded forest and plantation compared to primary forest (LMM, $X^2 = 6.35$, df = 2, P < 0.05; Figure A1.5C), 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, $X^2 = 4.87$, df = 2, P > 0.05; Figure A1.5A), or day-time minimum temperature (LMM, $X^2 = 4.60$, df = 2, P > 0.05; Figure A1.5B).

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).

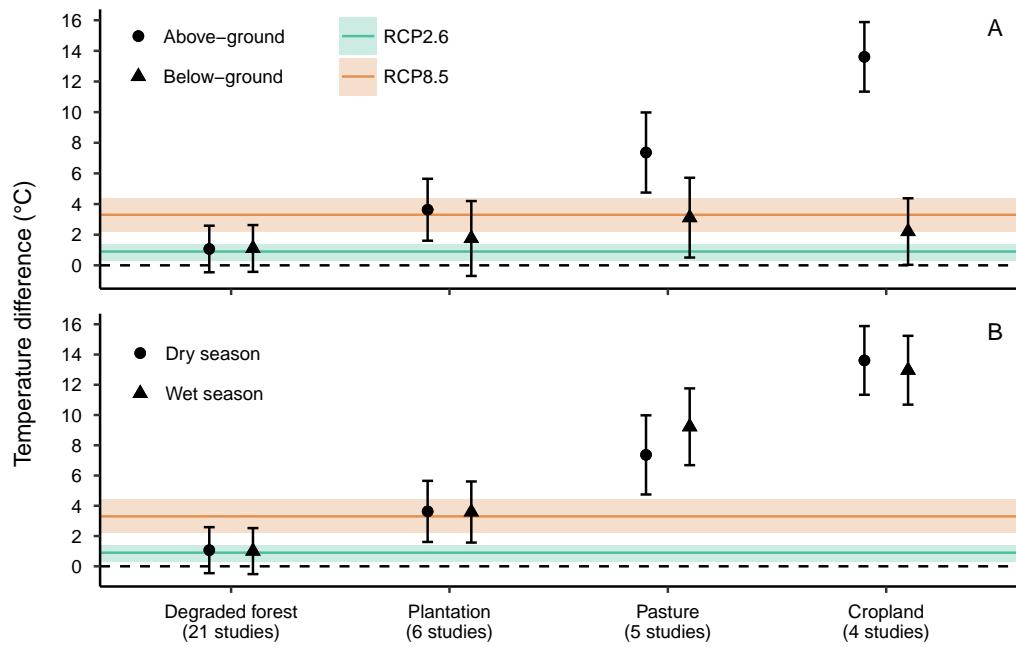


Figure 2.3: Model estimates of local day-time temperature in altered land-use types relative to primary forest (depicted by the black dashed line). In Panel A, different symbols denote position relative to the ground (above-or below-ground), and the season is held at the reference level (dry season). 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, 2013b). 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).

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: $+0.1^\circ\text{C}$ 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 ($+0.9^\circ\text{C}$ in RCP2.6; IPCC, 2013b), and frequently also exceeded the maximum warming scenario ($+3.3^\circ\text{C}$ in RCP8.5; IPCC, 2013b). 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.

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

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	Wet	1
BG	Dry	1.1	-0.4	2.6	1.1	BG	1.1	0.1		0.1
		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	Wet	2.6
BG	Dry	1.8	-0.7	4.2						0.1
		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	Wet	7.1
BG	Dry	3.1	0.5	5.7						-1.9
		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	Wet	7.3
BG	Dry	2.2	0	4.4						0.6
		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.

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 A1.3 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, 2013b). 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, 2013b) 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., 2014). 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 ([doi:10.5061/dryad.g4000](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>).

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 A1.3). 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 A1.3A) and season (LMM, $\chi^2 = 105.63$, df = 4, P < 0.001; Figure A1.3B). Specifically, the difference between altered land-use types and primary forest was greater above-ground than below-ground (Figure A1.3A), and variable between seasons according to the land-use type (Figure A1.3B).

A.2 Supplementary figures

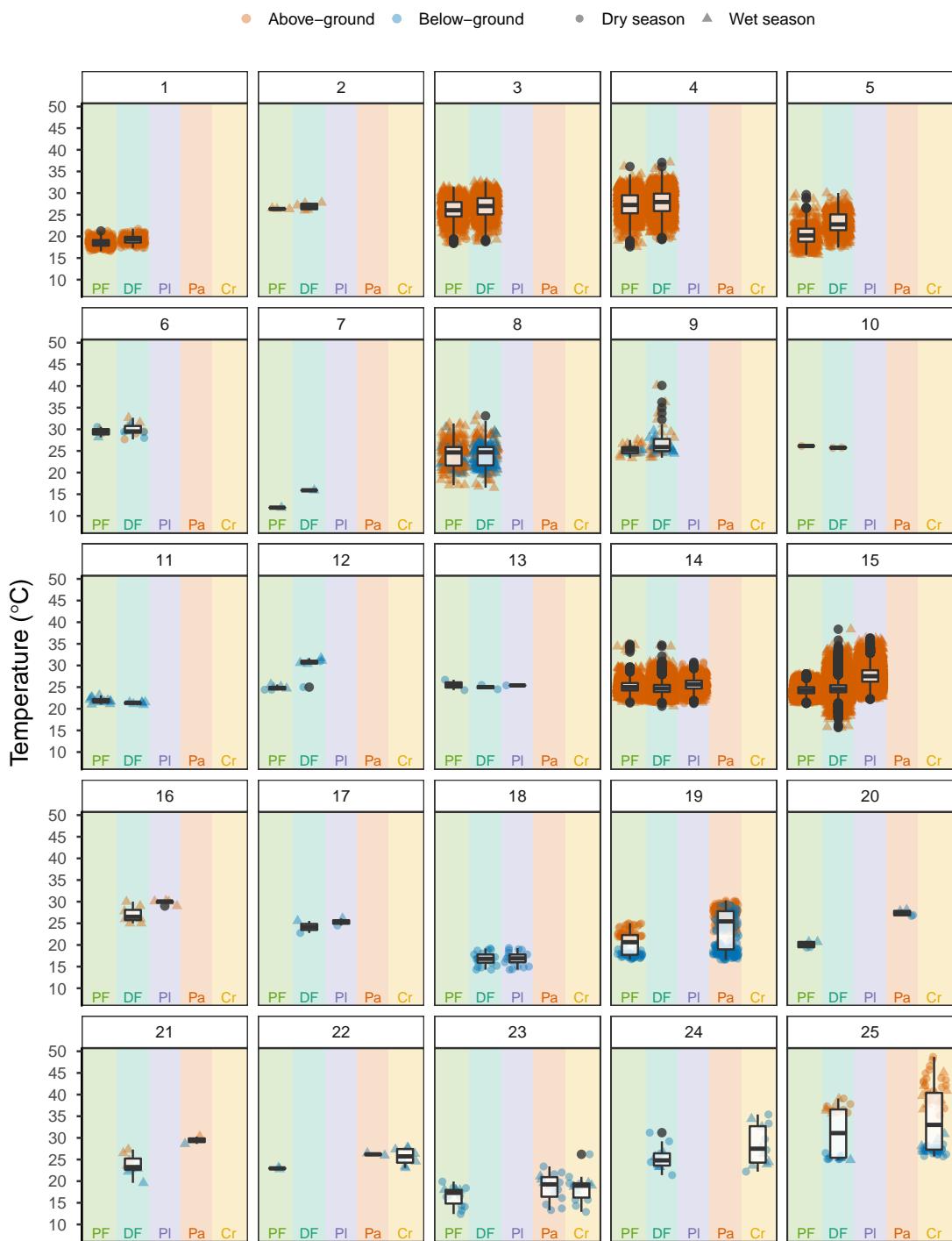


Figure A1.1: Day-time temperature against land-use type for each study contributing data to the analyses. Panel numbers refer to the study number in the reference list below. Land-use types are: primary forest (PF), degraded forest (DF), plantation (PI), pasture (Pa) and cropland (Cr). Panels are ordered 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).

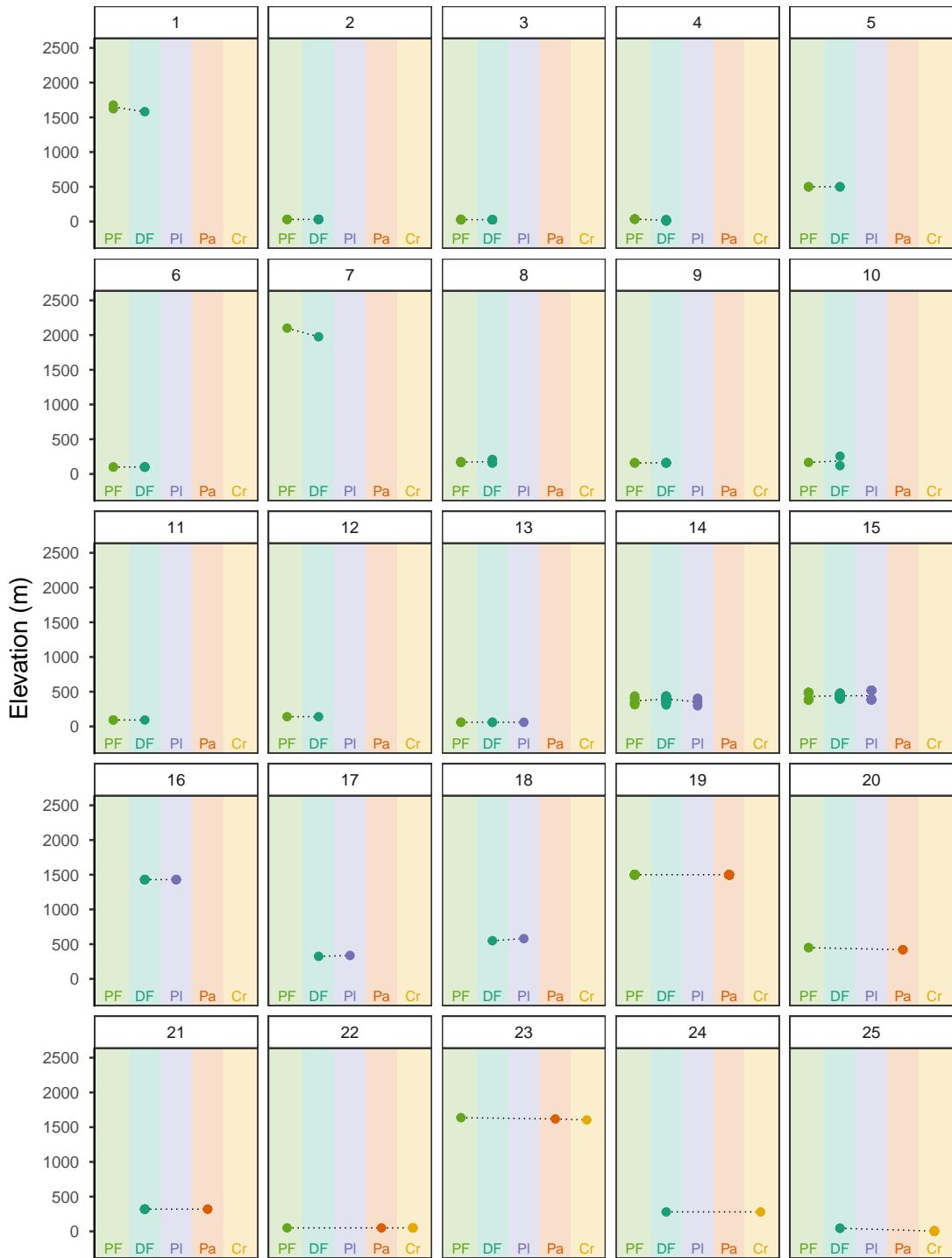


Figure A1.2: Site elevation against land-use type for each study contributing data to the analyses. Panel numbers refer to the study number in the reference list below. Land-use types are: primary forest (PF), degraded forest (DF), plantation (PI), pasture (Pa) and cropland (Cr). Panels are ordered by 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.

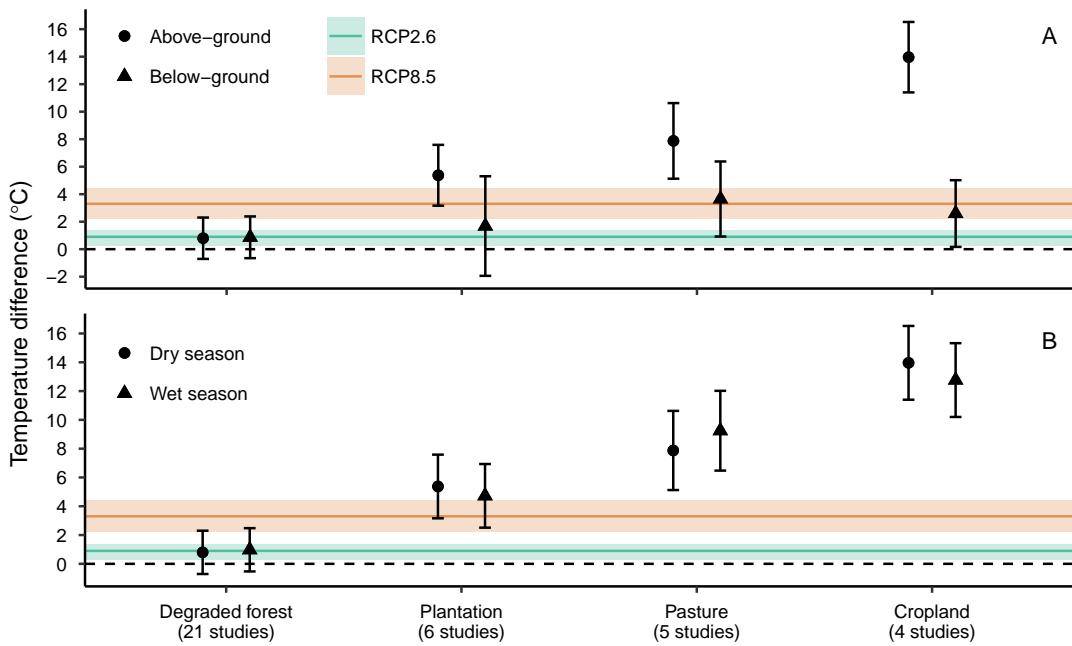


Figure A1.3: Model estimates of the temperature difference between altered land-use types and primary forest, using a reduced dataset to balance sample sizes between the different studies that contributed data. Parameter estimates are standardised against the estimate for primary forest, which is represented 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 (IPCC, 2013b). 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).

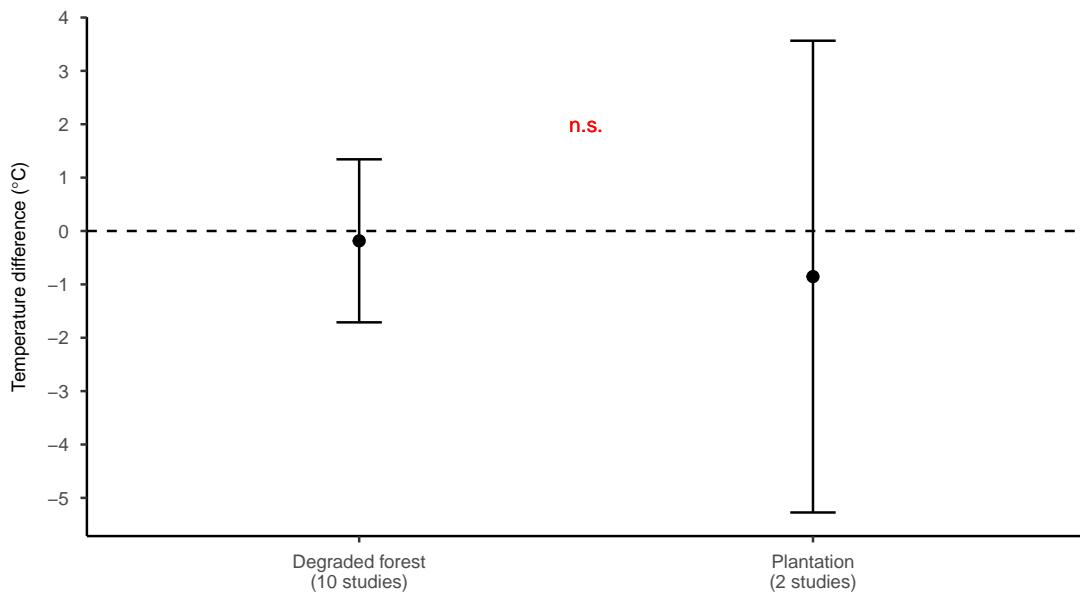


Figure A1.4: Model estimates of the nocturnal temperature difference between altered land-use types and primary forest. Note that cropland and pasture are missing from this analysis because nocturnal temperature data for these land-use types were not available. Parameter estimates are standardised against the estimate for primary forest, which is represented by the dotted line. Error bars are 95% confidence intervals.

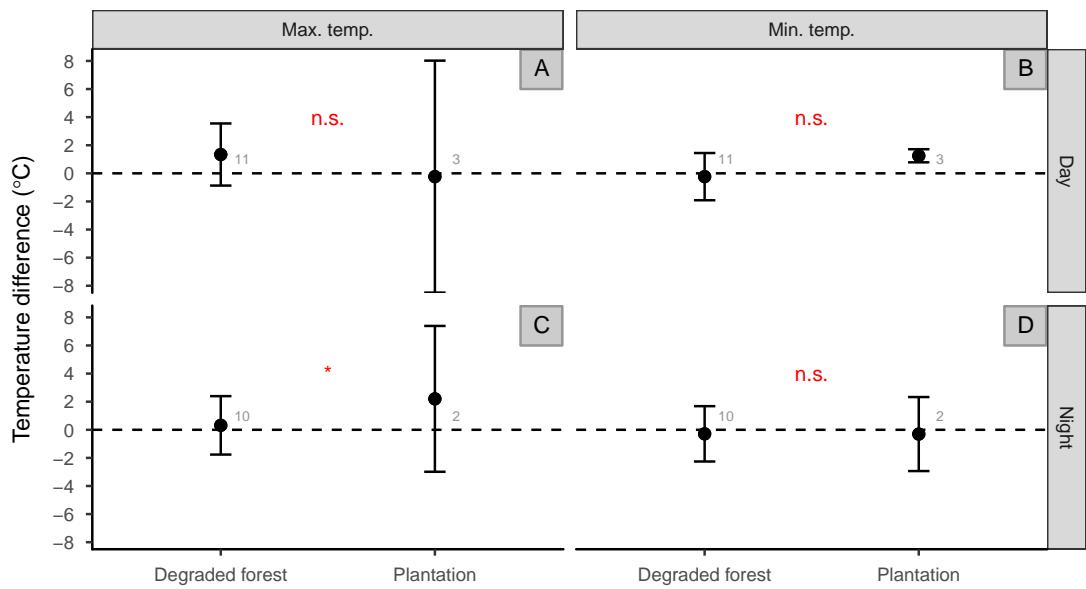


Figure A1.5: Model estimates of the difference between altered land-use types and primary forest in terms of temperature extremes. Day-time results are depicted in panels A and B, and night-time results in panels C and D. Panels A and C indicate the effect of land-use change on maximum temperature, and 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

B.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))
```

B.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 A1.3). 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 A1.3A) and season (LMM, $\chi^2 = 105.63$, df = 4, P < 0.001; Figure A1.3B). Specifically, the difference between altered land-use types and primary forest was greater above-ground than below-ground (Figure A1.3A), and variable between seasons according to the land-use type (Figure A1.3B).

B.2 Supplementary figures

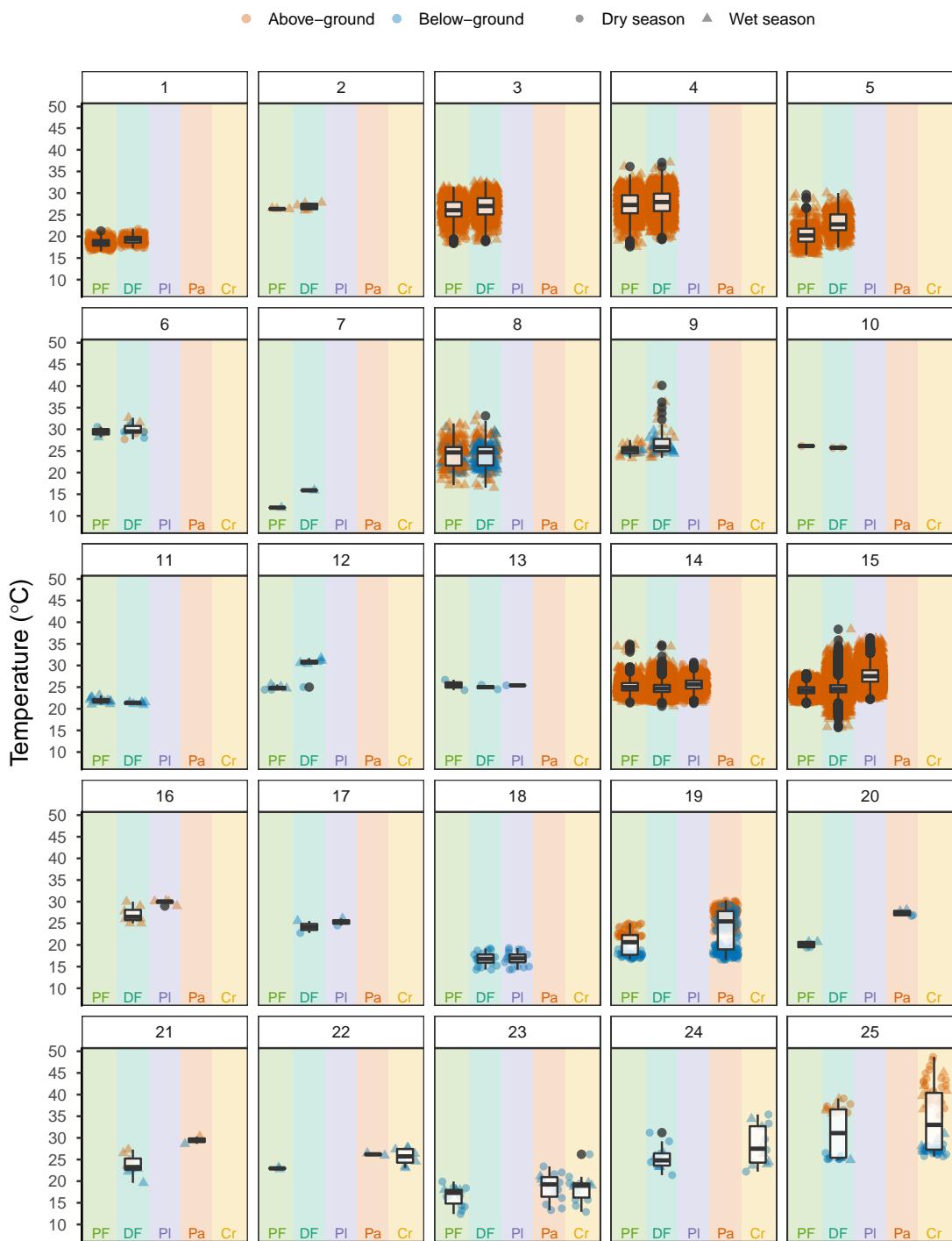


Figure A1.1: Day-time temperature against land-use type for each study contributing data to the analyses. Panel numbers refer to the study number in the reference list below. Land-use types are: primary forest (PF), degraded forest (DF), plantation (PI), pasture (Pa) and cropland (Cr). Panels are ordered 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).

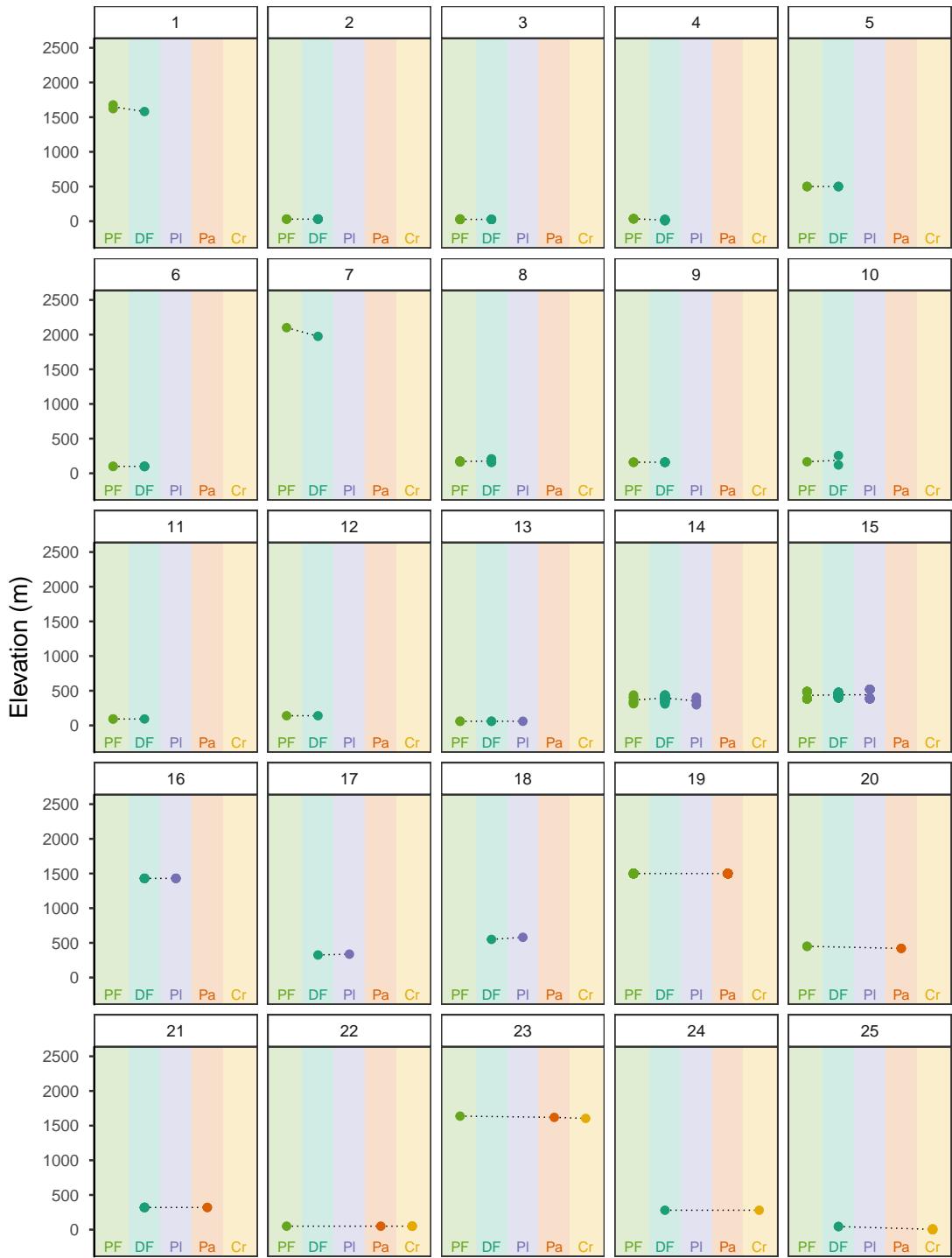


Figure A1.2: Site elevation against land-use type for each study contributing data to the analyses. Panel numbers refer to the study number in the reference list below. Land-use types are: primary forest (PF), degraded forest (DF), plantation (PI), pasture (Pa) and cropland (Cr). Panels are ordered by 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.

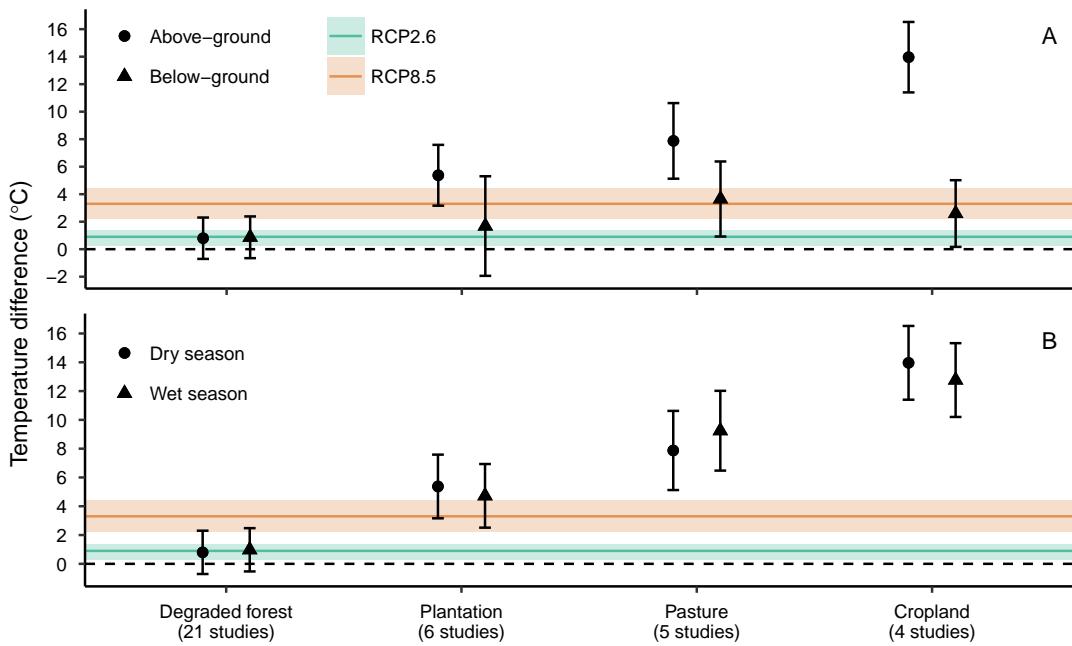


Figure A1.3: Model estimates of the temperature difference between altered land-use types and primary forest, using a reduced dataset to balance sample sizes between the different studies that contributed data. Parameter estimates are standardised against the estimate for primary forest, which is represented 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 (IPCC, 2013b). 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).

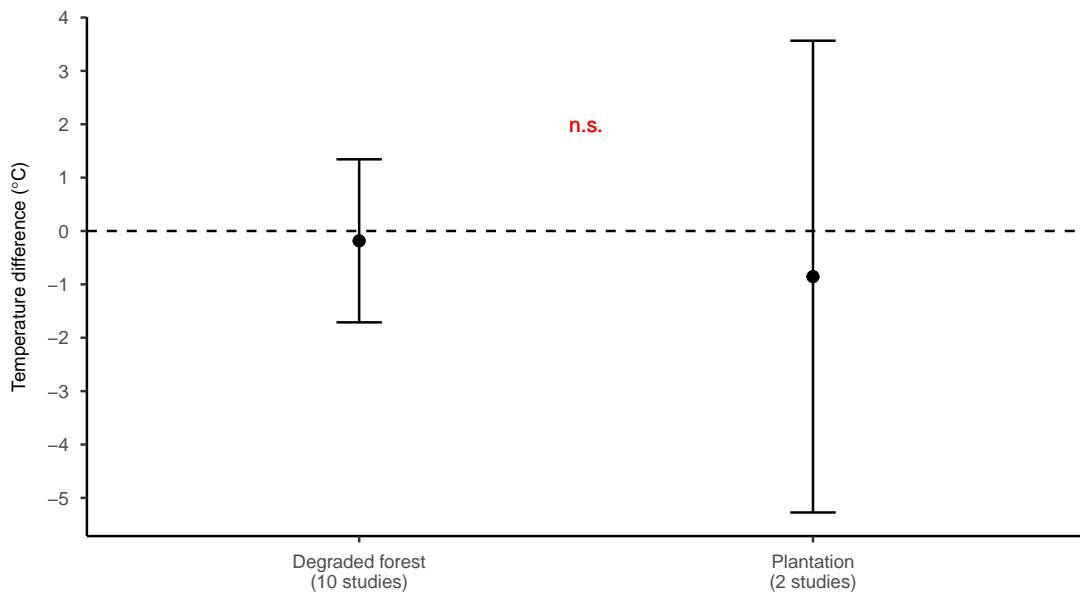


Figure A1.4: Model estimates of the nocturnal temperature difference between altered land-use types and primary forest. Note that cropland and pasture are missing from this analysis because nocturnal temperature data for these land-use types were not available. Parameter estimates are standardised against the estimate for primary forest, which is represented by the dotted line. Error bars are 95% confidence intervals.

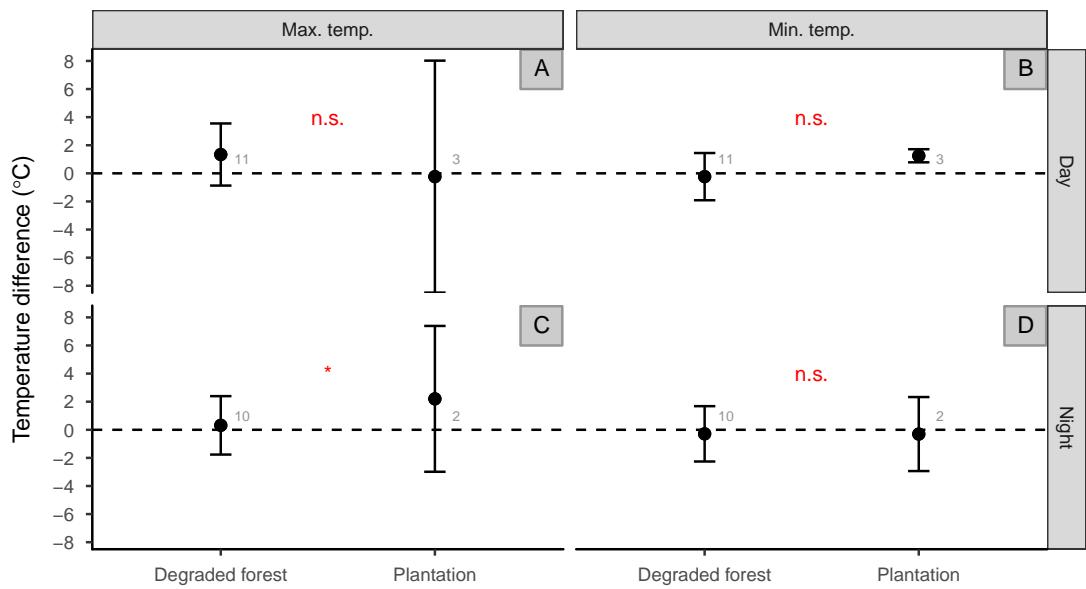


Figure A1.5: Model estimates of the difference between altered land-use types and primary forest in terms of temperature extremes. Day-time results are depicted in panels A and B, and night-time results in panels C and D. Panels A and C indicate the effect of land-use change on maximum temperature, and 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.

Bibliography

- Asner, G. P., Rudel, T. K., Aide, T. M., Defries, R., and Emerson, R. (2009). A contemporary assessment of change in humid tropical forests. *Conservation Biology*, 23(6):1386–1395.
- Baillie, J., Hilton-Taylor, C., Stuart, S. N., IUCN—The World Conservation Union, and Species Survival Commission (2004). *2004 IUCN red list of threatened species: a global species assessment*. IUCN—The World Conservation Union, Gland, Switzerland.
- Barnosky, A. D., Matzke, N., Tomiya, S., Wogan, G. O. U., Swartz, B., Quental, T. B., Marshall, C., McGuire, J. L., Lindsey, E. L., Maguire, K. C., Mersey, B., and Ferrer, E. A. (2011). Has the Earth’s sixth mass extinction already arrived? *Nature*, 471(7336):51–57.
- Bates, D., Mächler, M., Bolker, B., and Walker, S. (2015). Fitting Linear Mixed-Effects Models Using lme4. *Journal of Statistical Software*, 67(1):1–48.
- Bradshaw, W. E. and Holzapfel, C. M. (2006). Evolutionary Response to Rapid Climate Change. *Science*, 312(5779):1477–1478.
- Brodie, J., Post, E., and Laurance, W. F. (2012). Climate change and tropical biodiversity: a new focus. *Trends in Ecology & Evolution*, 27(3):145–150.
- Brodie, J. F., Giordano, A. J., Zipkin, E. F., Bernard, H., Mohd-Azlan, J., and Ambu, L. (2014). Correlation and Persistence of Hunting and Logging Impacts on Tropical Rainforest Mammals. *Conservation Biology*, pages n/a–n/a.
- Brook, B. W., Sodhi, N. S., and Bradshaw, C. J. A. (2008). Synergies among extinction drivers under global change. *Trends in Ecology & Evolution*, 23(8):453–460.
- Caillon, R., Suppo, C., Casas, J., Arthur Woods, H., and Pincebourde, S. (2014). Warming decreases thermal heterogeneity of leaf surfaces: implications for behavioural thermoregulation by arthropods. *Functional Ecology*, 28(6):1449–1458.
- Chen, I.-C., Shiu, H.-J., Benedick, S., Holloway, J. D., Chey, V. K., Barlow, H. S., Hill, J. K., and Thomas, C. D. (2009). Elevation increases in moth assemblages over 42 years on a tropical mountain. *Proceedings of the National Academy of Sciences*, 106(5):1479–1483.

- Chen, J., Franklin, J. F., and Spies, T. A. (1995). Growing-season microclimatic gradients from clearcut edges into old-growth douglas-fir forests. *Ecological Applications*, 5(1):74–86.
- Chou, C. and Lan, C.-W. (2012). Changes in the annual range of precipitation under global warming. *Journal of Climate*, 25(1):222–235.
- Christidis, N., Stott, P. A., Hegerl, G. C., and Betts, R. A. (2013). The role of land use change in the recent warming of daily extreme temperatures. *Geophysical Research Letters*, 40(3):589–594.
- Colwell, R. K., Brehm, G., Cardelús, C. L., Gilman, A. C., and Longino, J. T. (2008). Global warming, elevational range shifts, and lowland biotic attrition in the wet tropics. *Science*, 322(5899):258–261.
- Davin, E. L. and de Noblet-Ducoudré, N. (2010). Climatic impact of global-scale deforestation: radiative versus nonradiative processes. *Journal of Climate*, 23(1):97–112.
- Deutsch, C. A., Tewksbury, J. J., Huey, R. B., Sheldon, K. S., Ghalambor, C. K., Haak, D. C., and Martin, P. R. (2008). Impacts of climate warming on terrestrial ectotherms across latitude. *Proceedings of the National Academy of Sciences*, 105(18):6668–6672.
- du Plessis, K. L., Martin, R. O., Hockey, P. A. R., Cunningham, S. J., and Ridley, A. R. (2012). The costs of keeping cool in a warming world: implications of high temperatures for foraging, thermoregulation and body condition of an arid-zone bird. *Global Change Biology*, 18(10):3063–3070.
- Dubreuil, V., Debortoli, N., Funatsu, B., Nédélec, V., and Durieux, L. (2011). Impact of land-cover change in the Southern Amazonia climate: a case study for the region of Alta Floresta, Mato Grosso, Brazil. *Environmental Monitoring and Assessment*, 184(2):877–891.
- Edwards, D. P., Larsen, T. H., Docherty, T. D. S., Ansell, F. A., Hsu, W. W., Derhé, M. A., Hamer, K. C., and Wilcove, D. S. (2011). Degraded lands worth protecting: the biological importance of Southeast Asia's repeatedly logged forests. *Proceedings of the Royal Society B: Biological Sciences*, 278:82–90.
- Edwards, D. P., Tobias, J. A., Sheil, D., Meijaard, E., and Laurance, W. F. (2014). Maintaining ecosystem function and services in logged tropical forests. *Trends in Ecology & Evolution*, 29(9):511–520.
- Ewers, R. M. and Banks-Leite, C. (2013). Fragmentation Impairs the Microclimate Buffering Effect of Tropical Forests. *PLOS ONE*, 8(3):e58093.
- Fayle, T. M., Chung, A. Y. C., Dumbrell, A. J., Eggleton, P., and Foster, W. A. (2009). The Effect of Rain Forest Canopy Architecture on the Distribution of Epiphytic Ferns (*Asplenium* spp.) in Sabah, Malaysia. *Biotropica*, 41(6):676–681.

- Findell, K. L., Shevliakova, E., Milly, P. C. D., and Stouffer, R. J. (2007). Modeled impact of anthropogenic land cover change on climate. *Journal of Climate*, 20(14):3621–3634.
- Foley, J. A., DeFries, R., Asner, G. P., Barford, C., Bonan, G., Carpenter, S. R., Chapin, F. S., Coe, M. T., Daily, G. C., Gibbs, H. K., Helkowski, J. H., Holloway, T., Howard, E. A., Kucharik, C. J., Monfreda, C., Patz, J. A., Prentice, I. C., Ramankutty, N., and Snyder, P. K. (2005). Global consequences of land use. *Science*, 309(5734):570–574.
- Foley, J. A., Ramankutty, N., Brauman, K. A., Cassidy, E. S., Gerber, J. S., Johnston, M., Mueller, N. D., O’Connell, C., Ray, D. K., and West, P. C. (2011). Solutions for a cultivated planet. *Nature*, 478(7369):337–342.
- Foster, W. A., Snaddon, J. L., Turner, E. C., Fayle, T. M., Cockerill, T. D., Ellwood, M. D. F., Broad, G. R., Chung, A. Y. C., Eggleton, P., Khen, C. V., and Yusah, K. M. (2011). Establishing the evidence base for maintaining biodiversity and ecosystem function in the oil palm landscapes of South East Asia. *Philosophical Transactions of the Royal Society B: Biological Sciences*, 366(1582):3277–3291.
- França, F., Louzada, J., Korasaki, V., Griffiths, H., Silveira, J. M., and Barlow, J. (2016). Do space-for-time assessments underestimate the impacts of logging on tropical biodiversity? An Amazonian case study using dung beetles. *Journal of Applied Ecology*, 53(4):1098–1105.
- Freeman, B. G. and Freeman, A. M. C. (2014). Rapid upslope shifts in New Guinean birds illustrate strong distributional responses of tropical montane species to global warming. *Proceedings of the National Academy of Sciences*, 111(12):4490–4494.
- Frenne, P. D. and Verheyen, K. (2016). Weather stations lack forest data. *Science*, 351(6270):234–234.
- Gibbs, H. K., Ruesch, A. S., Achard, F., Clayton, M. K., Holmgren, P., Ramankutty, N., and Foley, J. A. (2010). Tropical forests were the primary sources of new agricultural land in the 1980s and 1990s. *Proceedings of the National Academy of Sciences*, 107(38):16732–16737.
- Gibson, L., Lee, T. M., Koh, L. P., Brook, B. W., Gardner, T. A., Barlow, J., Peres, C. A., Bradshaw, C. J. A., Laurance, W. F., Lovejoy, T. E., and Sodhi, N. S. (2011). Primary forests are irreplaceable for sustaining tropical biodiversity. *Nature*, 478(7369):378–381.
- Gillingham, P. (2010). *The relative importance of microclimate and land use to biodiversity*. PhD thesis, University of York, Department of Biology.
- Godfray, H. C. J., Beddington, J. R., Crute, I. R., Haddad, L., Lawrence, D., Muir, J. F., Pretty, J., Robinson, S., Thomas, S. M., and Toulmin, C. (2010). Food Security: The Challenge of Feeding 9 Billion People. *Science*, 327(5967):812–818.

- González del Pliego, P., Scheffers, B. R., Basham, E. W., Woodcock, P., Wheeler, C., Gilroy, J. J., Medina Uribe, C. A., Haugaasen, T., Freckleton, R. P., and Edwards, D. P. (2016). Thermally buffered microhabitats recovery in tropical secondary forests following land abandonment. *Biological Conservation*, 201:385–395.
- Gunderson, A. R. and Leal, M. (2016). A conceptual framework for understanding thermal constraints on ectotherm activity with implications for predicting responses to global change. *Ecology Letters*, 19(2):111–120.
- Hannah, L., Flint, L., Syphard, A. D., Moritz, M. A., Buckley, L. B., and McCullough, I. M. (2014). Fine-grain modeling of species' response to climate change: holdouts, stepping-stones, and microrefugia. *Trends in Ecology & Evolution*, 29(7):390–397.
- Hansen, M. C., Potapov, P. V., Moore, R., Hancher, M., Turubanova, S. A., Tyukavina, A., Thau, D., Stehman, S. V., Goetz, S. J., Loveland, T. R., Kommareddy, A., Egorov, A., Chini, L., Justice, C. O., and Townshend, J. R. G. (2013). High-resolution global maps of 21st-century forest cover change. *Science*, 342(6160):850–853.
- Hansen, M. C., Stehman, S. V., Potapov, P. V., Loveland, T. R., Townshend, J. R. G., DeFries, R. S., Pittman, K. W., Arunarwati, B., Stolle, F., Steininger, M. K., Carroll, M., and DiMiceli, C. (2008). Humid tropical forest clearing from 2000 to 2005 quantified by using multitemporal and multiresolution remotely sensed data. *Proceedings of the National Academy of Sciences*, 105(27):9439–9444.
- Hardwick, S. R., Toumi, R., Pfeifer, M., Turner, E. C., Nilus, R., and Ewers, R. M. (2015). The relationship between leaf area index and microclimate in tropical forest and oil palm plantation: Forest disturbance drives changes in microclimate. *Agricultural and Forest Meteorology*, 201:187–195.
- Hersteinsson, P. and MacDonald, D. W. (1992). Interspecific Competition and the Geographical Distribution of Red and Arctic Foxes *Vulpes Vulpes* and *Alopex lagopus*. *Oikos*, 64(3):505–515.
- Hill, J. K., Thomas, C. D., Fox, R., Telfer, M. G., Willis, S. G., Asher, J., and Huntley, B. (2002). Responses of butterflies to twentieth century climate warming: implications for future ranges. *Proceedings of the Royal Society B: Biological Sciences*, 269(1505):2163–2171.
- Hirsch, T. and Secretariat of the Convention on Biological Diversity (2010). *Global biodiversity outlook 3*. Secretariat of the Convention on Biological Diversity, Montreal, Quebec, Canada.
- Hurtt, G. C., Chini, L. P., Frolking, S., Betts, R. A., Feddema, J., Fischer, G., Fisk, J. P., Hibbard, K., Houghton, R. A., Janetos, A., Jones, C. D., Kindermann, G., Kinoshita, T., Goldewijk,

- K. K., Riahi, K., Shevliakova, E., Smith, S., Stehfest, E., Thomson, A., Thornton, P., Vuuren, D. P. v., and Wang, Y. P. (2011). Harmonization of land-use scenarios for the period 1500–2100: 600 years of global gridded annual land-use transitions, wood harvest, and resulting secondary lands. *Climatic Change*, 109(1-2):117–161.
- IPCC (2007). *Climate Change 2007: The Physical Science Basis. Contribution of Working Group I to the Fourth Assessment Report of the Intergovernmental Panel on Climate Change*. Cambridge University Press, Cambridge, United Kingdom and New York, NY, USA, 996 pp.
- IPCC (2013a). *Climate Change 2013: The Physical Science Basis. Contribution of Working Group I to the Fifth Assessment Report of the Intergovernmental Panel on Climate Change*. Cambridge University Press, Cambridge, United Kingdom and New York, NY, USA.
- IPCC (2013b). *Climate Change 2013: The Physical Science Basis. Contribution of Working Group I to the Fifth Assessment Report of the Intergovernmental Panel on Climate Change*. Cambridge University Press, Cambridge, United Kingdom and New York, NY, USA.
- Isaac, J. L., De Gabriel, J. L., and Goodman, B. A. (2008). Microclimate of daytime den sites in a tropical possum: implications for the conservation of tropical arboreal marsupials. *Animal Conservation*, 11(4):281–287.
- IUCN (2014). The IUCN Red List of Threatened Species. Version 2014.3. [Online].
- Katovai, E., Burley, A. L., and Mayfield, M. M. (2012). Understory plant species and functional diversity in the degraded wet tropical forests of Kolombangara Island, Solomon Islands. *Biological Conservation*, 145(1):214–224.
- Kearney, M., Shine, R., Porter, W. P., and Wake, D. B. (2009). The Potential for Behavioral Thermoregulation to Buffer "Cold-Blooded" Animals against Climate Warming. *Proceedings of the National Academy of Sciences of the United States of America*, 106(10):3835–3840.
- Kingsolver, J. G. (2009). The well-temperated biologist. *The American Naturalist*, 174(6):755–768.
- Kumar, R. and Shahabuddin, G. (2005). Effects of biomass extraction on vegetation structure, diversity and composition of forests in Sariska Tiger Reserve, India. *Environmental Conservation*, 32(03):248.
- Laurance, W. F., Clements, G. R., Sloan, S., O'Connell, C. S., Mueller, N. D., Gooseem, M., Venter, O., Edwards, D. P., Phalan, B., Balmford, A., Van Der Ree, R., and Arrea, I. B. (2014). A global strategy for road building. *Nature*, 513(7517):229–232.
- Lawrence, D. and Vandecar, K. (2015). Effects of tropical deforestation on climate and agriculture. *Nature Climate Change*, 5(1):27–36.

- Lewis, S. L., Edwards, D. P., and Galbraith, D. (2015). Increasing human dominance of tropical forests. *Science*, 349(6250):827–832.
- Li, Y., Zhao, M., Motesharrei, S., Mu, Q., Kalnay, E., and Li, S. (2015). Local cooling and warming effects of forests based on satellite observations. *Nature Communications*, 6:6603.
- Loarie, S. R., Duffy, P. B., Hamilton, H., Asner, G. P., Field, C. B., and Ackerly, D. D. (2009). The velocity of climate change. *Nature*, 462(7276):1052–1055.
- Luskin, M. S. and Potts, M. D. (2011). Microclimate and habitat heterogeneity through the oil palm lifecycle. *Basic and Applied Ecology*, 12(6):540–551.
- Mantyka-pringle, C. S., Martin, T. G., and Rhodes, J. R. (2012). Interactions between climate and habitat loss effects on biodiversity: a systematic review and meta-analysis. *Global Change Biology*, 18(4):1239–1252.
- Mason, T. H., Stephens, P. A., Apollonio, M., and Willis, S. G. (2014). Predicting potential responses to future climate in an alpine ungulate: interspecific interactions exceed climate effects. *Global Change Biology*, 20(12):3872–3882.
- Melin, M., Matala, J., Mehtätalo, L., Tiilikainen, R., Tikkanen, O.-P., Maltamo, M., Pusenius, J., and Packalen, P. (2014). Moose (*Alces alces*) reacts to high summer temperatures by utilizing thermal shelters in boreal forests - an analysis based on airborne laser scanning of the canopy structure at moose locations. *Global Change Biology*, 20(4):1115–1125.
- Mora, C., Frazier, A. G., Longman, R. J., Dacks, R. S., Walton, M. M., Tong, E. J., Sanchez, J. J., Kaiser, L. R., Stender, Y. O., Anderson, J. M., Ambrosino, C. M., Fernandez-Silva, I., Giuseffi, L. M., and Giambelluca, T. W. (2013). The projected timing of climate departure from recent variability. *Nature*, 502(7470):183–187.
- Murcia, C. (1995). Edge effects in fragmented forests: implications for conservation. *Trends in Ecology & Evolution*, 10(2):58–62.
- Murphy, G. E. P. and Romanuk, T. N. (2014). A meta-analysis of declines in local species richness from human disturbances. *Ecology and Evolution*, 4(1):91–103.
- Myers, N., Mittermeier, R. A., Mittermeier, C. G., Da Fonseca, G. A. B., and Kent, J. (2000). Biodiversity hotspots for conservation priorities. *Nature*, 403:853–858.
- NASA (2017). SRTM NASA Version 3.
- Newbold, T., Hudson, L. N., Hill, S. L. L., Contu, S., Lysenko, I., Senior, R. A., Börger, L., Bennett, D. J., Choimes, A., Collen, B., Day, J., De Palma, A., Díaz, S., Echeverría-Londoño, S., Edgar, M. J., Feldman, A., Garon, M., Harrison, M. L. K., Alhusseini, T., Ingram, D. J., Itescu, Y., Kattge, J., Kemp, V., Kirkpatrick, L., Kleyer, M., Correia, D. L. P., Martin, C. D., Meiri, S.,

- Novosolov, M., Pan, Y., Phillips, H. R. P., Purves, D. W., Robinson, A., Simpson, J., Tuck, S. L., Weiher, E., White, H. J., Ewers, R. M., Mace, G. M., Scharlemann, J. P. W., and Purvis, A. (2015). Global effects of land use on local terrestrial biodiversity. *Nature*, 520(7545):45–50.
- NOAA ("nd"). Solar Calculations.
- Nussey, D. H., Postma, E., Gienapp, P., and Visser, M. E. (2005). Selection on Heritable Phenotypic Plasticity in a Wild Bird Population. *Science*, 310(5746):304–306.
- O'Connor, M. I., Selig, E. R., Pinsky, M. L., and Altermatt, F. (2012). Toward a conceptual synthesis for climate change responses. *Global Ecology and Biogeography*, 21(7):693–703.
- Oke, T. R. (1987). *Boundary layer climates*. Methuen, London, 2nd ed. edition.
- Okuda, T., Suzuki, M., Adachi, N., Quah, E. S., Hussein, N. A., and Manokaran, N. (2003). Effect of selective logging on canopy and stand structure and tree species composition in a lowland dipterocarp forest in peninsular Malaysia. *Forest Ecology and Management*, 175(1–3):297–320.
- Opdam, P. and Wascher, D. (2004). Climate change meets habitat fragmentation: linking landscape and biogeographical scale levels in research and conservation. *Biological Conservation*, 117(3):285–297.
- Parmesan, C. (2006). Ecological and Evolutionary Responses to Recent Climate Change. *Annual Review of Ecology, Evolution, and Systematics*, 37(1):637–669.
- Parmesan, C., Ryrholm, N., Stefanescu, C., Hill, J. K., Thomas, C. D., Descimon, H., Huntley, B., Kaila, L., Kullberg, J., Tammaru, T., Tennent, W. J., Thomas, J. A., and Warren, M. (1999). Poleward shifts in geographical ranges of butterfly species associated with regional warming. *Nature*, 399(6736):579–583.
- Peck, L. S. (2011). Organisms and responses to environmental change. *Marine Genomics*, 4(4):237–243.
- Peck, L. S., Clark, M. S., Morley, S. A., Massey, A., and Rossetti, H. (2009). Animal temperature limits and ecological relevance: effects of size, activity and rates of change. *Functional Ecology*, 23(2):248–256.
- Pielke, R. A., Pitman, A., Niyogi, D., Mahmood, R., McAlpine, C., Hossain, F., Goldewijk, K. K., Nair, U., Betts, R., Fall, S., Reichstein, M., Kabat, P., and de Noblet, N. (2011). Land use/land cover changes and climate: modeling analysis and observational evidence. *Wiley Interdisciplinary Reviews: Climate Change*, 2(6):828–850.

- Pimm, S. L., Russell, G. J., Gittleman, J. L., and Brooks, T. M. (1995). The Future of Biodiversity. *Science*, 269(5222):347–350.
- Pounds, J. A., Fogden, M. P. L., and Campbell, J. H. (1999). Biological response to climate change on a tropical mountain. *Nature*, 398(6728):611–615.
- Putz, F. E., Sist, P., Frederickson, T., and Dykstra, D. (2008). Reduced-impact logging: Challenges and opportunities. *Forest Ecology and Management*, 256(7):1427–1433.
- Putz, F. E., Zuidema, P. A., Synnott, T., Peña-Claros, M., Pinard, M. A., Sheil, D., Vanclay, J. K., Sist, P., Gourlet-Fleury, S., Griscom, B., Palmer, J., and Zagt, R. (2012). Sustaining conservation values in selectively logged tropical forests: the attained and the attainable. *Conservation Letters*, 5(4):296–303.
- Puurtinen, M., Elo, M., Jalasvuori, M., Kahilainen, A., Ketola, T., Kotiaho, J. S., Mönkkönen, M., and Pentikäinen, O. T. (2015). Temperature-dependent mutational robustness can explain faster molecular evolution at warm temperatures, affecting speciation rate and global patterns of species diversity. *Ecography*, pages 001–009.
- R Core Team (2017). *R: A Language and Environment for Statistical Computing*. R Foundation for Statistical Computing, Vienna, Austria.
- Ramdani, F., Moffiet, T., and Hino, M. (2014). Local surface temperature change due to expansion of oil palm plantation in Indonesia. *Climatic Change*, 123(2):189–200.
- Sala, O. E., Chapin, F. S., Iii, Armesto, J. J., Berlow, E., Bloomfield, J., Dirzo, R., Huber-Sanwald, E., Huenneke, L. F., Jackson, R. B., Kinzig, A., Leemans, R., Lodge, D. M., Mooney, H. A., Oesterheld, M., Poff, N. L., Sykes, M. T., Walker, B. H., Walker, M., and Wall, D. H. (2000). Global biodiversity scenarios for the year 2100. *Science*, 287(5459):1770–1774.
- Saner, P., Lim, R., Burla, B., Ong, R. C., Scherer-Lorenzen, M., and Hector, A. (2009). Reduced soil respiration in gaps in logged lowland dipterocarp forests. *Forest Ecology and Management*, 258(9):2007–2012.
- Scheffers, B. R., Edwards, D. P., Diesmos, A., Williams, S. E., and Evans, T. A. (2014a). Microhabitats reduce animal's exposure to climate extremes. *Global Change Biology*, 20(2):495–503.
- Scheffers, B. R., Evans, T. A., Williams, S. E., and Edwards, D. P. (2014b). Microhabitats in the tropics buffer temperature in a globally coherent manner. *Biology Letters*, 10(12):20140819.
- Schnitzer, S. A., Parren, M. P. E., and Bongers, F. (2004). Recruitment of lianas into logging gaps and the effects of pre-harvest climber cutting in a lowland forest in Cameroon. *Forest Ecology and Management*, 190(1):87–98.

- Scriven, S. A., Hodgson, J. A., McClean, C. J., and Hill, J. K. (2015). Protected areas in Borneo may fail to conserve tropical forest biodiversity under climate change. *Biological Conservation*, 184:414–423.
- Snyder, P. K., Foley, J. A., Hitchman, M. H., and Delire, C. (2004). Analyzing the effects of complete tropical forest removal on the regional climate using a detailed three-dimensional energy budget: An application to Africa. *Journal of Geophysical Research: Atmospheres*, 109(D21):D21102.
- Sturm, M., Racine, C., and Tape, K. (2001). Climate change: Increasing shrub abundance in the Arctic. *Nature*, 411(6837):546–547.
- Suggitt, A. J., Gillingham, P. K., Hill, J. K., Huntley, B., Kunin, W. E., Roy, D. B., and Thomas, C. D. (2011). Habitat microclimates drive fine-scale variation in extreme temperatures. *Oikos*, 120(1):1–8.
- Sunday, J. M., Bates, A. E., Kearney, M. R., Colwell, R. K., Dulvy, N. K., Longino, J. T., and Huey, R. B. (2014). Thermal-safety margins and the necessity of thermoregulatory behavior across latitude and elevation. *Proceedings of the National Academy of Sciences of the United States of America*, 111(15):5610–5615.
- Tewksbury, J. J., Huey, R. B., and Deutsch, C. A. (2008). Putting the heat on tropical animals. *Science*, 320(5881):1296–1297.
- Thomas, C. D., Cameron, A., Green, R. E., Bakkenes, M., Beaumont, L. J., Collingham, Y. C., Erasmus, B. F. N., de Siqueira, M. F., Grainger, A., Hannah, L., Hughes, L., Huntley, B., van Jaarsveld, A. S., Midgley, G. F., Miles, L., Ortega-Huerta, M. A., Townsend Peterson, A., Phillips, O. L., and Williams, S. E. (2004). Extinction risk from climate change. *Nature*, 427(6970):145–148.
- Thomas, C. D., Gillingham, P. K., Bradbury, R. B., Roy, D. B., Anderson, B. J., Baxter, J. M., Bourn, N. A. D., Crick, H. Q. P., Findon, R. A., Fox, R., Hodgson, J. A., Holt, A. R., Morecroft, M. D., O'Hanlon, N. J., Oliver, T. H., Pearce-Higgins, J. W., Procter, D. A., Thomas, J. A., Walker, K. J., Walmsley, C. A., Wilson, R. J., and Hill, J. K. (2012). Protected areas facilitate species' range expansions. *Proceedings of the National Academy of Sciences*, 109(35):14063–14068.
- Thomas, C. D. and Lennon, J. J. (1999). Birds extend their ranges northwards. *Nature*, 399(6733):213–213.
- Tuff, K. T., Tuff, T., and Davies, K. F. (2016). A framework for integrating thermal biology into fragmentation research. *Ecology Letters*, 19(4):361–374.
- United Nations (2014). United Nations Millennium Development Goals. [Online].

- Van Houtan, K. S., Pimm, S. L., Halley, J. M., Bierregaard, R. O., and Lovejoy, T. E. (2007). Dispersal of Amazonian birds in continuous and fragmented forest. *Ecology Letters*, 10(3):219–229.
- Walther, G. R., Post, E., Convey, P., Menzel, A., Parmesan, C., Beebee, T. J. C., Fromentin, J. M., Hoegh-Guldberg, O., and Bairlein, F. (2002). Ecological responses to recent climate change. *Nature*, 416(6879):389–395.
- Wickham, J. D., Wade, T. G., and Riitters, K. H. (2012). Comparison of cropland and forest surface temperatures across the conterminous United States. *Agricultural and Forest Meteorology*, 166–167:137–143.
- Wiens, J. A. and Bachelet, D. (2010). Matching the multiple scales of conservation with the multiple scales of climate change. *Conservation Biology*, 24(1):51–62.
- Xu, M., Qi, Y., Chen, J., and Song, B. (2004). Scale-dependent relationships between landscape structure and microclimate. *Plant Ecology*, 173(1):39–57.
- Zuur, A. F. (2009). *Mixed effects models and extensions in ecology with R*. Statistics for biology and health. Springer, New York, NY.