



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**

September 2018

# Contents

<b>Abstract</b>	x
<b>Acknowledgements</b>	xi
<b>Author's declaration</b>	xii
<b>1 General introduction</b>	1
<b>2 PLAN</b>	2
2.1 Threats to biodiversity . . . . .	2
2.2 Land-use change in the tropics . . . . .	3
2.3 Climate change in the tropics . . . . .	3
2.4 Thesis aims and rationale . . . . .	5
2.5 Threats to biodiversity . . . . .	7
2.6 Responses to climate change . . . . .	8
2.7 Influence of land-use change . . . . .	12
2.8 Thesis aims and rationale . . . . .	14
<b>3 A pantropical analysis of the impacts of forest degradation and conversion on local temperature</b>	15
3.1 Abstract . . . . .	16
3.2 Introduction . . . . .	16
3.3 Methods . . . . .	19
3.4 Results . . . . .	21
3.5 Discussion . . . . .	26
3.6 Data availability and R code . . . . .	30
3.7 Acknowledgements . . . . .	30
<b>4 A framework for quantifying fine-scale thermal heterogeneity in the field</b>	31
4.1 Abstract . . . . .	32
4.2 Introduction . . . . .	32
4.3 Methods . . . . .	34

4.4	Results . . . . .	36
4.5	Discussion . . . . .	38
<b>5</b>	<b>Tropical forests are thermally buffered despite intensive selective logging</b>	<b>40</b>
5.1	Abstract . . . . .	41
5.2	Introduction . . . . .	41
5.3	Methods . . . . .	43
5.4	Results . . . . .	49
5.5	Discussion . . . . .	54
5.6	Data availability . . . . .	57
5.7	Acknowledgements . . . . .	57
<b>6</b>	<b>The impact of recent forest cover change on climate connectivity in the tropics</b>	<b>58</b>
6.1	Abstract . . . . .	59
6.2	Introduction . . . . .	59
6.3	Materials and Methods . . . . .	61
6.4	Results . . . . .	63
6.5	Discussion . . . . .	64
<b>7</b>	<b>Discussion</b>	<b>66</b>
7.1	Summary of thesis findings . . . . .	66
7.2	Climate at the fine scale . . . . .	67
7.3	Climate at the coarse scale . . . . .	68
7.4	Wider applicability of findings . . . . .	69
7.5	Recommendations for conservation and futher research . . . . .	70
7.6	Conclusions . . . . .	71
<b>A</b>	<b>Supporting information for Chapter 2</b>	<b>72</b>
A.1	Impact of unbalanced sampling . . . . .	72
A.2	Supplementary figures . . . . .	74
<b>B</b>	<b>Supporting information for Chapter 4</b>	<b>78</b>
B.1	Sampling methods for forest structure . . . . .	78
B.2	Extracting and processing data from thermal images . . . . .	80
B.3	Sampling methods for microhabitat volume . . . . .	81
B.4	Impact of logging on macroclimate . . . . .	82
B.5	Impact of logging on microclimate over 24 hours . . . . .	84
B.6	Supplementary figures . . . . .	86

# List of Tables

3.1	Land use classification definitions (modified from Extended Data Table 1 in Newbold et al. (2015). . . . .	18
3.2	Summary of the 25 studies contributing data to analyses. Study number corresponds to point labels in Figure 3.1. Crosses indicate the land-use types, position(s) relative to ground level and season(s) considered by each study. . . . .	24
3.3	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. . . . .	27

# List of Figures

2.1 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). . . . .	10
3.1 Locations of the 25 studies contributing data to the analyses. Point labels correspond to the study number in Table 3.1. The shading and size of concentric points corresponds to different land-use types, to indicate the data provided by each study. . . . .	22
3.2 Raw day-time temperature against land-use type, across all studies contributing data to the analyses (plotted by study in Figure A.4). 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). . . . .	22
3.3 Model estimates of local day-time temperature in altered land-use types relative to primary forest (depicted by the black dashed line). In panel (a), different symbols denote position relative to the ground (above-or below-ground), and the season is held at the reference level (dry season). In panel (b), different symbols denote the season (dry or wet), and the position relative to the ground is held at the reference level (above-ground). Error bars are 95% confidence intervals. Solid lines indicate projected warming in the tropics for the period 2081–2100 compared to the period 1986–2005, as a result of global climate change (IPCC, 2013). Shaded bands indicate 5%–95% ranges from the distribution of the climate model ensemble. Colors represent the lowest and highest warming scenarios (RCP2.6 and RCP8.5, respectively). . .	25

4.1	The influence of time and forest structure (measured as tree stand basal area; m <sup>2</sup> /ha) on the average area of hot patches (a) and the density of hot patches (patches/m <sup>2</sup> ; b). Points are shaded according to forest structure, from simpler, more open forests in light green to more complex and closed forests in dark green. Fitted values for patch characteristics against time of day are depicted by the black line, with a grey band for the 95% confidence intervals.	37
5.1	Study location in Malaysian Borneo (a), and distribution of sites (b): six sites in primary forest (blue) and six sites in logged forest (orange). Each site comprised five plots along an existing transect, with plot centres separated by 125 m (c). Tree and sapling stand basal area was calculated from the distance to and circumference of the nearest two trees and saplings in each of four quadrants centred on the plot centre (d; see section B.1 for more details). Curved arrows indicate the direction of magnification, from panels a-d. . . . .	44
5.2	Example thermal image. Pixels are shaded from cold (purple) to hot (yellow). Warm patches (outlined in pink) and cool patches (outlined in blue) were identified using the Getis-Ord local statistic of each pixel. . . . .	46
5.3	Comparison between primary forest (blue) and logged forest (orange) in terms of: (a-d) the relationship between microclimate temperature and macroclimate temperature; and (e-h) absolute microclimate temperature across varying levels of forest quality (measured as tree stand basal area). Microclimates were measured at the surface (a, e), and inside deadwood (b, f), tree holes (c, g) and leaf litter (d, h). The grey dashed lines in panels a-d indicate zero temperature buffering, where the microclimate temperature is equal to the macroclimate temperature. In all panels, shaded bands are 95% confidence intervals. . . . .	51
5.4	The influence of forest type (primary or logged) and forest quality (measured as tree stand basal area) on microclimate temperature range. Daily range for surface microclimates (a) was calculated as the difference between the maximum and the minimum microclimate temperature (itself calculated as the 5 <sup>th</sup> percentile temperature across four photos taken at each visit to each plot). For microclimates inside deadwood (b), tree holes (c) and leaf litter (d), the daily range was the difference between the 95 <sup>th</sup> percentile and 5 <sup>th</sup> percentile of raw temperature measurements. Primary forest data points are depicted as blue circles and logged forest as orange triangles. Shaded bands represent 95% confidence intervals. . . . .	52

5.5 The influence of forest type (primary or logged forest) and forest quality (measured as tree stand basal area) on microclimate availability. Results for surface microclimates (top row) include: the temperature range from the warmest warm patch to the coolest cool patch (a); the average surface area of cool patches (b); and the Aggregation Index of cool patches (c). The volume (per m <sup>2</sup> forest) of microhabitats typically associated with microclimates (bottom row) is shown for deadwood (d), tree holes (e) and leaf litter (f). Primary forest data points are depicted as blue circles and logged forest as orange triangles. Shaded bands represent 95% confidence intervals. Asterisks in panel f denote a statistically significant difference at 0.001 < P < 0.01 (**). . . . .	53
A.1 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, 2013). 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). . . . .	74
A.2 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. . . . .	74
A.3 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. . . . .	75

A.4 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). . . . .	76
A.5 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. . . . .	77
B.1 Sampling design schematic. . . . .	78
B.2 The influence of forest type (primary or logged forest) and forest quality (measured as tree stand basal area; m <sup>2</sup> /ha) on macroclimate temperature (top row) and macroclimate vapour pressure deficit (VPD; bottom row). Macroclimate measurements collected using a whirling hygrometer are shown in the left column, and from dataloggers in the right column. Data points from primary forest points are depicted as blue circles, and from logged forest as orange triangles. Shaded bands are 95% confidence intervals.	86
B.3 Comparison of the relationship between microclimate temperature and macroclimate temperature within primary forest (blue circles) and logged forest (orange triangles), during the day (top row) and night (bottom row), and for three microhabitats: deadwood (left column), tree holes (centre column) and leaf litter (right column). The grey dashed line indicates zero temperature buffering, where the microclimate temperature is equal to the macroclimate temperature. Shaded bands are 95% confidence intervals. . .	86



# **Abstract**

Stuff about tropical forests being important and blah blah blah.

# Acknowledgements

Thanks everyone for being alright.

# Author's declaration

The research presented in this thesis is my own. This thesis has not been submitted for any other award at this or any other institution. In addition to myself (R.A.S.) there were several collaborators in this research: David Edwards (D.P.E.), Jane Hill (J.K.H.), Pamela González del Pliego (P.G.), Laurel Goode (L.K.G.) and Suzan Benedick (S.B.).

## Chapter 2

This chapter has been published as:

**Senior RA, Hill JK, González del Pliego P, Goode LK, Edwards DP. A pantropical analysis of the impacts of forest degradation and conversion on local temperature. Ecology and Evolution. 2017;7:7897–7908.**

This chapter is reproduced in full in this thesis, with minor formatting alterations. The overall contribution of authors was as follows: R.A.S., D.P.E., and J.K.H conceived the study. R.A.S., P.G. and L.K.G. collated the data. R.A.S. performed statistical analyses. R.A.S. wrote the manuscript, with contributions from D.P.E. and J.K.H.

## Chapter 4

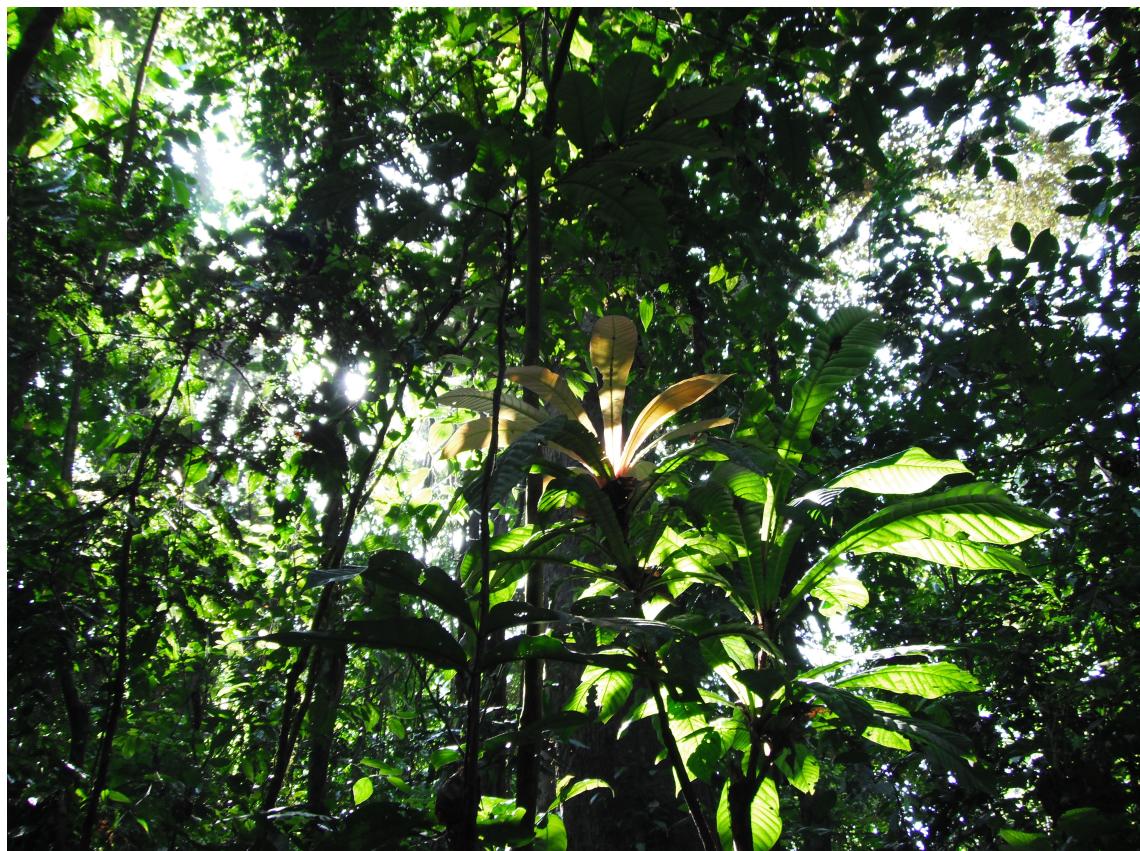
This chapter has been published as:

**Senior RA, Hill JK, Benedick S, Edwards DP. Tropical forests are thermally buffered despite intensive selective logging. Global Change Biology. 2018;24:1267–1278.**

This chapter is reproduced in full in this thesis, with minor formatting alterations. The overall contribution of authors was as follows: R.A.S., D.P.E., and J.K.H conceived the study. R.A.S. collected the data, with S.B. providing logistical support. R.A.S. performed all statistical analyses and wrote the manuscript, with contributions from D.P.E. and J.K.H.

# Chapter 1

## General introduction



Sunshine through rainforest canopy in Danum Valley.

# Chapter 2

## PLAN

### 2.1 Threats to biodiversity

- Global extinction crisis, caused by humans (Barnosky et al., 2011)
  - Recent rates of extinction are between 100 and 1000 times greater than pre-human levels (Barnosky et al., 2011; Pimm et al., 1995)
  - Has not slowed despite increasing awareness and action (?)
- Main ways in which humans drive extinction
  - Land-use change, climate change, pollution, over-exploitation and invasive species (Hirsch and Secretariat of the Convention on Biological Diversity, 2010)
  - Greatest overall threat to terrestrial systems is currently land-use change, climate change is forecast to become increasingly important (Sala et al., 2000)
- Why extinction matters
  - Intrinsic value (?)
  - Extrinsic value (ecosystem services) (??)
  - Resilience (?) and planetary boundaries (?)
- Why the tropics are particularly important
  - Harbour most of the world's terrestrial biodiversity (Jenkins et al., 2013)
  - Many species yet to be discovered [REF]
  - Remaining pristine habitat, on which a disproportionate number of species depend [WILDERNESS AREAS]
- -> important to understand how biodiversity responds to human impacts, and how we can support adaptive responses to prevent extinction

## 2.2 Land-use change in the tropics

- Tropics is undergoing a huge amount of land-use change, which historically was concentrated more in temperate regions (Gibbs et al., 2010; Foley et al., 2011)
- Land-use change has driven extensive and severe losses of biodiversity across the planet (Newbold et al., 2015)

### 2.2.1 Forest conversion

- Driven primarily by agriculture (Godfray et al., 2010)
- Devastating loss of habitat, particularly in SE Asia and Amazon (Gibbs et al., 2010; Hansen et al., 2013)
- Greenhouse gas emission [Foley et al. (2005); (IPCC, 2013)]
- Secondary impacts (roads, edge effects, fragmentation) (?Murcia, 1995; ?; Ewers and Banks-Leite, 2013)

### 2.2.2 Forest degradation

- Includes fragmentation and edge effects (see above), as well as selective logging
- Selective logging more extensive than conversion, esp. in SE Asia (Hansen et al., 2008; Asner et al., 2009)
- These forests still retain conservation value (Edwards et al., 2011; Gibson et al., 2011; Edwards and Laurance, 2013), so part of a pragmatic conservation approach is maximising their ability to sustain biodiversity under additional threats e.g. climate change (?)

## 2.3 Climate change in the tropics

- Debate about vulnerability of tropical species
- Vulnerability is about both exposure (extrinsic factors) and sensitivity (intrinsic factors) (?)
- Exposure and sensitivity interact to determine whether species *need* to resist or recover from perturbations, as well as their *ability* to do so
- It is likely that most tropical species will need to respond to the effects of climate change in some way

- Exposure in terms of absolute change will be less than elsewhere (?Corlett, 2012; IPCC, 2013), but long periods of climatic stability mean that actually exposure in terms of relative change will likely be greatest in the tropics, with the earliest appearance of novel climates (Mora et al., 2013)
- Following limited temperature variation – over space (shallow latitudinal temperature gradients (Colwell et al., 2008)), and time (geologic and seasonally (?))
- tropical species tend to have narrow thermal limits (Deutsch et al., 2008; Tewksbury et al., 2008; Khaliq et al., 2014), and already operate near the upper limits of these [REF]
- Ability to respond depends on ability to either adapt in situ, or move

### **2.3.1 In situ adaptation**

- Includes genetic adaptation, physiological plasticity, and behaviour
- Evidence for genetic adaptation is limited
  - Many of the tropical species of particular global conservation interest are highly specialised; specialisation tends to reduce variation in heritable traits and therefore decreases potential for genetic adaptation (?)
  - Tends to be limited to selection for traits that underlie adaptive responses: namely, physiological plasticity or dispersal ability
- Evidence for physiological plasticity is more common, but still tends to be limited to phenological changes (and those in temperate regions) rather than thermal tolerance directly
- For animals, behaviour is a very common response to suboptimal climatic conditions, since it is employed on a regular basis to respond to changes within days and years

### **2.3.2 In situ adaptation**

- Behaviour is often overlooked, perhaps because it tends to act on a much shorter timescale than seems relevant to the pace of climate change
  - But short-term impacts of long-term climate change can be very important -> changes to climate distribution
  - Thus, day-to-day behavioural strategies for coping with suboptimal temperatures can have long-term implications for population viability
- Importance of microclimates and microhabitats (set scene for chapters 2 and 4)
- Improvements in technology inc. thermal cameras and dataloggers (set scene for chapter 3)

### 2.3.3 Range shifts

- Within and between generations, many species may shift their ranges
  - This can happen as well as in situ adaptation, or because such adaptation is difficult and selection tends to favour individuals that simply remove themselves from novel, suboptimal conditions
- Prevalence globally and tropically of range-shifting as a response to climate change
- Climate gradients: latitudinal, elevational and vertical
- Factors influencing likelihood of range shifts:
  - Availability of target habitat
  - Accessibility of target habitat
  - Ecological traits of the focal species
- Many studies focus on availability of climate analogues, or present day connectedness of natural habitat, without considering the two things simultaneously (set scene for chapter 5)

## 2.4 Thesis aims and rationale

1. Investigate the potential for land-use change to impact microclimates and microhabitats, and hence the subsequent impacts on:
  - The baseline of local climate change that global climate change is projected onto
  - The potential for thermal buffering as an adaptive response
2. Investigate the potential for land-use change to impact range shifts under climate change
  - Focus on the tropics
  - First use a literature review to collect local site-level temperature data in different land-use types across the tropics
  - Then consider temperature and temperature variation at an even finer scale, using a field study in Borneo
  - Develop methodology and software to utilise thermal images as a tool for assessing thermal heterogeneity
  - Finally, use pantropical forest cover and climate datasets to consider how recent forest loss has impacted species' ability to track climate change by shifting their ranges

The specific objectives of the main data chapters are outlined below:

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

- Many studies considering impacts of climate change hint at the importance of temperature for species' ecology
- When considering interactions between land-use change and global climate change, most studies tend to focus on how the former may cause or hinder adaptation to the latter
- This chapter focused on how degradation and conversion of tropical forests directly causes climate change, on a fine spatiotemporal scale
- Implications for the impact of further warming under global climate change, but suggests that degraded forests and microhabitats may be able to buffer species from further change

### **2.4.2 Chapter 3 – A framework for quantifying fine-scale thermal heterogeneity in the field**

- Despite acknowledged importance of temperature for species' ecology, and recognition that most species experience temperature at a the spatial scale of mm to m, focus on fine-scale temperature regimes has been much neglected in ecology
- Part of the reason is limitations in technology, although such limitations are being increasingly overcome
- Dataloggers were a big part of this, but now thermal cameras are also becoming increasingly affordable
- The focus of this chapter is to develop a framework and software for utilising thermography to quantify thermal heterogeneity at a fine spatial scale using images collected in the field
- We present a developmental R package and worked example, demonstrating the utility of the package for comparing thermal heterogeneity over time between different locations

### **2.4.3 Chapter 4 – Tropical forests are thermally buffered despite intensive selective logging**

- Temperature variation at a fine spatial scale is crucially important in allowing species to cope with temperature change at a coarser scale

- Selective logging affects a huge area of tropical rainforests, particularly in SE Asia, but we do not know how this form of land-use change impacts fine-scale temperature
- Using data collected in Borneo, this chapter compares various components of thermal buffering between intensively logged and unlogged forests, and finds little thermal difference despite pervading differences in forest structure
- Confirms results hinted at in Chapter 2, underscoring the conservation value of degraded forests particularly when left to recover

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

- In addition to in situ adaptation, or where such adaptation is either impossible or insufficient, species may shift their ranges in response to climate change
- Range shifting is well-documented in both modern times and paleontological records, but its ubiquitousness across the tropics as a means to prevent species from going extinct under climate change depends on species being able to reach suitable habitat with a suitable climate
- This chapter utilises global climate and forest cover data to assess the extent to which current forest cover facilitates movement to analogous future climate, and how this has been impacted by recent forest cover loss
- Find that climate connectivity is very poor in many regions of the tropics, and has largely declined over just 12 years of forest loss

### **2.5 Threats to biodiversity**

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

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

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

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

Alternatively, the biodiversity crisis could be alleviated through a better understanding of how and why organisms respond to human impacts. In this way, we could modify our actions to minimise impact, and also facilitate organism responses that permit persistence through change. This is the step that I will address in the following review. Initially I will focus on organism responses to climate change, given the increasing importance of this pressure in the future (Sala et al., 2000). However, neither the impacts of climate change nor land-use change can be fully understood in isolation; the synergies between the two pressures are thought to be extensive, but generally poorly understood (Brodie et al., 2012; Mantyka-pringle et al., 2012). In the tropics forest degradation is some 20 times more pervasive than deforestation (Asner et al., 2009), yet there is particularly little discussion of how habitat degradation might interact with climate change. This is the key unexplored area that I will move on to discuss, before finally outlining my PhD framework.

## 2.6 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.

### 2.6.1 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” (Baillie et al., 2004). Between 1880 and 2012, global average temperature increased by 0.85°. This trend will continue into the future, with predictions of global average temperature for the period 2081-2100, relative to 1986-2005, ranging from an increase of 1-3.7°C, depending on the scenario used (IPCC, 2013).

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

Where extinctions have been attributed to climate change, this is through changes in local weather patterns. Weather is distinguished from climate as being “the state of the atmosphere at a given time and place”, whereas climate comprises “the statistics of weather conditions over a decade or more” (IPCC, 2013). Concomitant with increasing global average temperature is the increase in the frequency and intensity of extreme weather events (IPCC, 2013). This can be explained statistically, because an ‘extreme weather event’ is an event in which the climatic conditions fall towards either extreme end of the probability distribution (the 10th or 90th percentile; IPCC (2013)]. Provided the probability distribution of temperatures remains the same (or similar), an increase in average temperature corresponds to an upwards shift in the overall temperature distribution, and therefore we more commonly see temperatures that were originally very rare, and begin to see temperatures never before recorded (Figure 2.1). It is almost certain that there will be more extremes of heat (and fewer extremes of cold) towards the late 21st Century (IPCC, 2013).

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

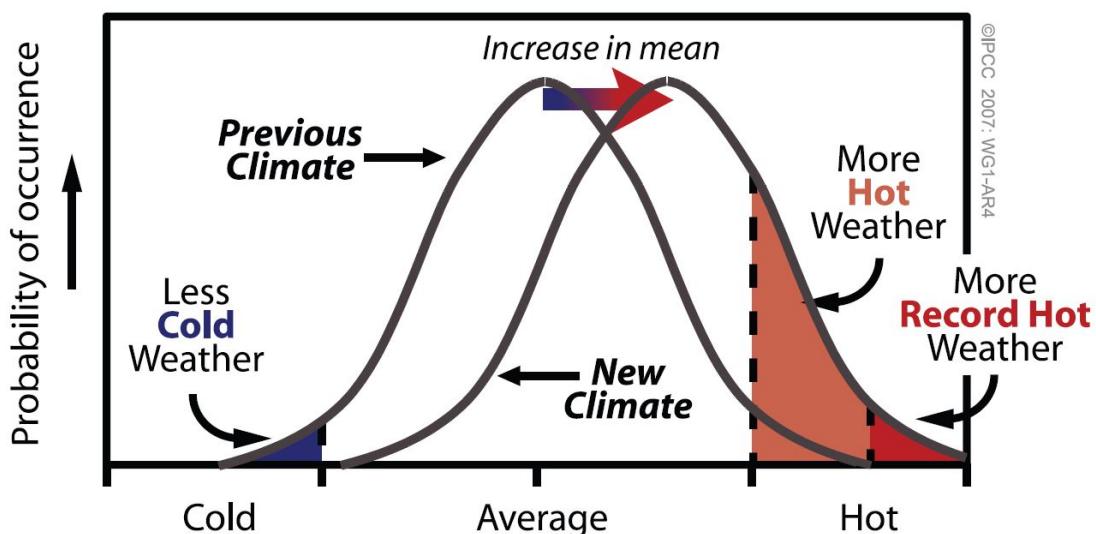


Figure 2.1: Schematic showing the increase in frequency of extreme temperatures (shaded light pink) and the magnitude of extreme temperatures (shaded dark pink), in response to increasing mean temperature for a normal distribution of temperatures. ‘extreme’ refers to events that would have been anomalous under the previous probability distribution. Figure taken directly from IPCC (2007).

### 2.6.2 Range shifts due to climate change

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

Until recently, there were very few studies of range shifts due to climate change in tropical species, with some suggesting that the response should be less extreme given the slower rates of warming in the tropics (Freeman and Freeman, 2014; IPCC, 2013). It is now apparent that tropical species do shift their ranges to track climate, particularly to higher elevations (Chen et al., 2009; Pounds et al., 1999) owing to shallow temperature gradients across latitudes (Colwell et al., 2008). In fact, tropical species track climate more closely than temperate species (Freeman and Freeman, 2014). This effect could be due to: (1) greater thermal specialisation as a result of long-term thermal stability in the tropics (Freeman and Freeman, 2014); (2) slower velocity of climate change up mountains (Loarie et al., 2009) meaning it is easier for species to keep pace; or (3) fewer barriers to dispersal in the tropics, since tropical

biomes have thus far retained a greater proportion of natural habitat than temperate regions. In any case, even tropical species do not track climate precisely (Chen et al., 2009).

### 2.6.3 In situ adaptation to climate change

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

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

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

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

The literature discussed above fails to mention one additional and very significant tool that animals can employ to adapt to climate change – behaviour. All organisms ordinarily experience a range of temperatures, and so possess thermoregulatory behaviours that can also be

deployed to mitigate the impacts of climate change. Chamois, for example, move to higher altitudes and reduce activity when temperature increases (Mason et al., 2014).

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

## 2.7 Influence of land-use change

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

In this review, however, I have focused on how organisms can adaptively respond to change. The question then becomes: how does land-use change influence an organism’s capacity to respond to climate change? On a regional scale under wholesale conversion, the answer is relatively well-discussed. Namely, regional habitat loss creates barriers to climate-driven range shifts (Thomas et al., 2012). Recall that in response to climate change that has already happened, organisms have not moved as quickly as expected (Chen et al., 2009), and barriers to dispersal may contribute to this.

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

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

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

Wholesale conversion is very likely to impede the ability of persisting organisms to adapt to future climate change, but then few of the original species do persist through conversion (e.g. Gibson et al., 2011; Katovai et al., 2012; Murphy and Romanuk, 2014) and — at least in the tropics — habitat degradation is far more pervasive. In particular, some 20% of the humid tropical biome experienced selective logging from 2000–2005 (Asner et al., 2009), whilst deforestation affected only 1.4% in the same period (Hansen et al., 2008). Although the habitat type broadly remains as 'forest', selective logging can be extremely disruptive. Indeed the term 'selective' is somewhat of a misnomer, meaning that particular species and stems (usually above a minimum trunk diameter) are targeted (Edwards et al., 2014b). These targets are typically the largest, oldest trees, the removal of which reduces canopy height and canopy density (Kumar and Shahabuddin, 2005; Okuda et al., 2003), and also fragments the forest canopy and opens up large gaps (Edwards et al., 2014b) that are often invaded by non-tree species, such as climbers and bamboo. Commercial selective logging also causes collateral damage, particularly where trees are connected by climbers (Schnitzer et al., 2004), as well

as requiring roads and skid trails that bring further challenges for wildlife (Brodie et al., 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.

## 2.8 Thesis aims and rationale

### 2.8.1 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).

## Chapter 3

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



Bornean horned frog (*Megophrys nasuta*).

This chapter has been published as:

**Senior RA, Hill JK, González del Pliego P, Goode LK, Edwards DP. A pantropical analysis of the impacts of forest degradation and conversion on local temperature. Ecology and Evolution. 2017;7:7897–7908.**

### 3.1 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.

### 3.2 Introduction

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

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

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

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

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

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

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

In the present study, we carry out analyses of published data to test the effect of land-use change on local temperature across the tropics. We collected local, in situ temperature data from the literature for paired sites (< 1ha) that differed in land-use type. Categories of land use we studied were primary forest, degraded forest, plantation, pasture and cropland (Table 3.1; 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.

### 3.3 Methods

#### 3.3.1 Literature search

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

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

Table 3.1: Land use classification definitions (modified from Extended Data Table 1 in Newbold et al. (2015)).

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

### 3.3.2 Selection criteria

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

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

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

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

### 3.3.3 Data collation

Where possible, temperature data were extracted from text, tables or graphs in the publication. Data in graphs were extracted using Digitizel ([www.digitizeit.de](http://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 (Jarvis et al., 2008). 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 3.1). ‘Urban’ could not be included due to insufficient data.

### 3.3.4 Statistical analysis

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

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

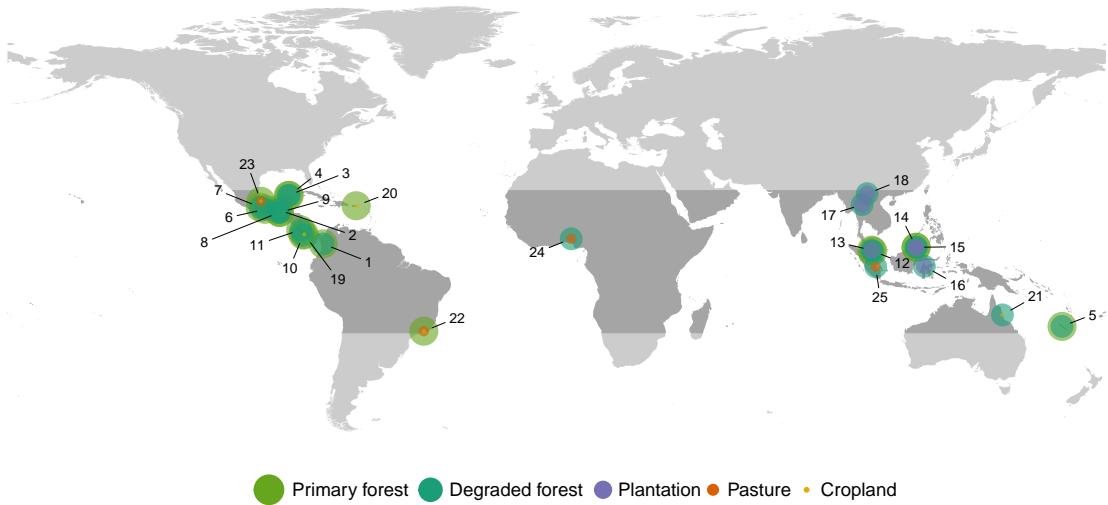


Figure 3.1: Locations of the 25 studies contributing data to the analyses. Point labels correspond to the study number in Table 3.1. The shading and size of concentric points corresponds to different land-use types, to indicate the data provided by each study.

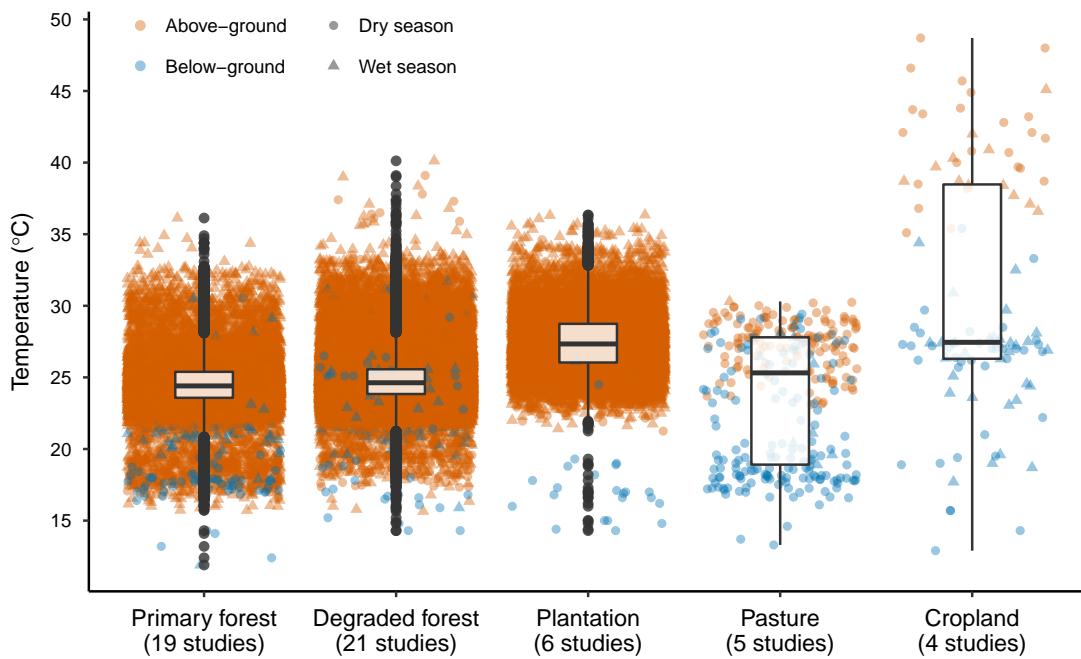


Figure 3.2: Raw day-time temperature against land-use type, across all studies contributing data to the analyses (plotted by study in Figure A.4). Point shading indicates temperatures measured above-ground (orange) or below-ground (blue), and different symbols indicate temperatures measured during the dry season (circles) or wet season (triangles).

## 3.4 Results

In total, 25 studies met the criteria for inclusion (Table 3.2). Studies spanned 12 countries, across every continent within the tropics (Figure 3.1), and provided 113,894 observations of day-time temperature (Figure 3.2 and Figure A.4). Most observations represented either a single temperature observation within, or mean temperature across, a single day at the point location where measurements were taken. Six studies reported temperature at a coarser temporal resolution (mean = 107 days; minimum = 14 days; maximum = 183 days), and six studies reported temperature at a coarser spatial resolution (mean = 527 m<sup>2</sup>; minimum = 64 m<sup>2</sup>; maximum = 1,000 m<sup>2</sup>). The maximum elevational difference between sites within a single study ranged from 0 to 141 m (mean = 33 m), and site elevation was random with respect to land-use type (LMM,  $X^2 = 19.33$ , df = 14, P > 0.05; Figure A.5). 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))
```

### 3.4.1 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 3.3; Figure 3.3), 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 3.3). By contrast, converted habitats in our dataset – plantation, pasture and cropland – were, on average, hotter than primary forest by 2.7°C, 6.2°C and 7.6°C, respectively. Results were

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

Table 3.2: Summary of the 25 studies contributing data to analyses. Study number corresponds to point labels in Figure 3.1. Crosses indicate the land-use types, position(s) relative to ground level and season(s) considered by each study.

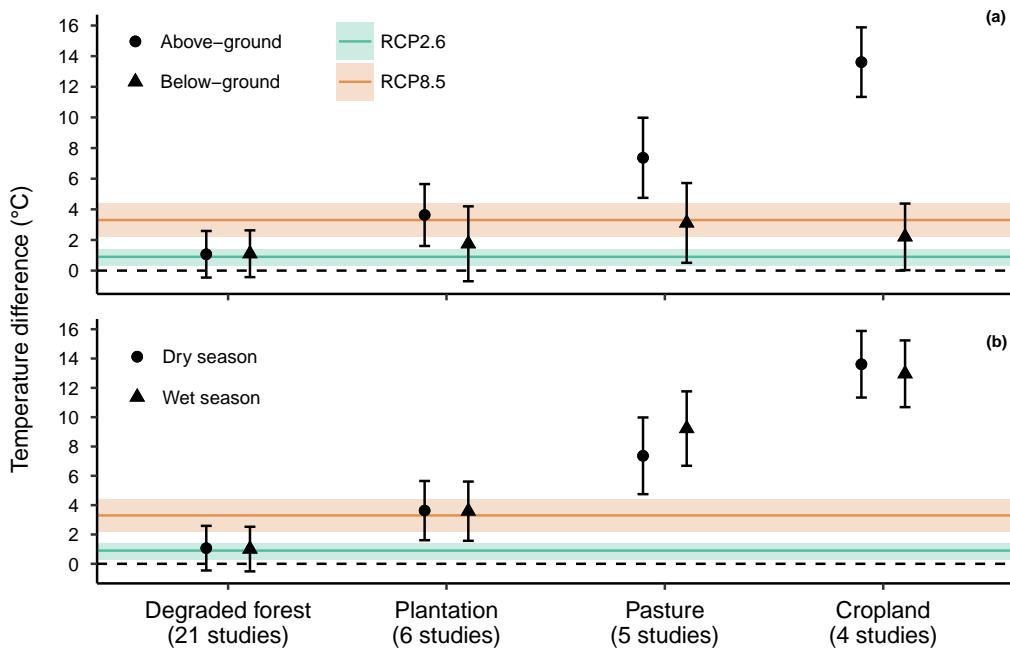


Figure 3.3: Model estimates of local day-time temperature in altered land-use types relative to primary forest (depicted by the black dashed line). In panel (a), different symbols denote position relative to the ground (above-or below-ground), and the season is held at the reference level (dry season). In panel (b), different symbols denote the season (dry or wet), and the position relative to the ground is held at the reference level (above-ground). Error bars are 95% confidence intervals. Solid lines indicate projected warming in the tropics for the period 2081–2100 compared to the period 1986–2005, as a result of global climate change (IPCC, 2013). Shaded bands indicate 5%–95% ranges from the distribution of the climate model ensemble. Colors represent the lowest and highest warming scenarios (RCP2.6 and RCP8.5, respectively).

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

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 A.2), and neither did night-time minimum temperature (LMM,  $X^2 = 2.31$ ,  $df = 2$ ,  $P > 0.05$ ; Figure A.3d). 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 A.3c), 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 A.3a), or day-time minimum temperature (LMM,  $X^2 = 4.60$ ,  $df = 2$ ,  $P > 0.05$ ; Figure A.3b).

### 3.4.2 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 3.3; Figure 3.3a). 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 3.3a).

### 3.4.3 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 3.3; Figure 3.3b), but the direction of the interaction varied by land-use type, and in all cases the effect size was very small. In degraded forest and plantation, seasonality had no appreciable effect on temperature relative to primary forest (dry vs. wet season: +0.1°C in both degraded forest and plantation). In contrast, the temperature difference between pasture and primary forest was 1.9°C greater in the wet versus dry season, while in cropland the differential was 0.6°C greater in the dry versus wet season.

## 3.5 Discussion

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

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

Table 3.3: 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.

### 3.5.1 Thermal differences between land-use types

Human-impacted land-use types are likely hotter than intact primary forest because of changes in evapotranspiration and the amount of solar radiation reaching the Earth's surface (Oke, 1987; Findell et al., 2007; Davin and de Noblet-Ducoudré, 2010). Degradation and deforestation cause a lowering and thinning of the canopy, and reduction in rooting depth, leaf area index and surface roughness, all of which reduce evapotranspiration (Okuda et al., 2003; Snyder et al., 2004; Kumar and Shahabuddin, 2005; Findell et al., 2007; Davin and de Noblet-Ducoudré, 2010; Hardwick et al., 2015), and thereby increase temperature (Oke, 1987; Foley et al., 2005). Changes to canopy architecture and a reduction in the number of sub-canopy vegetation strata also cause warming by increasing the amount of solar radiation reaching the ground (Oke, 1987; Murcia, 1995). Our land use categories encompass a spectrum of vegetation change, from relatively little change in degraded forests (where some trees and a closed canopy are maintained) to maximal change in pasture and cropland (where trees are replaced with herbaceous plants). Accordingly, degradation had the smallest average effect (+1.1°C), followed by plantation (+2.7°C), and then pasture (+6.2°C) and cropland (+7.6°C). We expected that the same mechanisms underlying the warming effect of land-use change would also result in increased day-time temperature extremes and decreased night-time temperatures in altered land-use types, relative to primary forest (Oke, 1987; Chen et al., 1995). Unfortunately, the data available were very limited, including only three of the five land-use types (primary forest, degraded forest and plantation), and resulting in extremely large confidence intervals (Figure A.1 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.

### 3.5.2 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 3.3; Figure 3.3a). 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 3.3; Figure 3.3b). 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.

### 3.5.3 Implications for biodiversity

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

That said, we find several circumstances where warming through land-use change is mitigated. Degraded forests were not significantly hotter than primary forests (according to 95% confidence intervals; Figure 3.3). This is encouraging because degraded forests are likely to become the most widespread land-use type in future (Hurtt et al., 2011), and many studies have demonstrated their capacity to retain species of conservation concern (Edwards et al., 2011; Gibson et al., 2011; Putz et al., 2012; Edwards et al., 2014b). For all altered land-use types, the warming effect was limited below-ground, highlighting a crucial thermal refuge for species that are able to occupy the soil, and suggesting that above-ground microhabitats, such as deadwood and epiphytes, might fulfil a similar role (Scheffers et al., 2014a; González del Pliego et al., 2016). Thermal refugia may not be a permanent solution for avoiding climate change, and sensitive species may find that even relatively cold microhabitats are

still too hot (e.g. below-ground in pasture was 4°C warmer than primary forest; Table 3.3; Figure 3.3), but refugia could at least provide species with more time to respond to suboptimal climatic conditions (Hannah et al., 2014).

### 3.5.4 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 3.1), 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.

### 3.5.5 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.

### 3.6 Data availability and R code

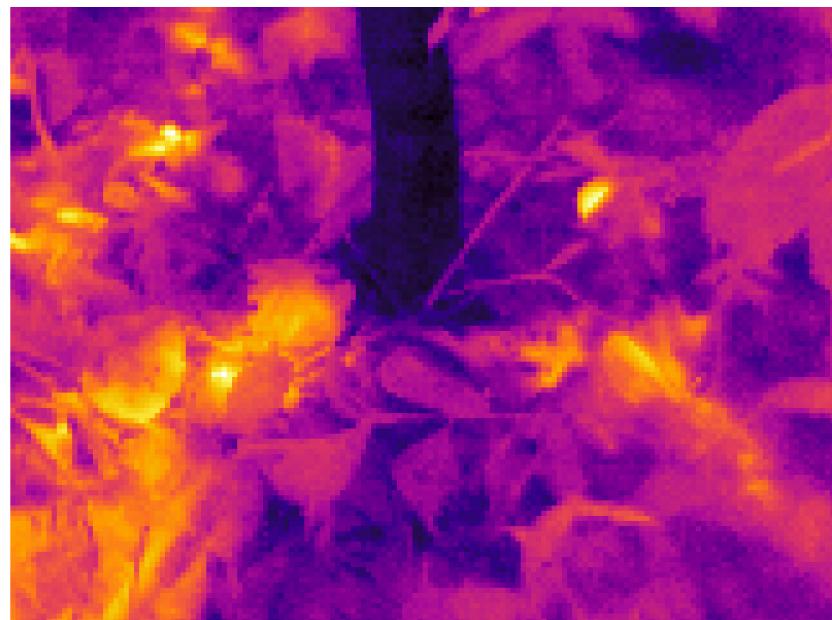
The collated dataset can be found on Dryad (<https://doi.org/10.5061/dryad.g4000>). Note that in many cases these data were aggregated for analyses. For finer resolution data please refer to the original data sources. R functions used to estimate time of sunset and sunrise can be downloaded from GitHub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

### 3.7 Acknowledgements

We thank the following people for providing temperature data: Julieta Benítez Malvido, Stephen Hardwick, Karen Holl, Thomas Ibanez, and Bráulio Santos. A considerable amount of data was provided by the Stability of Altered Forest Ecosystem (SAFE) Project, for which we acknowledge their primary sponsor: the Sime Darby Foundation. We thank Tim Newbold for statistical advice. R.A.S. was funded by a NERC studentship through the ACCE (Adapting to the Challenges of a Changing Environment) Doctoral Training Partnership (Grant No. NE/L002450/1); P.G. was supported by CONACyT, Scholarship 359063. We also thank two anonymous referees for their comments, which greatly improved the manuscript.

## Chapter 4

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



Thermal image of rainforest floor.

## 4.1 Abstract

Variation in temperature at a fine spatial scale creates critically important microclimates for many organisms. Quantifying thermal heterogeneity at this scale is challenging, and has so far been largely restricted to the use of dataloggers. Thermography is becoming an increasingly affordable and viable alternative. A single thermal photo contains thousands of spatially-explicit surface temperature measurements, and is therefore ideal for rapidly assessing fine-scale spatial temperature variation, including the surfaces within a few cms of which most organisms actually experience temperature. Both the technology and data have been underexploited in terrestrial ecology, in part because there is limited technical support for processing and interpreting these data. Here we present a simple R package for batch extracting and converting data from FLIR thermal cameras, and for quantifying thermal heterogeneity in gridded temperature data more generally. We apply this framework to investigate how forest structure affects thermal heterogeneity in primary forests in Borneo, using both (1) fine-scale FLIR thermal images collected in the field, and (2) remotely-sensed thermal data. Our various metrics of thermal heterogeneity show.... Our framework simplifies the process of getting data into a usable format, and demonstrates that... The importance of microclimates to species' ecology necessitates an efficient methodology for sampling thermal heterogeneity at the relevant spatial scale; streamlining data processing and analysis – as we do here – is a major part of this.

## 4.2 Introduction

- A key mechanism by which organisms will respond to future climate change is adaptation *in situ* (Hannah et al., 2014).
- Many organisms in structurally complex tropical rainforests respond to extremes of heat by exploiting fine-scale (mm to m) thermal heterogeneity (Scheffers et al., 2014b; González del Pliego et al., 2016).
- The ability of many tropical organisms to adaptively respond to climate change is therefore critically dependent on variation in temperature at this scale.
- Previously, fine-scale thermal heterogeneity was captured using temperature dataloggers. Dataloggers suspended in the understorey record air temperature that has been equilibrated by the movement of air masses, and thus represents forest temperature at a local scale (m to ha; Scheffers et al., 2014b; González del Pliego et al., 2016). Dataloggers placed inside microhabitats – such as tree holes and epiphytes – record air temperature at the finest spatial scale (mm to cm), and we know from these studies that the cool microclimates inside these microhabitats are able to thermally buffer

inhabitant frogs and lizards from temperature change at a local scale.

- The use of temperature dataloggers has clearly been instrumental in advancing this field. However, dataloggers can only record the air temperature in their immediate vicinity, and must therefore be highly replicated in space (and in a variety of microhabitats) to adequately quantify spatial temperature variation. The number of dataloggers available to the user imposes a financial and logistical limit on the spatial representativeness of sampling. Furthermore, the vast majority of terrestrial organisms are very small, flat, or thigmothermic (thermoregulate via direct contact with a surface), and therefore surface temperature is often more relevant than air temperature (e.g. Kaspari et al., 2015).
- Technological advances mean that the use of thermal cameras is increasingly affordable and practical (Scheffers et al., 2017; Faye et al., 2016).
- Thermal photos are ideal for capturing fine-scale surface temperature in tropical rainforests. Each photo provides thousands of spatially-explicit temperature measurements at the mm-cm scale. However, both the technology itself and the data provided have thus far been underexploited. Owing to the novelty of the methodology, there is little guidance for what metrics ought to be calculated and how.
- Faye et al. (2016) provide an excellent starting point from which to formulate such a framework. Using standard RGB images in combination with thermal images, collected using an unmanned aerial vehicle (UAV), Faye et al. demonstrate how this technology can be used to compare thermal heterogeneity between different surfaces (in this case, bare soil versus crop surface), and suggest metrics that they consider to be most appropriate to capture different facets of thermal heterogeneity.
- Their toolbox, however, does not immediately facilitate a general assessment of thermal heterogeneity using photos collected in the field. While the use of UAVs in the tropics is indeed becoming more feasible and affordable (Sanchez-Azofeifa et al., 2017), for the foreseeable future it is likely that thermography in tropical rainforests will most commonly consist of manually collected thermal photos.
- Additionally, while Faye et al. (2016) and Scheffers et al. (2017) provide introductory R scripts to facilitate the processing of thermal photos, there remains little technical support and guidance for ecologists for what is, in reality, an otherwise difficult and time-consuming element of any study seeking to utilise this technology.
- The development of the Thermimage package in R has considerably eased the extraction and conversion of raw data from FLIR thermal cameras, but this package does not directly facilitate batch processing and does not calculate (nor suggest) what metrics are most appropriate to quantify thermal heterogeneity from thermal images.
- In this study, we introduce a developmental R package – thermstats – for batch extraction, processing and analysing images from FLIR thermal cameras, extending the functionality of the Thermimage package. We outline the utility of our package

by comparing metrics of thermal heterogeneity over time and varying forest structure. In addition, we demonstrate that our functions for quantifying thermal heterogeneity can also be applied to other kinds of thermal image, including those at a coarser spatial scale.

## 4.3 Methods

### 4.3.1 Step 1: Data collection

- Key technical considerations for data collection
  - Environmental parameters:
    - \* Atmospheric temperature
    - \* Relative humidity
    - \* Object distance
    - \* Emissivity
  - Camera calibration
  - Format of FLIR thermal images (e.g. for a model E40: 160 x 120 pixels)

### 4.3.2 Step 2: Data extraction

- Requires ExifTool installation (freely available: <https://sno.phy.queensu.ca/~phil/exiftool/>)
- Batch extract data from thermal jpeg files using `batch_extract` function in `thermstats`
  - Batch implementation of `readflirJPG` in `Thermimage` package

### 4.3.3 Step 3: Conversion of raw data

- Describe format of the raw data
- Retrieve camera calibration constants using `flirsettings` in `Thermimage` package
- Specify environmental parameters (see Step 1)
- Batch convert raw data to temperature in °C using `batch_convert` in `thermstats`
  - Batch implementation of `raw2temp` in `Thermimage` package

#### 4.3.4 Step 4: Calculate metrics of thermal heterogeneity

- Function `stats_by_group` in `thermstats` calculates statistics across multiple photos within a specified grouping
  - Based on the assumption that multiple photos are required at each sampling location to adequately represent spatial variation in temperature...
  - ...but also works if the photo itself is the unit of replication
- Calculates summary statistics (specified by the user) across all pixels of all photos within the group, e.g.:
  - Mean
  - Standard deviation
  - Median
  - Percentiles
  - Kurtosis and skewness
  - Diversity indices
- Identifies hot and cold patches using Getis-Ord local statistic (Getis and Ord, 1996), via function `get_patches`
  - Implements `localG` function from `spdep` package
  - Option to return patches as a `SpatialPolygonsDataFrame` and plot using `plot_patches`
- Calculates spatial statistics of hot and cold patches:
  - Patch area (number of pixels)
  - Patch density (number of hot/cold patches per m<sup>2</sup>)
  - Patch configuration (Aggregation Index of hot/cold patches)

#### 4.3.5 Case studies

1. How does forest structure affect fine-scale thermal heterogeneity?
  - Expect that more open and less structurally complex forest would be more homogenous (e.g. narrower temperature range, smaller and fewer cold patches that are highly clustered, but more hot patches)
2. How does time of day affect fine-scale thermal heterogeneity?
  - Midday is when ambient temperature is highest, and thus heterogeneity is most important for organisms seeking to avoid extremes of heat (especially important under climate change)
  - Thermal heterogeneity will increase from dawn to midday as hot and cold spots increasingly deviate from the average temperature
  - The effect will be more extreme in forests with a more complex physical structure

ture, with a greater variety of radiative properties across the components of the surface

#### **4.3.5.1 Field study**

- Description of study area and sampling design for collecting thermal images with FLIR E40 camera in 2014 and 2015
- Description of forest structure variables
  - Tree stand basal area and its coefficient of variation
  - Sapling stand basal area and its coefficient of variation
  - Proportion of trees that were dipterocarps
  - % canopy cover
  - % veg. cover at different strata
- Statistical analyses
  - Generalized Additive Mixed Models of each metric of thermal heterogeneity against forest structure and time of day
  - Random intercept for plot nested in site

#### **4.3.5.2 Remote study**

- Example of applying same metrics to coarser scale thermal data
- Description of the thermal data and forest structure data
  - Note that only forest structure is available here, not time of day
  - Forest structure data from LiDAR, including canopy height and canopy openness
- Statistical analyses
  - Linear Models of each metric of thermal heterogeneity against forest structure

## **4.4 Results**

### **4.4.1 Frequency distribution of temperature**

- (Response variables include 5<sup>th</sup> and 95<sup>th</sup> percentiles, the range between them, Shannon Diversity Index and Simpson Diversity Index)
- Impact of time of day and forest structure
  - Field study only
- Impact of forest structure

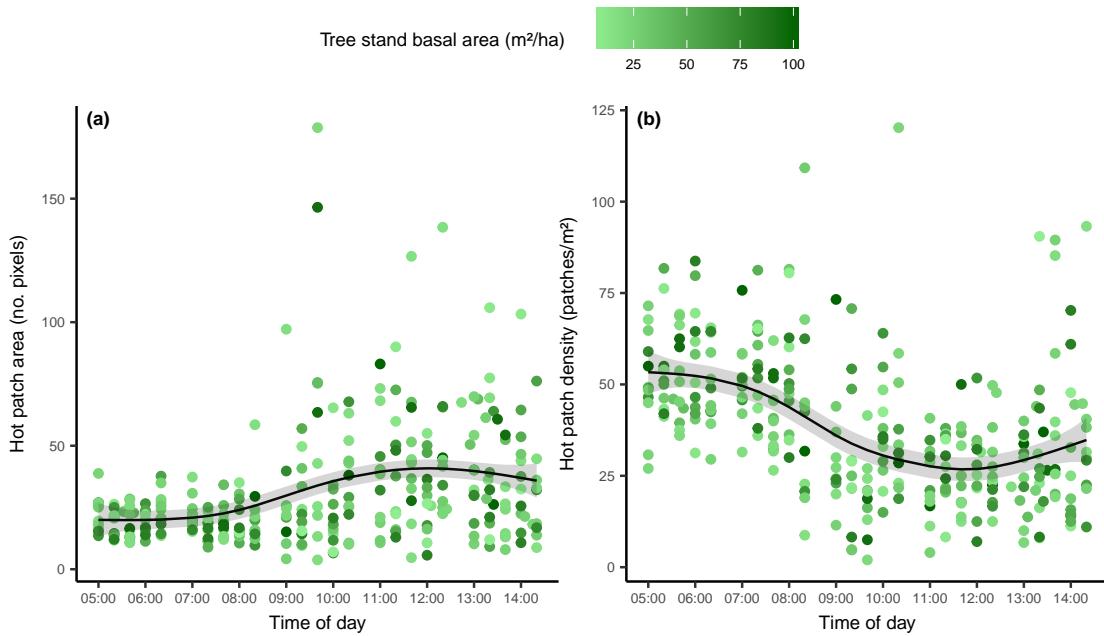


Figure 4.1: The influence of time and forest structure (measured as tree stand basal area;  $\text{m}^2/\text{ha}$ ) on the average area of hot patches (a) and the density of hot patches ( $\text{patches}/\text{m}^2$ ; b). Points are shaded according to forest structure, from simpler, more open forests in light green to more complex and closed forests in dark green. Fitted values for patch characteristics against time of day are depicted by the black line, with a grey band for the 95% confidence intervals.

- Field and remote study

#### 4.4.2 Spatial distribution of temperature

- (Response variables include patch area, patch density and patch Aggregation Index, for hot and cold patches separately)
- Impact of time of day and forest structure
  - Field study only
- Impact of forest structure
  - Field and remote study
- Example field study results:
  - From dawn onwards the average area of hot patches increased slightly towards a plateau around midday (GAMM,  $F = 28.02$ ,  $P < 0.001$ ; Figure 4.1a). This was countered by a fall in the density of hot patches (per  $\text{m}^2$ ), which reached its minimum value at around midday (GAMM,  $F = 28.02$ ,  $P < 0.001$ ; Figure 4.1b). Forest structure (measured by tree stand basal area;  $\text{m}^2/\text{ha}$ ), however, did not affect hot patch area (GAMM,  $F = 0.029$ ,  $P > 0.05$ ) or density (GAMM,  $F = 0.101$ ,  $P > 0.05$ ).

## 4.5 Discussion

- Our developmental R package offers users a structured and simple way to process thermal photos, tailored towards photos collected using a FLIR camera but with applicability for other kinds of thermal photos
- There are various metrics of thermal heterogeneity that we consider to be of prime biological importance, including our novel application of hot spot analysis
  - Frequency distribution statistics describe the overall availability of different temperatures
    - \* Important for meeting the thermal requirements of a variety of species
    - \* Temperature extremes are particularly important for buffering organisms against temperature change at a coarser spatial scale
  - Hot spot analysis allows us to identify spatial clusters of temperature extremes, the characteristics of which (e.g. area, density and configuration) determines the ease with which they can be utilised by different organisms
  - Reiterate that these metrics are not readily captured by existing methodologies i.e. dataloggers
- Discuss case studies
  - Compare field and remote study results
  - Over the course of day, changes in temperature at a coarser scale translate to changes in fine-scale thermal heterogeneity, which we are able to detect using our various metrics, which capture different facets of temperature variation.
- Discuss the limitations of thermal cameras (best used in combination with dataloggers)
  - Cannot directly capture sub-surface temperatures (though surface temperature is influenced by sub-surface temperature)
  - Inferior to dataloggers for capturing temporal variation in temperature
  - Still somewhat expensive and sensitive to heat and humidity
  - Ensure that the camera is calibrated and environmental parameters are recorded

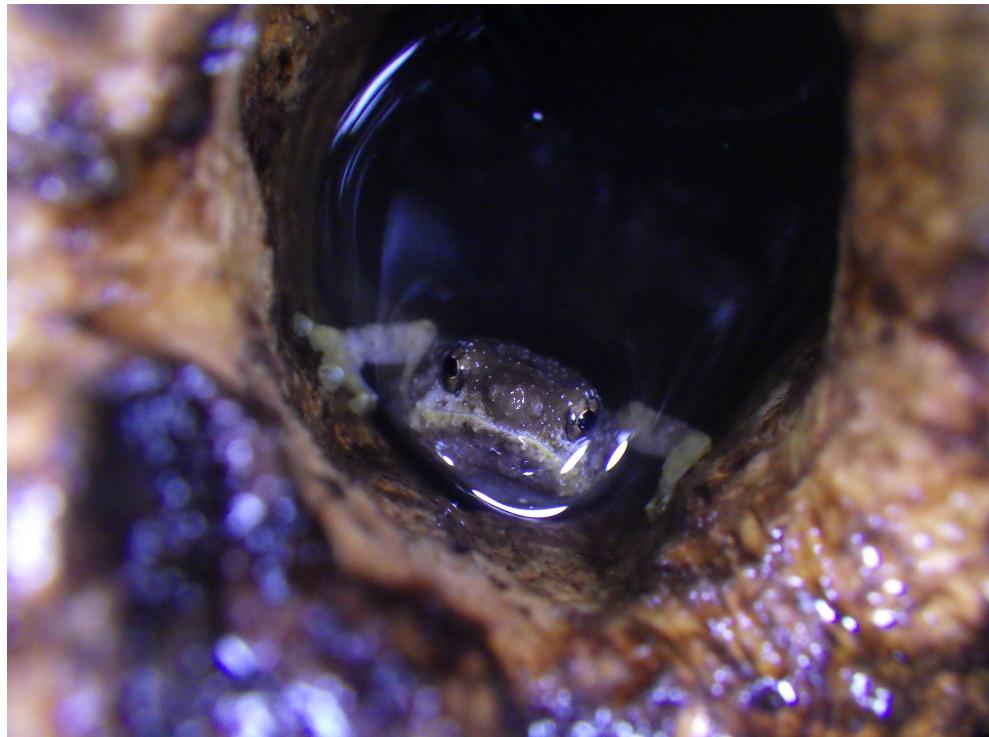
### 4.5.1 Summary

- Thermal heterogeneity is crucial for thermoregulation by many species, and increasingly so under climate change. Our package and framework provides support and guidance for researchers, enabling them to address key issues in ecology with the help of increasingly efficient technology.
- We provide a fully-reproducible example of how our approach can be used to quantify

thermal heterogeneity in tropical forests using data at a fine spatial scale, collected using a FLIR thermal camera. We also show how our metrics can be calculated for other kinds of thermal data, such as those collected at a coarser spatial scale.

## Chapter 5

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



Bornean tree hole frog (*Metaphrynella sundana*).

This chapter has been published as:

**Senior RA, Hill JK, Benedick S, Edwards DP. Tropical forests are thermally buffered despite intensive selective logging. Global Change Biology. 2018;24:1267–1278.**

## 5.1 Abstract

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

## 5.2 Introduction

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

this is heavily contingent on the assumption that these forests will maintain their current conservation value into the future.

Several factors may influence the value of selectively logged forests for biodiversity in the long-term, and a key consideration is the interaction of multiple drivers of biodiversity loss (Brook et al., 2008; Mantyka-pringle et al., 2012; Sirami et al., 2017). The impacts of climate change are particularly important, and increasingly so as this century progresses (Sala et al., 2000; Chou et al., 2013; IPCC, 2013). Novel (non-analogous) climatic conditions are predicted to appear first in the tropics (Mora et al., 2013), where many species have narrow thermal limits (Deutsch et al., 2008; Tewksbury et al., 2008; Khaliq et al., 2014) and where there is limited dispersal potential owing to poor dispersal ability of many species (Van Houtan et al., 2007). This vulnerability of tropical species is compounded by an absence of target habitats containing analogous climates (Colwell et al., 2008), and widespread deforestation creating a hostile matrix through which dispersal must occur (Brook et al., 2008; Scriven et al., 2015). The ability of tropical species to withstand climate change, and so avoid extinction, is likely to be highly dependent on their ability to adapt *in situ* within existing forest areas. The extent to which species persistence can be facilitated within selectively logged forests will, therefore, greatly influence the conservation value of these habitats.

In primary forests and secondary forests re-growing on abandoned farmland, previous studies found that organisms – particularly ectotherms – avoid suboptimal temperatures in the wider ‘macroclimate’ (climate at a spatial scale of m to ha) by moving locally into ‘microclimates’: climate at a fine-scale, mm to m, that is distinct from the macroclimate (Scheffers et al., 2014a,b; González del Pliego et al., 2016). Climate at this fine-scale is more relevant for the majority of terrestrial biodiversity, which primarily consists of small-bodied ectotherms (Suggitt et al., 2011; Potter et al., 2013; Nadeau et al., 2017). Indeed, the vast proportion of terrestrial species are small in size, flat in shape, or thermoregulate via contact with vegetation, and so it is important to consider microclimates close to, and including, the surfaces on which these species live (Kaspari et al., 2015; Scheffers et al., 2017).

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

all increase in the day-time temperature of logged forests, increasing the necessity for thermal buffering. Simultaneously, the potential for thermal buffering may be compromised if forest structural changes also influence the temperature and distribution of cool microclimates, particularly if their temperature becomes more similar to that of the wider macroclimate (e.g. Caillon et al., 2014), or there are simply fewer cool microclimates available overall. Conversely, enhanced air-mixing in more open logged forests might create cooler and less variable microclimates. Previous evidence suggests that the availability of cool ‘microhabitats’ (localised environments within which cool microclimates are contained; Scheffers et al., 2014a; González del Pliego et al., 2016; Shi et al., 2016) can be reduced (e.g. leaf litter; Saner et al., 2009) or increased (e.g. deadwood; Carlson et al., 2017) by selective logging, implying that forest quality alters thermal environments.

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

## 5.3 Methods

### 5.3.1 Study area

Sampling took place in an extensive area of contiguous forest in Sabah (Malaysian Borneo; Figure 5.1a). This area represents over 10,000 km<sup>2</sup> of lowland dipterocarp forest, comprising production forest and areas of undisturbed protected forest (Reynolds et al., 2011). In this

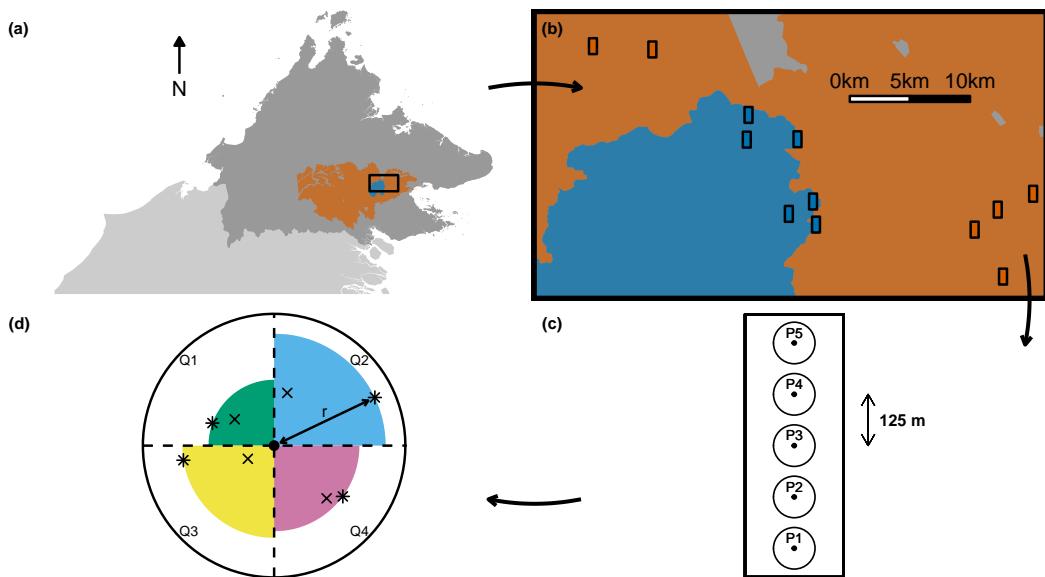


Figure 5.1: Study location in Malaysian Borneo (a), and distribution of sites (b): six sites in primary forest (blue) and six sites in logged forest (orange). Each site comprised five plots along an existing transect, with plot centres separated by 125 m (c). Tree and sapling stand basal area was calculated from the distance to and circumference of the nearest two trees and saplings in each of four quadrants centred on the plot centre (d; see section B.1 for more details). Curved arrows indicate the direction of magnification, from panels a-d.

study, we sampled sites in forest that had been commercially selectively logged twice (Ulu Segama-Malua Forest Reserve,  $4^{\circ}57'42.8''N$ ,  $117^{\circ}56'51.7''E$ ). The area was first logged from 1987-1991, using tractors and high-lead extraction techniques to harvest commercial trees (those in the family Dipterocarpaceae) with stems  $> 0.6$  m diameter at breast height (D.B.H.), and yielding  $\sim 113$  m $^3$  of timber per hectare (Fisher et al., 2011; Edwards et al., 2014a). Between 2001 and 2007, the area was re-logged and the minimum harvested tree diameter reduced to  $> 0.4$  m D.B.H., yielding an additional 31 m $^3$ /ha of timber (Fisher et al., 2011). Thus, we sampled sites that had been heavily disturbed about 10 years prior to the study, at which point 67% of the forest had an average density of  $< 10$  trees per hectare with a D.B.H. greater than 40 cm (Reynolds et al., 2011). The area has been recovering naturally since logging operations ceased. Control sites were located in undisturbed, protected primary forest (Danum Valley Conservation Area;  $4^{\circ}57'45.2''N$ ,  $117^{\circ}48'10.4''E$ ).

### 5.3.2 Sampling design

We sampled twelve sites, six in twice-logged forest and six in primary forest, along existing transects (Figure 5.1b; Edwards et al., 2011, 2014a). Sites were more than 2 km apart, and at least 100 m from forest edges. Within each site, we established five plots 50 m in diameter, with plot centres spaced at 125 m intervals along the transect (Figure 5.1c; 60 plots in total).

Fieldwork was conducted from April to July 2015, during the severe El Niño-Southern Oscillation (ENSO) event of 2015-2016 (NOAA Climate Prediction Center, 2015) when mean daily temperature was 2.26°C higher and mean daily rainfall was 2.09 mm lower than the 5-year average (across April to July for the years 2007 to 2011; data from weather station at Danum Valley Field Centre).

### **Forest structure**

To quantify the level of disturbance to the forest from selective logging, we used an established methodology for assessing forest structure in each plot (Hamer et al., 2003; Lucey and Hill, 2012). The variables we measured were: the stand basal area ( $\text{m}^2/\text{ha}$ ) of mature trees (circumference > 0.6 m) and saplings (circumference 0.1-0.6 m), based on the distance to and circumference at breast height of the two nearest trees and saplings in each of four quadrants centred on the plot centre (Figure 5.1d); the coefficient of variation for the basal area of trees and of saplings; the proportion of mature trees that were dipterocarps (indicative of mature, complex forest); percentage canopy cover; and visual estimates of percentage vegetation cover at ground (1.5 m above ground), understorey (15 m above ground) and canopy (the main stratum of leaf cover > 15 m above ground) height. For full methodological details see section B.1.

### **Quantifying surface microclimates**

Fine-scale surface temperature of the forest floor is particularly relevant for small-bodied, surface-dwelling organisms, such as many insect and reptile species. We measured surface temperature within each plot using an infrared camera (FLIR Systems, model E40). Macroclimate temperature was defined as the air temperature at 1.5 m above-ground, measured using a whirling hygrometer. Each site was visited on two days, and each plot within the site was sampled five times each day between 05:00 hrs to 14:30 hrs. During each sample of any given plot, the observer stood at the centre of the plot, took a single hygrometer reading and then, holding the camera at breast height and pointing 45° downwards (relative to the ground), took a photo in four orthogonal directions (Scheffers et al., 2017). Each thermal image comprised 19200 distinct observations of surface temperature (one per pixel), and covered a surface area of approximately 1  $\text{m}^2$ . In total, we recorded 2400 thermal images (4 images per plot x 5 repeats x 2 site visits x 60 plots).

For all subsequent analyses, a unique data point comprised thermal information from the four photographs taken each time a plot was sampled: 76800 observations of surface temperature measurements for each plot (i.e. combining 19200 observations from the four photos

taken in each orthogonal direction). For details of thermal image data extraction and processing see section B.2. The temperature of cool surface microclimates was defined as the 5<sup>th</sup> percentile (i.e. coolest) across all 76800 pixels. For some organisms, the efficacy of thermal buffering also depends on the thermal stability of microclimates (Shi et al., 2016). We calculated daily variation in surface microclimate temperature as the difference between the minimum and maximum microclimate temperature, for each day and for each plot.

To identify spatially-explicit patches of warm and cool pixels (Figure 5.2) we calculated the Getis-Ord local statistic for each pixel within the neighbourhood of the nearest eight pixels, using the function ‘localG’ in the spdep package in R (Bivand and Piras, 2015; R Core Team, 2017). Pixels with a Z-value of  $\geq 3.886$  were defined as being within warm patches, and those with a Z-value of  $\leq -3.886$  within cool patches (Getis and Ord, 1996). Thermal diversity was defined as the difference between the median temperature of the warmest warm patch minus the median temperature of the coolest cool patch (hereafter: ‘patch temperature range’). The average surface area of cool patches was calculated as the total number of pixels within cool patches, multiplied by the surface area of one pixel ( $0.516 \text{ cm}^2$ ), and divided by the total number of cool patches across the four photos. Finally, spatial configuration of cool patches was quantified using the Aggregation Index: the number of edges that cool patches share, divided by the maximum number of edges that they could possibly share (He et al., 2000; Caillon et al., 2014). Higher values of the Aggregation Index indicate increased clustering of microclimates in space, which makes them more difficult for organisms to track (Sears et al., 2016).

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

Many ectotherms, such as amphibians, spend some or all of their time exploiting cool microclimates inside microhabitats, which thermal images are unable to capture. We selected three types of microhabitat known to provide cool microclimates (Scheffers et al., 2014b,a; González del Pliego et al., 2016), and placed one temperature datalogger (HOBO pendant datalogger, Onset, model UA-001-64K or model UA-002-64K) per plot in each microhabitat type: deadwood ( $> 10 \text{ cm}$  stem diameter), tree holes ( $> 2 \text{ cm}$  at widest point of entrance hole,  $< 2 \text{ m}$  above the ground) and leaf litter ( $1.5 \text{ m}$  left of the plot centre). The hygrometer measurements of macroclimate temperature were not always synchronised with the dataloggers inside microhabitats, hence we additionally measured macroclimate temperature using a datalogger suspended  $1.5 \text{ m}$  above the ground at the centre of each plot, shielded against direct radiation and precipitation by an inverted plastic funnel (Shoo et al., 2010; Scheffers et al., 2014a).

All dataloggers recorded temperature every 20 minutes for six consecutive days, occurring

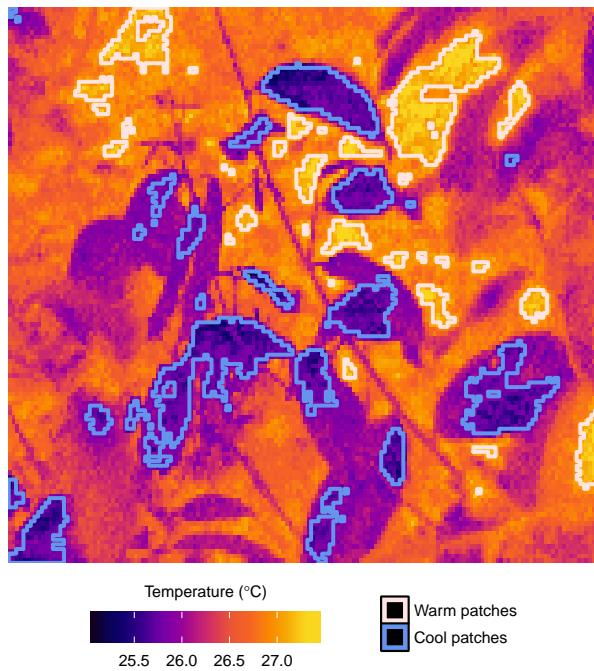


Figure 5.2: Example thermal image. Pixels are shaded from cold (purple) to hot (yellow). Warm patches (outlined in pink) and cool patches (outlined in blue) were identified using the Getis-Ord local statistic of each pixel.

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

To estimate the occurrence of microclimates inside microhabitats, we measured the volume of leaf litter, tree holes and deadwood within a  $50 \times 5$  m subplot centred on each plot centre (60 sub-plots in total), with the long edge running parallel to the transect. For full methodological details see section B.3. We divided microhabitat volume by the total area surveyed to generate microhabitat volume per  $\text{m}^2$  forest, for each plot.

### 5.3.3 Variables analysed

#### Forest structure

We examined the impact of selective logging on forest structure using linear mixed effects models to compare nine structural response variables between logged and primary forests: stand basal area of trees and of saplings; the coefficient of variation across individual basal areas of trees and of saplings; proportion of trees that were dipterocarps (binomial data: dipterocarp versus non-dipterocarp); percentage canopy cover (proportion data); and percentage vegetation cover at ground, understorey and canopy strata (proportion data). We found that tree stand basal area ( $\text{m}^2/\text{ha}$ ) was a good measure of changes in forest structure from logging activity ( $\text{LR} = 8.102, P < 0.01$ ; Figure B.4a; see Results for full details), hence we use this variable as a continuous measure of disturbance (henceforth: forest quality) in all our analyses exploring the thermal buffering potential of logged and unlogged forests.

#### Macroclimate and microclimate temperature

Macroclimate temperature is the temperature at a relatively coarse spatial scale, and was captured in this study using both a hygrometer and suspended datalogger (measuring the same variable but at different times). The macroclimate does not affect thermal buffering potential *per se*, but it does dictate the overall necessity for thermal buffering. We modelled hygrometer and datalogger temperature separately, including forest type (logged or primary forest) and forest quality as explanatory variables (see section B.4).

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

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

range was the daily range (95<sup>th</sup> percentile minus 5<sup>th</sup> percentile) of the raw temperature observations. All models were run separately for surface, leaf litter, tree hole and deadwood microclimates.

### Microclimate availability

Microclimate occurrence was modelled separately for surface microclimates (i.e. the average surface area of cool patches), and those inside leaf litter, tree holes and deadwood (each quantified by their average volume per m<sup>2</sup> forest). The thermal diversity of surface microclimates was captured by the temperature range between the warmest warm patch and the coolest cool patch. The spatial configuration of surface microclimates refers to the Aggregation Index of cool patches (binomial data: edges shared by cool patches versus edges not shared by cool patches). For all models, the fixed effects were forest type (logged or primary forest) and forest quality (i.e. tree stand basal area).

### 5.3.4 Statistical analyses

All data were analysed using mixed effects models in R (version 3.3.0; R Core Team, 2017). To account for spatial pseudoreplication, forest structure models included ‘site’ as a random intercept term, and all other models included ‘plot’ nested within ‘site’. Temperature data were recorded at multiple time points, hence the full models were visually assessed for evidence of temporal autocorrelation of residuals (function ‘acf’ in the nlme package; Pinheiro et al., 2017), and a correlation structure for both date and time was incorporated where necessary (the specific structure was chosen using AIC; Zuur, 2009). For binomial data (proportion of dipterocarps and surface microclimate Aggregation Index) we used generalized linear mixed effects models (GLMMs) with a binomial error distribution, fitted using the package lme4 (Bates et al., 2015) and tested for overdispersion. Diagnostic plots were assessed for all models to confirm model fit and, where necessary, we modified the variance structure of the residuals (Zuur, 2009) and transformed variables to normality. For true proportion data (percentage canopy cover and percentage vegetation cover), the transformation used was a modification of the empirical logit (Warton and Hui, 2011).

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

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

## 5.4 Results

### 5.4.1 Changes in forest structure after logging

Following two rounds of commercial selective logging, tree stand basal area – our measure of forest quality – was  $39.5 \text{ m}^2/\text{ha}$  in logged forest, compared to  $39.5 \text{ m}^2/\text{ha}$  in primary forest ( $\text{LR} = 8.102, P < 0.01$ ; Figure B.4a). Logged forests thus contained far fewer large trees than did primary forests. There were also more large saplings in logged forest ( $6.77 \text{ m}^2/\text{ha}$ ) than in primary forests ( $6.77 \text{ m}^2/\text{ha}$ ;  $\text{LR} = 4.239, P < 0.05$ ; Figure B.4b), and trees were less variable in size ( $\text{LR} = 13.038, P < 0.001$ ; Figure B.4c). There was no difference between forest types in terms of the variability of size among saplings ( $\text{LR} = 0.114, P = 0.736$ ; Figure B.4d).

Changes to forest structure from selective logging were also evident in the overall amount of vegetation cover. Although there was no observed difference between logged forest and primary forest in percentage vegetation at ground level ( $\text{LR} = 2.758, P = 0.097$ ; Figure B.4g), the proportion of trees that were dipterocarps ( $X^2 = 2.42, P = 0.12$ ; Figure B.4e) or the percentage canopy cover ( $\text{LR} = 0.874, P = 0.35$ ; Figure B.4f), we did find that percentage vegetation cover was higher in primary forest than in logged forest in both the understorey (primary = 68.2%; logged = 68.2%;  $\text{LR} = 5.288, P < 0.05$ ; Figure B.4h), and in the canopy (primary = 23.1%; logged = 23.1%;  $\text{LR} = 9.174, P < 0.01$ ; Figure B.4i). Thus, 9-12 years after logging there were significant differences in forest structure between logged and primary forests. This was especially true for the components of forest structure that typically indicate the presence of large, mature trees and high structural complexity, and which might be expected to influence microclimates and the availability of microhabitats.

### 5.4.2 Macroclimate and microclimate temperature in logged and primary forest

Despite differences in forest structure, we found no difference in macroclimate temperature of logged and primary forests, whether measured by the hygrometer ( $\text{LR} = 0.081, P = 0.776$ ; Figure B.2a) or suspended datalogger ( $\text{LR} = 0, P = 0.983$ ; Figure B.2b). Macroclimate temperature was also consistent across varying levels of forest quality, for temperature measured via the hygrometer ( $\text{LR} = 0.022, P = 0.883$ ; Figure B.2a) and suspended datalogger ( $\text{LR} = 0.527$ ,

$P = 0.468$ ; Figure B.2b). Thus, the necessity for thermal buffering was comparable between the two forest types.

Absolute microclimate temperature was comparable between forest types for all of the microclimates considered: surface ( $LR = 0.447, P = 0.504$ ; Figure 5.3e), deadwood ( $LR = 0.206, P = 0.65$ ; Figure 5.3f), tree holes ( $LR = 2.759, P = 0.097$ ; Figure 5.3g) and leaf litter ( $LR = 1.616, P = 0.204$ ; Figure 5.3h). We found that the relationship between microclimate temperature and macroclimate temperature was slightly steeper in primary forest compared to logged forest for deadwood ( $LR = 7.268, P < 0.01$ ; Figure 5.3b), tree holes ( $LR = 13.657, P < 0.001$ ; Figure 5.3c) and leaf litter ( $LR = 28.914, P < 0.001$ ; Figure 5.3d). However, for  $1^\circ\text{C}$  macroclimate warming (from the median value) the maximum difference in microclimate warming between forest types was  $< 0.1^\circ\text{C}$ , and no such interaction was apparent for surface microclimates ( $LR = 1.197, P = 0.274$ ; Figure 5.3a). Similarly, for a  $1 \text{ m}^2/\text{ha}$  increase in forest quality (i.e. tree stand basal area), tree hole temperature was slightly warmer ( $LR = 4.661, P < 0.05$ ; Figure 5.3g), but the size of this effect was negligible ( $+0.00194^\circ\text{C}$ ), and not evident for other microclimates ( $P > 0.05$ ; Figure 5.3e-h). Thus we conclude that effects of logging on microclimate temperature were generally not evident, or minimal.

The final facet of microclimate temperature that we considered was daily temperature variation. This too was comparable between logged and primary forests for microclimates at the surface ( $LR = 0.437, P = 0.508$ ; Figure 5.4a), as well as those inside deadwood ( $LR = 0.02, P = 0.889$ ; Figure 5.4b), tree holes ( $LR = 3.242, P = 0.072$ ; Figure 5.4c) and leaf litter ( $LR = 2.449, P = 0.118$ ; Figure 5.4d). Microclimate temperature variation was also consistent across different levels of forest quality ( $P > 0.05$ ; Figure 5.4).

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

#### 5.4.3 Microclimate availability in logged and primary forest

The thermal buffering potential within a habitat depends not only on the temperature of microclimates relative to the macroclimate, but also on the overall availability and thermal diversity of those microclimates. The occurrence of surface microclimates was not impacted by forest type ( $LR = 0.872, P = 0.35$ ; Figure 5.5b), and the average volume of microhabitats (per  $\text{m}^2$  forest) was similar in logged and primary forest for deadwood ( $LR = 0.263, P = 0.608$ ; Figure 5.5d), tree holes ( $LR = 3.053, P = 0.081$ ; Figure 5.5e) and leaf litter ( $LR = 0.162, P = 0.687$ ; Figure 5.5f). There was no observed impact of forest quality on the occurrence of

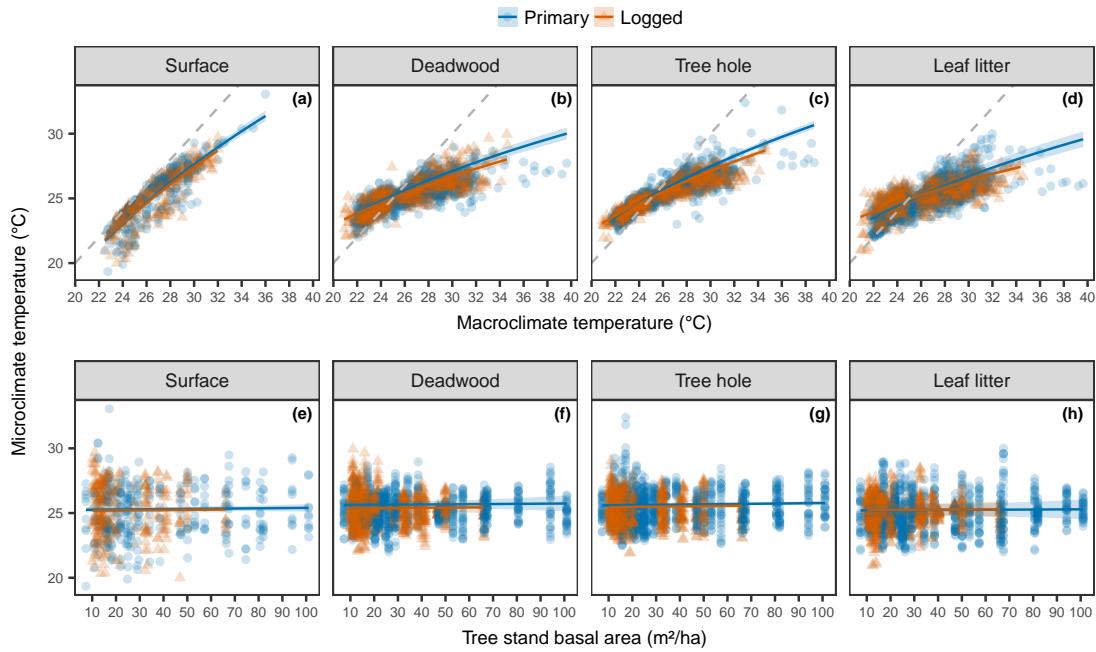


Figure 5.3: Comparison between primary forest (blue) and logged forest (orange) in terms of: (a-d) the relationship between microclimate temperature and macroclimate temperature; and (e-h) absolute microclimate temperature across varying levels of forest quality (measured as tree stand basal area). Microclimates were measured at the surface (a, e), and inside deadwood (b, f), tree holes (c, g) and leaf litter (d, h). The grey dashed lines in panels a-d indicate zero temperature buffering, where the microclimate temperature is equal to the macroclimate temperature. In all panels, shaded bands are 95% confidence intervals.

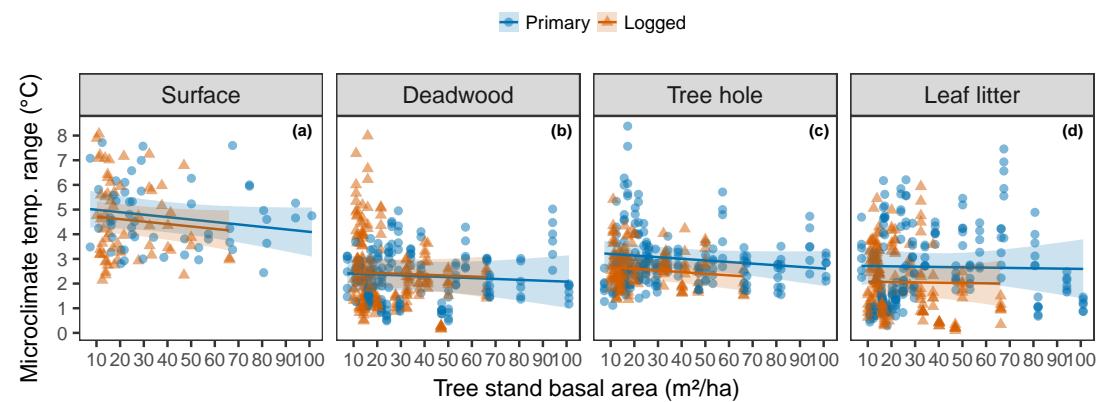


Figure 5.4: The influence of forest type (primary or logged) and forest quality (measured as tree stand basal area) on microclimate temperature range. Daily range for surface microclimates (a) was calculated as the difference between the maximum and the minimum microclimate temperature (itself calculated as the 5<sup>th</sup> percentile temperature across four photos taken at each visit to each plot). For microclimates inside deadwood (b), tree holes (c) and leaf litter (d), the daily range was the difference between the 95<sup>th</sup> percentile and 5<sup>th</sup> percentile of raw temperature measurements. Primary forest data points are depicted as blue circles and logged forest as orange triangles. Shaded bands represent 95% confidence intervals.

surface microclimates ( $LR = 1.324, P = 0.25$ ; Figure 5.5b) or the volume of deadwood ( $LR = 3.78, P = 0.052$ ; Figure 5.5d) and tree holes ( $LR = 2.172, P = 0.141$ ; Figure 5.5e). In contrast, we found that leaf litter volume increased by  $12.3 \text{ cm}^3/\text{m}^2$  for a  $1 \text{ m}^2/\text{ha}$  increase in forest quality (i.e. tree stand basal area;  $LR = 7.056, P < 0.01$ ; Figure 5.5f).

Using thermal images we were able to quantify the thermal diversity and spatial configuration of surface microclimates. Thermal diversity has a bearing on the diversity of organisms that are able to find microclimates meeting their thermal requirements (which vary according to species, age, time of day, seasonality, etc.). Spatial configuration influences the ease with which organisms can utilise microclimates. We found that the temperature range spanned by surface microclimates (both warm and cool patches) was comparable between logged and primary forests ( $LR = 0.276, P = 0.599$ ; Figure 5.5a) and with varying forest quality ( $LR = 3.552, P = 0.059$ ; Figure 5.5a). The same was true for the Aggregation Index of cool surface patches, both between logged and primary forest ( $X^2 = 0.312, P = 0.576$ ; Figure 5.5c) and with different levels of forest quality ( $X^2 = 0.183, P = 0.669$ ; Figure 5.5c).

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

## 5.5 Discussion

Forest degradation by commercial selective logging affects huge expanses of the tropics (Asner et al., 2009; Lewis et al., 2015). Southeast Asia has experienced the most intensive selective logging of all tropical rainforests (Lewis et al., 2015), and in our study area  $\sim 145 \text{ m}^3$  of timber was removed per hectare. Despite these forests having only a maximum of 12 years post-logging recovery (Fisher et al., 2011), and the coincidental occurrence during data collection of abnormally hot and dry conditions associated with the strongest El Niño-Southern Oscillation (ENSO) event since 1998 (NOAA Climate Prediction Center, 2015), we found very few thermal differences associated with selective logging. This is an important finding for tropical conservation because it suggests that the potential for thermal buffering will not limit the ability of selectively logged forests to maintain high biodiversity under climate change.

### 5.5.1 Forest structure

At a local scale (m to ha), climate is highly dependent upon vegetation (Oke, 1987; Sears et al., 2011). Selective logging operations generally target larger and older trees, leading to

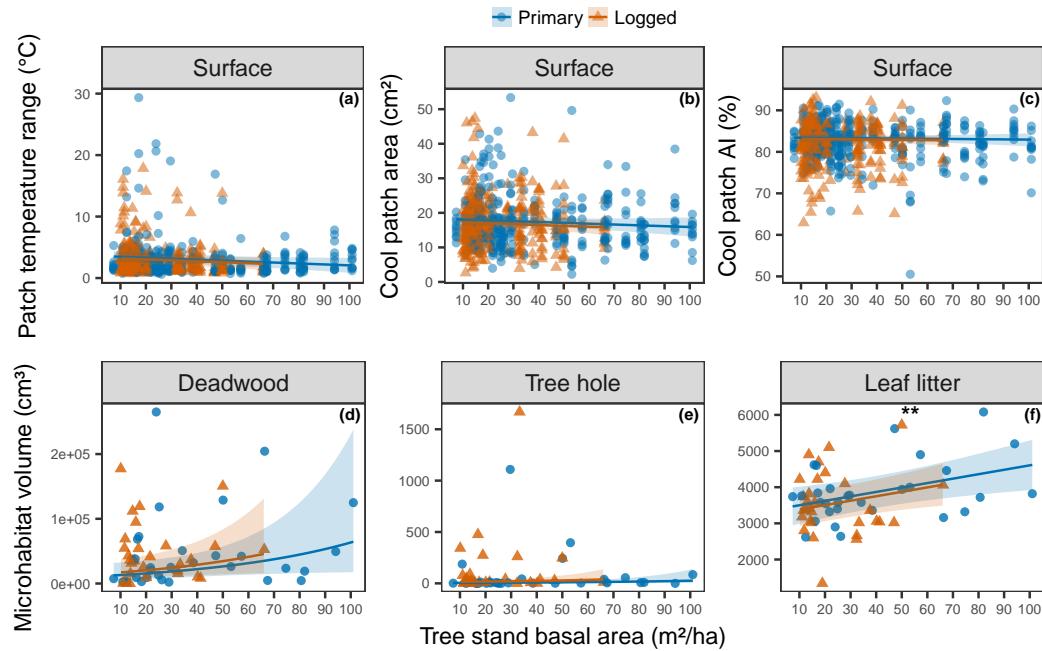


Figure 5.5: The influence of forest type (primary or logged forest) and forest quality (measured as tree stand basal area) on microclimate availability. Results for surface microclimates (top row) include: the temperature range from the warmest warm patch to the coolest cool patch (a); the average surface area of cool patches (b); and the Aggregation Index of cool patches (c). The volume (per m<sup>2</sup> forest) of microhabitats typically associated with microclimates (bottom row) is shown for deadwood (d), tree holes (e) and leaf litter (f). Primary forest data points are depicted as blue circles and logged forest as orange triangles. Shaded bands represent 95% confidence intervals. Asterisks in panel f denote a statistically significant difference at  $0.001 < P < 0.01$  (\*\*).

many associated changes in vegetation structure (Okuda et al., 2003; Kumar and Shahabud-din, 2005; Edwards et al., 2014b). A clear signal of historical logging in our study area was a reduction in stand basal area of mature trees by 0% (Figure B.4a; Berry et al., 2008), accompanied by reduced variation in tree basal area (Figure B.4c), and reduced vegetation cover at  $\geq 15$  m height (Figure B.4h,i). The increase in stand basal area of saplings by 0% (Figure B.4b) is evidence that there has been substantial natural regeneration in the intervening years.

### 5.5.2 Macroclimate and microclimate temperature

Although primary forest contained more large trees (Figure B.4a), the absence of any long-term effect of selective logging on percentage canopy cover (Figure B.4f) suggests that forest vegetation as a whole – regardless of how it was distributed vertically – intercepted comparable amounts of incoming solar radiation in both logged and primary forests. This finding is in keeping with previous studies observing rapid horizontal canopy growth following selective logging (e.g. Asner et al., 2004). Alternatively, vegetation in logged forest may have intercepted less incoming radiation than in primary forest (i.e. if there was less vegetation overall), but reflected a greater proportion of what was intercepted, owing to the higher albedo of habitats with an abundance of non-tree species (Oke, 1987; Davin and de Noblet-Ducoudré, 2010; Edwards et al., 2014b). In either case (or in combination), given comparable levels of solar radiation reaching the forest floor of logged and primary forests, it follows that the temperature at coarse and fine scales (macroclimate and microclimate temperatures) should also be comparable (Figure 5.3 and Figure B.2).

The temperature of cool microclimates relative to average conditions is what largely determines their ability to buffer macroclimate warming (Scheffers et al., 2014a; González del Pliego et al., 2016; Shi et al., 2016). Given that selective logging did not affect absolute temperature of the macroclimate (Figure B.2) or microclimates (Figure 5.3), we can infer that there was no overall effect of selective logging on the difference between micro- and macroclimate temperature. There was also no evidence that selective logging impacted overall daily variation in microclimate temperature (Figure 5.4). There were some impacts of logging on the relationship between microclimate and macroclimate temperature for microclimates inside deadwood, tree holes and leaf litter (Figure 5.3), but the effect sizes for these interactions were extremely small. The maximum difference in microclimate warming between logged and primary forests was  $< 0.1^\circ\text{C}$  for  $1^\circ\text{C}$  of macroclimate warming. As such, we conclude that even when selective logging had a statistically significant influence on thermal buffering potential, the effect was small and of limited biological relevance.

### 5.5.3 Microclimate availability

Even if microclimates are present and effective at buffering temperature change, overall rarity or isolation could render them functionally redundant to some species (Sears et al., 2011, 2016). We demonstrate that lower forest quality was associated with less leaf litter (Figure 5.5; cf. Saner et al., 2009), but forest quality and forest type had little effect on the occurrence of microclimates at the surface or inside deadwood and tree holes. This is contrary to expectations from previous studies (Ball et al., 1999; Blakely and Didham, 2008). However, high volumes of deadwood could be maintained in logged forest by lower decomposition rates (Ewers et al., 2015; Yeong et al., 2016; but see Hérault et al., 2010), and large remnant pieces from harvest operations. In undisturbed forests, tree holes tend to be associated with larger, older trees (Lindenmayer et al., 2000; Blakely and Didham, 2008). A comparable quantity of tree holes might be found in logged forests because of damage from logging operations (Edwards et al., 2014b), increased wind in gaps (Chen et al., 1995) and remnant large trees that were specifically avoided by logging companies because of hollow boles. Additionally, we assessed tree holes in the understorey only, and differences may well manifest at higher forest strata.

The availability of microclimates to organisms is also influenced by their thermal diversity and distribution in space. We found that patches of warm and cool microclimates on the surface of the forest floor spanned a temperature range of about 3°C, regardless of logging activity (Figure 5.5a). Cool patches were generally highly clustered in space (Aggregation Index of 83.3%), but this was not affected by logging (Figure 5.5c). Thermal diversity and spatial configuration of microclimates are relatively novel facets of thermal buffering potential (but see: Caillon et al., 2014; Sears et al., 2016; Faye et al., 2016); they are likely determined by the composition of the forest floor and the relative radiative properties of these different components (e.g. bare soil versus leaves versus water; Oke, 1987; Snyder et al., 2004). We therefore suggest that these characteristics of the forest floor were comparable between forests despite the large differences in forest structure that were evident after logging.

### 5.5.4 Caveats and future research directions

The potential for thermal buffering and its general necessity are influenced by moisture levels, as well as temperature (McLaughlin et al., 2017). Many ectotherms, including amphibians (Duellman and Trueb, 1986) and isopods (Hassall et al., 2010), can survive in hot temperatures for longer if relative humidity is sufficiently high to prevent desiccation. Although we did not measure fine-scale vapour pressure deficit (a variable combining both temperature and relative humidity), we did find that coarse-scale vapour pressure deficit measure-

ments from the hygrometer and from hydrochron iButtons (section B.4) showed little variation within or between forests (Figure B.2).

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

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

The ability of selectively logged tropical forests to retain current levels of biodiversity will critically depend on their ability to protect species from the impacts of increasingly severe climate change. As average temperatures increase over this century, so too will the intensity and frequency of extreme climatic events. Thermal buffering will likely be crucial in allowing species to move locally to avoid suboptimal climates. We sampled in some of the most intensively logged forest in the tropics, during abnormally hot and dry conditions of a severe ENSO event; it is highly unlikely that our study would have failed to detect any appreciable thermal differences between primary and logged forests had they existed. Regardless of whether commercially selectively logged forests remain biologically or structurally distinctive from undisturbed forests, this study shows for the first time that they are functionally equivalent in the provisioning of cool microclimates, and underscores their vital role in conservation both now and under future climate warming.

## 5.6 Data availability

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

## 5.7 Acknowledgements

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

## Chapter 6

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



Mixed use tropical landscape in Bali.

## 6.1 Abstract

To survive in a warming world the range of many species will shift polewards or upwards. Tropical rainforests harbour most of the world's remaining terrestrial biodiversity, included many thermally restricted forest specialists. Despite this, we currently lack a biome-wide assessment of the potential for tropical species to reach climate analogues within existing forest cover. Moreover, no study to date has empirically tested where, how and why climate connectivity has changed as a result of change in forest cover. In this study, we quantified pantropical climate connectivity in 2000 and 2012. We tested various hypotheses relating climate connectivity change to the magnitude and location of forest cover change. We found that... To conserve global biodiversity under climate change, we suggest that unavoidable forest loss in the tropics should be..., and that forest protection and reforestation should...

## 6.2 Introduction

To avoid extinction under future climate change, species must either adapt *in situ* or shift their range (Hobbs et al., 2018). Both strategies have been widely studied, with range shifts polewards or upwards appearing to be a widespread response to climate change across the globe, in both palaeoecological records and under modern climate change (Parmesan, 2006; Davis and Shaw, 2001), and across a range of taxa (Chen et al., 2009; Freeman and Freeman, 2014; Raxworthy et al., 2008). There is potential for other human impacts, including land-use change, to influence the ability of species to shift their ranges in response to climate change. Understanding such interactions is a conservation priority (Brook et al., 2008; Mantyka-pringle et al., 2012; Sirami et al., 2017; Titeux et al., 2017).

Land-use change impedes range shifts in most cases, by creating highly fragmented landscapes through which many species struggle to navigate (Thomas et al., 2004; Heller and Zavaleta, 2009; Tucker et al., 2018). The tropics is an area of particular concern because it harbours most remaining terrestrial biodiversity (Jenkins et al., 2013) while also being the focus of intensive and extensive land-use change via the conversion and degradation of tropical forests (Hansen et al., 2013; Lewis et al., 2015). Although the absolute magnitude of climate change will be greatest at the poles (IPCC, 2013), long periods of climatic stability mean that is the tropics where relative climate change will be the most severe (Mora et al., 2013). Many tropical species have limited tolerance for temperature change (Deutsch et al., 2008; Tewksbury et al., 2008; Khaliq et al., 2014), and are also highly sensitive to fragmentation because of habitat specialism and poor dispersal ability (Opdam and Wascher, 2004). Climate-driven range shifts in the tropics generally follow elevation al gradients, probably because latitudinal temperature gradients are very shallow (Loarie et al., 2009). Range shifts

of tropical species have been documented in response to as little warming as 0.1°C to 0.76°C (Parmesan and Yohe, 2003; Raxworthy et al., 2008; Chen et al., 2009; Peh, 2007; Freeman and Freeman, 2014; Raxworthy et al., 2008).

The ability of species to shift their ranges in response to climate change depends both on the future availability of suitable habitat with an analogous climate, and the connectivity between the species' current distribution and any potential future habitat. Species Distribution Models (SDMs) have been key in addressing the former, using the correlation between current distribution and current abiotic conditions (including climate) to forecast where species might go in the future (Hijmans and Graham, 2006). However, not only do SDMs fail to consider connectivity, they are also fine-filter approaches focusing on specific species and requiring a wealth of data relating to the distribution of those species (Nuñez et al., 2013). Equally, there is a plethora of studies that quantify habitat connectivity – both structural and actual connectivity (Calabrese and Fagan, 2004) – which have been instrumental in highlighting the extent of fragmentation by land-use change (e.g. Tucker et al., 2018; Brodie et al., 2015; Cosgrove et al., 2017). These studies, however, do not explicitly consider climate. This is important because large areas of structurally connected habitat could still become unsuitable under climate change if there is insufficient climatic heterogeneity within that habitat (e.g. lowland rainforest).

The handful of studies that do integrate habitat connectivity with climate are highly informative both for quantifying the current connectedness of natural areas to future climate analogues, and for predicting specific movement routes or 'climate corridors' between source and target areas (McGuire et al., 2016; Littlefield et al., 2017; Nuñez et al., 2013). Such corridors could prove vital for many range-shifting species. That said, 'climate connectivity', defined as the extent to which "spatial configuration of natural lands allows species to track their current climatic conditions during projected climate change" (McGuire et al., 2016), has yet to be reviewed for a whole biome, nor has any study to date utilised empirical data to examine the change in climate connectivity over time. The latter is significant if we are to understand the factors that drive change in climate connectivity: where does an increase in natural habitat maximise climate connectivity, and where does loss of natural habitat minimise loss of climate connectivity?

In this study, we combined current and future climate data with data from tropical land-use change that has already occurred, to quantify both the current climate connectivity across the tropics and the patterns of climate connectivity change in the recent past. To enable a broad, coarse-filter assessment of climate connectivity, we consider land use only in terms of forest versus non-forest, using 2000 and 2012 tree cover data from Hansen et al. (2013) and excluding tree plantations (World, 2015). Climate connectivity was quantified by adapting the approach of McGuire et al. (2016): forested areas were categorised into patches

according to 0.5°C increments in Mean Annual Temperature (Hijmans et al., 2005), and for each patch we calculated the coolest destination patch that could be reached by traversing a gradient from hotter to cooler adjacent patches. Patches achieved climate connectivity if they were able to reach a destination with a future temperature cooler than or equal to its current temperature. The aim of this approach is to quantify only the physical potential for thermally-restricted tropical forest species to reach climate analogues via forested habitat; it does not take into account any species-specific restrictions such as dispersal distance. We hypothesised that forest cover change from 2000 to 2012, elevation and the geometry of forest patches (patch area) would explain much of the variation in climate connectivity.

## 6.3 Materials and Methods

We focused our study on the pantropics, including all land masses located between  $\pm 23.43694^\circ$  latitude and more than 65,610 km<sup>2</sup> in area [*this is to reduce computational load and focus on places where range shifts are likely to be most feasible - it's currently arbitrarily set as the area of Sri Lanka*]. Maps were analysed at 1-km resolution projected into the World Cylindrical Equal Area projection. All spatial layers were processed with Python code implemented using the arcpy module in ArcMap version 10.4.1 (ESRI, 2011).

### 6.3.1 Climate-partitioned forest patches

Since we were interested in climate connectivity for tropical forest specialists, we calculated climate connectivity based on movement along a temperature gradient within forested areas only. We defined regions as forest or non-forest using tree cover data from Hansen et al. (2013). For the year 2000 (the recent past) cells were defined as forested if they had > 50% tree cover (Hansen et al., 2013), and did not fall within the boundaries of tree plantations (World, 2015). For the year 2012 (present day), cells were classed as forest based on forest loss and forest gain (Hansen et al., 2013) relative to the forest cover in 2000. If a cell had experienced forest loss from 2000 to 2012, it had gone from a forested to non-forested state and the cell was classed as non-forest. Conversely, if a cell had experienced forest gain from 2000 to 2012, it had gone from a non-forested to forested state; providing there had been no loss and the cell was not within a tree plantation, the cell was classed as forest.

Based on the approach of McGuire et al. (2016), we partitioned forest patches using a present-day (~1950-2000), 30-arc-second global layer for Mean Annual Temperature (hereafter: temperature) from the WorldClim database (Version 1.4; Hijmans et al., 2005), resampled to 1 km<sup>2</sup>. The same approach was applied separately to 2000 forest cover and

2012 forest cover: temperature values were assigned to forested cells and reclassified to increments of 0.5°C, based on evidence that tropical species are sensitive to this degree of temperature difference (e.g. Peh, 2007; Freeman and Freeman, 2014; Raxworthy et al., 2008). The resulting raster was then converted to polygons, whereby neighbouring forest cells with the same temperature value were assigned to the same polygon (hereafter: forest patch). While our approach is not specific to any particular taxon, it may be helpful to consider it in the context of range shifts by non-volant terrestrial animals (cf. Nuñez et al., 2013). We removed forest patches < 10 km<sup>2</sup> in area, based on the assumption that they could not support a population for long enough to enable range shifts [REF]. Patches within 2 km of each other were assigned to the same patch, assuming that populations could move across 2 km of non-forest to reach suitable habitat [REF].

### 6.3.2 Climate connectivity

The logic behind the measure of climate connectivity in McGuire et al. (2016) is that it represents the maximum temperature differential between current and future conditions that can be achieved by traversing a gradient of hotter to cooler patches within existing forest cover. We assigned mean current and future temperature to all forest patches, again using data from WorldClim. Future temperature was for the year 2050 (2041-2060), derived from the HadGEM2-AO general circulation model (IPCC, 2013) and Representative Concentration Pathway (RCP) 8.5, which is the most severe ('business-as-usual') IPCC scenario.

To trace each forest patch to its final destination patch we identified which patches were neighbours, and - for each neighbour pair - defined the hotter patch as the origin and the cooler patch as the destination. Most patches will have multiple neighbours, creating a network of connected patches with many possible pathways between them. We iterated over each unique temperature from cooler to hotter, propagating cool temperatures backward through the network of connected patches to identify the coolest temperature that could be reached for each origin patch (see Supplementary Text 1 for a worked example; McGuire et al., 2016).

Once each origin patch has a designated final destination patch, climate connectivity is calculated from the temperature differential between them. The key question is whether forest cover is sufficient for organisms to reach a place that, under future climate warming, is the same as or cooler than the temperature where it currently resides. Thus, climate connectivity is simply current temperature of the origin patch minus the future temperature of the destination patch. Where this value is zero or positive, the patch has achieved climate connectivity: there is sufficient structural connectivity between forested areas for organisms to reach an analogous future climate.

Climate connectivity was necessarily calculated at a patch-level, independently, for 2000 and 2012. However, because patches themselves were not constant through time, we used median climate connectivity within 50 m elevation al bands as our response variable. This not only enables comparison between the years, but also captures the potential interacting effect of elevation. Most human development occurs at lower elevations and most tropical species will likely track temperature gradients by moving uphill (Loarie et al., 2009), therefore both the patterns and significance of climate connectivity are likely to vary according to elevation. Elevation was derived from NASA's SRTM 90m Digital Elevation Database v4.1 (Jarvis et al., 2008).

### 6.3.3 Statistical analyses

All data were analysed using linear models in R version 3.4.3 (R Core Team, 2017). To understand current patterns we modelled 2012 climate connectivity against both elevation and continent. Any continental differences in climate connectivity are important from a policy perspective, but may also be expected owing to the different biogeography and land-use history of each continent within the pantropics: North and South America (hereafter: Latin America), Africa, Asia and Australia.

We hypothesised that the key drivers of change in climate connectivity would be change in forest cover and the geometry of forest patches in the year 2000. Within the same elevation al bands used to define climate connectivity, we calculated median patch area ( $\text{km}^2$ ) in the year 2000 (henceforth: patch area) and the total number of cells that went from a forested to non-forested state between 2000 and 2012 (henceforth: forest loss). In the full model, we tested change in climate connectivity against elevation and forest loss (and the interaction between them), and against patch area.

## 6.4 Results

### 6.4.1 Current state of climate connectivity

Across the whole study area, climate connectivity in 2012 ranged from a minimum of ??°C to a maximum of ??°C, with a median value of ??°C. Only ??% of the total area of forest patches achieved successful climate connectivity, with a value more than or equal to zero (Figure ??). Climate connectivity differed substantially by elevation band ( $F = ??; P = ??$ ), initially decreasing sharply as elevation increased, before reaching a plateau of around -3°C at elevations of 100 m or more (Figure ??).

### 6.4.2 Change in climate connectivity

Many areas experienced no change in climate connectivity from 2000 to 2012 (Figure ??), although change ranged from ??°C to +??°C. Forest loss was widespread, with a total area of ?? km<sup>2</sup> deforested between 2000 and 2012 (Figure ??).

Change in climate connectivity over time was unaffected by the area of forest patches in the year 2000 ( $F = ??; P = ??$ ), but decreased with increasing forest loss ( $F = ??; P = ??$ ; Figure ??).

## 6.5 Discussion

- We quantify for the first time the state of climate connectivity across the tropics, and how it has changed over a 12-year period.
- We make use of global datasets to empirically test factors that influence the probability of forest gaining or losing climate connectivity, such as the magnitude of forest cover change and elevation.
- *Interpretation of predictors of climate connectivity and change in climate connectivity, and what this means for biodiversity.*
- Quantifying and understanding climate connectivity in the tropics is important for estimating the potential for thermally-restricted forest specialists to adaptively respond to climate change. Such species represent a large proportion of the world's total biodiversity, but are highly threatened and highly vulnerable.

### 6.5.1 Caveats and limitations

It is important to note that we are not quantifying climate connectivity for particular species. This study is focused on how land-use change and climate change will interact to affect groups of species with particular thermal requirements. As such, our protocol analyses how forest cover and forest cover change affects the physical connectedness of forest patches within a particular climatic niche (cf. McGuire et al., 2016). The measure of climate connectivity is essentially a measure of the potential for thermally-restricted groups of species to track their preferred climate through near-continuous forest cover; we do not suggest that this alone is sufficient to predict the likelihood that such species will be capable of avoiding extinction under climate change. Many other factors will affect both the need and capacity for species to shift their ranges in response to rising temperatures. For example, even thermally-restricted species can adapt *in situ* via phenotypic plasticity, genetic adaptation or exploitation of climate refugia (Parmesan, 2006; Hannah et al., 2014). Species-specific factors such as dispersal

limits could preclude species from tracking their preferred climate even where climate connectivity exists, while some species may be capable of traversing greater distances through non-forest than we have allowed in our approach.

We focus on Mean Annual Temperature to create climate-partitioned forest patches, but note that other climate variables – particularly precipitation – are also extremely important in determining the climatic niche of any given species. Unfortunately, projections of future precipitation under climate change remain highly uncertain (IPCC, 2013; Corlett, 2012), and are also highly variable in space, both of which make it unclear the gradient that species would have to follow to avoid deleterious changes in precipitation.

The breadth of our study enabled us to determine broad trends and patterns across the most biodiverse biome in the terrestrial realm. However, to achieve such breadth requires that assumptions and simplifications are made. Our results should not be used to infer regional and local climate connectivity directly, but rather as a signpost to locations that appear to deviate from trends at a pantropical scale, and would therefore benefit from further, targeted investigation at a finer spatial scale, potentially incorporating species-specific information appropriate to the questions of interest (e.g. Martensen et al., 2017). Violations of our assumptions in particular regions would, of course, render our estimates of climate connectivity less accurate in those places. Overall, however, our focus is on climate connectivity at a pantropical scale, and therefore regional discrepancies will likely have limited impact on our overall conclusions. Our study, along with other, similar studies (McGuire et al., 2016; Martensen et al., 2017; Nuñez et al., 2013), represents the first steps towards capturing the current state of climate connectivity, but inevitably these approaches will be greatly enhanced by continuing developments in computational power and global, remotely-sensed datasets (Sanchez-Azofeifa et al., 2017).

### 6.5.2 Summary

Assessing the current status of climate connectivity across a whole biome enables us to establish a baseline, against which we can better appreciate the current and future threats to global biodiversity from the combined influence of land-use change and climate change. By using empirical data to characterise where, how and why forest cover change impacts climate connectivity, we can ensure that landscape planning of future, unavoidable forest loss is done with climate resilience in mind. Similarly, we can plan for forest gain (i.e. reforestation) and forest protection (e.g. Protected Areas) that incorporates and enhances climate corridors.

# Chapter 7

## Discussion



Frilled tree frog (*Kurixalus appendiculatus*).

### 7.1 Summary of thesis findings

- Aims of thesis were:
  1. Investigate the potential for land-use change to impact microclimates and microhabitats, and hence the subsequent impacts on:
    - The baseline of local climate change that global climate change is projected onto
    - The potential for thermal buffering as an adaptive response

2. Investigate the potential for land-use change to impact range shifts under climate change

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

\*\* Main objectives:\*\* 1. 2. 3. \* Assessed how degradation and conversion of tropical forests directly impacts temperature on a fine spatiotemporal scale \* Implications for the impact of further warming under global climate change, but suggests that degraded forests and micro-habitats may be able to buffer species from further change

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

\*\* Main objectives:\*\* 1. 2. 3. \* Developed software and metrics for analysing thermal images \* Enables other researchers to more easily utilise thermography as a technique for researching thermal regimes, which are vitally important to species' ecology

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

Main objectives:\*\* 1. 2. 3. \* Compared fine-scale temperature in primary and selectively logged forests of Borneo, using field data collected with dataloggers and a thermal camera \* Found that despite clear structural differences between these forest types, there was very little temperature variation which suggests rapid thermal recovery and underscores the importance of logged forests for biodiversity both now and under future climate change

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

\*\* Main objectives:\*\* 1. 2. 3. \* Combined global tree cover and climate datasets to quantify, pantropically, the current physical potential for species to reach climate analogues through near-continuous forest, and the extent to which this has been affected by recent forest cover change \* Found that current levels of climate connectivity are generally very poor, particularly in lowland regions with low forest cover and on mountain summits, hence many tropical species will struggle to reach analogous climate given current levels of forest cover

## 7.2 Climate at the fine scale

- Chapter 2 highlights that climate at the very coarse scale can mask important patterns occurring at a local scale
  - Land-use change has a direct impact on local climate
  - Suggestion that below-ground and within degraded forests species may avoid direct warming that results from loss of forest cover

- Bias towards particular regions & LUT
  - Doesn't account for intensity
- Chapter 3 establishes a framework to assess thermal regimes at an even finer spatial scale, using thermography
  - Importance of very fine spatial scale
  - Importance of surface temperature
  - Importance of spatial temperature variation
- Chapter 4 applies the framework of Chapter 3, alongside traditional dataloggers cf. Chapter 2, to further explore the potential for thermal buffering in selectively logged forests of Borneo
  - Confirm that local temperature is unaffected by selective logging, but so too is the fine-scale temperature variation that is vital for thermal buffering by animals
- Neither approach considered other climatic variables that are important to species' ecology under climate change (e.g. water & wind)
- Should also consider the vertical climate gradient in tropical rainforest (??)

### 7.3 Climate at the coarse scale

- Fine-scale climate is important for the day-to-day, individual-level responses of organisms to suboptimal temperatures, but over decades it is highly likely that many species will respond to coarse-scale climate change by shifting their ranges
  - This could happen alongside in situ adaptation, which could provide a buffer and allow more time for species to reach new target habitat
  - It could also be that in situ adaptation is not possible or is insufficient, for example in converted lands where the local temperature has increased to a level way beyond the thermal tolerance of forest specialists
- Chapter 4 considers the extent to which land-use change impacts landscape permeability, and the subsequent potential for species to reach analogous climates through natural habitat
  - Current levels of forest cover in the tropics offer poor connectivity between analogous climates, which has largely worsened from 2000 to 2012
- Only considering structural connectivity - no species data (this would make the approach species-specific and impose data limitations)
- Do not consider other climate variables, because their projections are uncertain and spatially variable, which makes it impossible at this stage to determine the gradient that species would have to follow to maintain climate parity

## 7.4 Wider applicability of findings

### 7.4.1 Biological relevance

- Chapters 2-4 are most relevant to small-bodied ectotherms, that are heavily influenced by local and fine-scale temperature and which are widely known to utilise thermal variation at this scale as a means to avoid suboptimal climatic conditions at a coarser scale
  - Also relevant to small-bodied endotherms, although less is known about the extent to which they can and do utilise microclimates in tropical forests
  - Could be relevant to plants, particularly in early life stages e.g. germination
  - A need to consider how behavioural exploitation of fine-scale temperature variation interacts with local adaptation and acclimation, and coarser scale responses such as range shifts
- Chapter 5 is more relevant to larger and more mobile animal species, such as medium-sized mammals, which are perhaps less able to adapt in situ but likely to shift their ranges in response to climate change
  - Relevance to plants will also depend on ability to disperse across matrix
  - Unknowns about how forest itself will shift under climate change also influences the relevance of these results to forest specialists
  - Different kinds of forest, which will limit different species to different extents
  - Inclusion of tree plantations may not be appropriate for many forest specialists, since they tend to lack structural and biological diversity

### 7.4.2 Relevance across tropics

- Chapter 2 was pantropical, but Africa was poorly represented
  - Where natural vegetation is not forest (e.g. páramo, cerrado, savannah, desert), it is expected that land-use change will have a much less substantial impact on local temperature
- Chapter 4 focused on a region of the tropics where logging intensity has in the past been very severe, but where logging activity has since ceased
  - Less relevant to areas with ongoing intensive logging
  - Less relevant to areas where recovery of canopy cover has not been permitted or not possible
- Chapter 4 only focused on the understorey, but in vertically complex forests there may well be a different result above the understorey

## 7.5 Recommendations for conservation and further research

- Land-use change is still a primary cause of species loss, and the lack of consideration of climatic impacts of land-use change may have underestimated this impact or caused it to be confounded with climate change (Chapter 2)
- Growing literature on the ways in which land-use change and climate change interact, but the impacts on risk of extinction for particular species will depend on many factors:
  - Spatiotemporal scale (Chapter 3 and 4)
  - Plasticity
  - Local adaptation
  - Functional connectivity (e.g. dispersal limits, metapopulation dynamics)
- On a local scale, enhancing thermal heterogeneity may help species to thermoregulate and so buffer species from climate change (at least offering them more time to adapt or disperse)
  - Chapter 4 suggests that natural restoration over a decade is sufficient for thermal recovery in the understorey, but this should be integrated with recovery of other abiotic and biotic requirements
  - More research is needed on the speed of thermal recovery, and whether active restoration or RIL techniques might have a role to play in enhancing thermal recovery from logging
- With improvements in technology, it would be fruitful to consider:
  - Other climatic factors, particularly moisture, at a fine spatial scale
  - Linking different spatiotemporal scales e.g. combining thermal imagery with drones to characterise thermal landscapes more extensively, or developing correlative models to link subcanopy climate to remotely sensed temperature data e.g. LAI
- Chapter 5 emphasises that habitat fragmentation has had a huge impact on the structural potential for range shifts, so future conservation efforts should aim to deforest, reforest and protect forest with climate connectivity in mind
  - Particularly hot and cold spots of climate connectivity can be used to pursue this research area in finer detail, considering particular taxonomic groups and habitat types, and could use scenarios to forecast further changes to climate connectivity from changes in land use and land cover
  - Again, restoration and protection of degraded forests likely has a key role to play in achieving climate connectivity across the tropics, while improving conditions in other elements of the matrix may also help some species (although this is unlikely to be of net benefit if used in place of a land-sparing strategy)

## 7.6 Conclusions

- The ways in which ongoing degradation and conversion of tropical forests impact the ability of species to respond to climate change will have a major influence on the long-term viability of forest specialists
- Tropical species represent a huge and vulnerable pool of global biodiversity, the loss of which would invariably push us towards, and perhaps beyond, various planetary boundaries
- We find that land-use change itself can have a major influence on climate at the level of the individual, but note that degraded forests still provide opportunities for thermal buffering and therefore have value both now and under climate change
- Protection of degraded forests, perhaps combined with restoration on abandoned agricultural sites, may also help connect species to future climate analogues – something that is clearly needed, since most tropical forests already fail to achieve climate connectivity
- In this context, the main aim of land managers should be to maximise the options available to species threatened with climate change, and so maintain climate resilience within changing tropical landscapes

# 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 A.1). 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 A.1a) and season (LMM,  $\chi^2 = 105.63$ , df = 4, P < 0.001; Figure A.1b). Specifically, the difference between altered land-use types and primary forest was greater above-ground than below-ground (Figure A.1a), and variable between seasons according to the land-use type (Figure A.1b).

## A.2 Supplementary figures

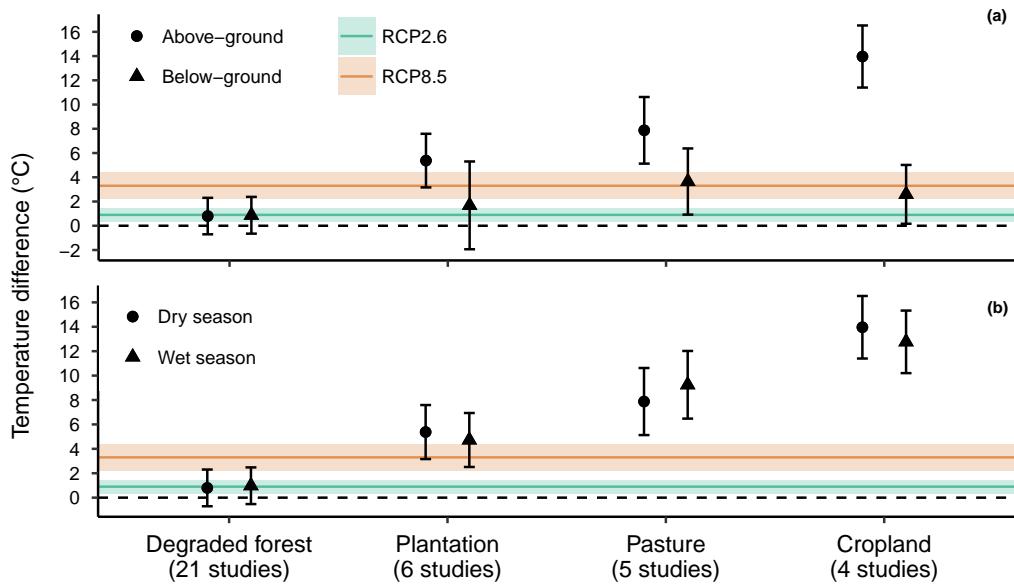


Figure A.1: Model estimates of the temperature difference between altered land-use types and primary forest, using a reduced dataset to balance sample sizes between the different studies that contributed data. Parameter estimates are standardised against the estimate for primary forest, which is represented 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, 2013). Shaded bands indicate 5%–95% ranges from the distribution of the climate model ensemble. Colours represent the lowest and highest warming scenarios (RCP2.6 and RCP8.5, respectively).

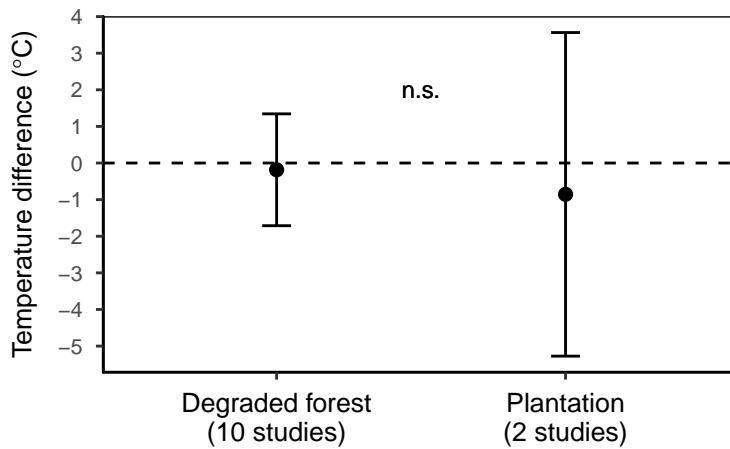


Figure A.2: Model estimates of the nocturnal temperature difference between altered land-use types and primary forest. Note that cropland and pasture are missing from this analysis because nocturnal temperature data for these land-use types were not available. Parameter estimates are standardised against the estimate for primary forest, which is represented by the dotted line. Error bars are 95% confidence intervals.

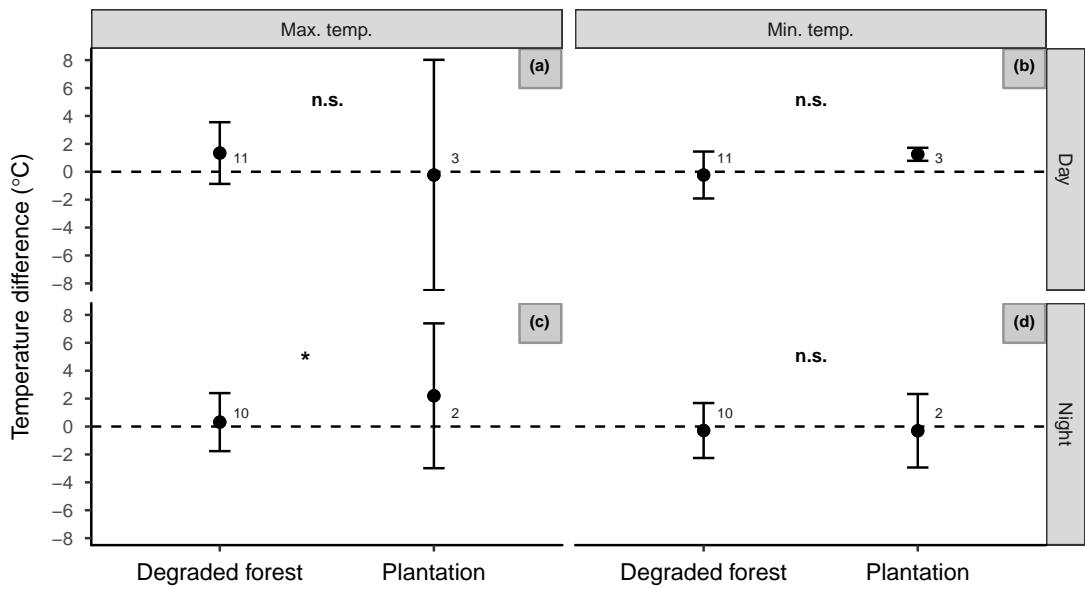


Figure A.3: Model estimates of the difference between altered land-use types and primary forest in terms of temperature extremes. Day-time results are depicted in panels A and B, and night-time results in panels C and D. Panels A and C indicate the effect of land-use change on maximum temperature, and 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.

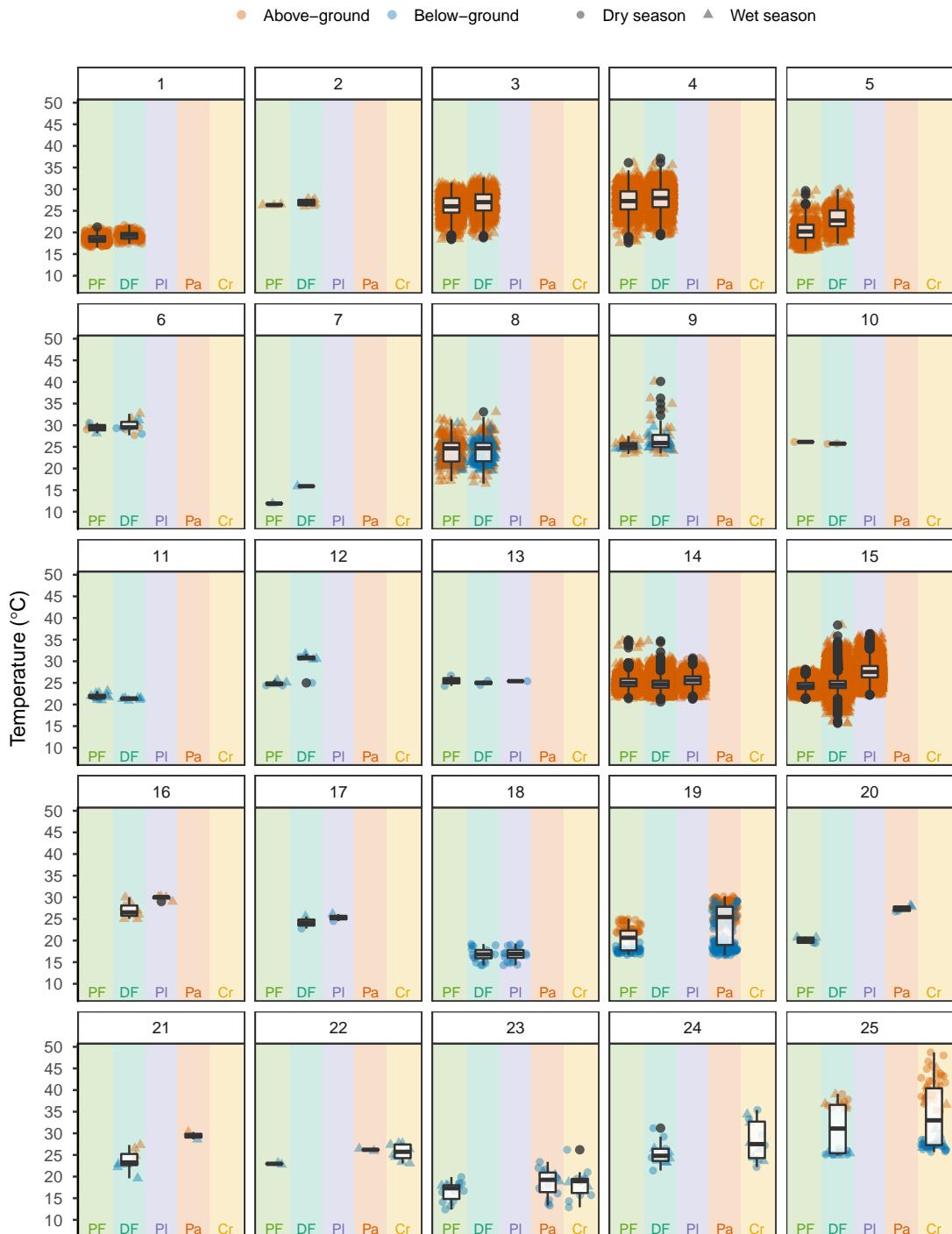


Figure A.4: Day-time temperature against land-use type for each study contributing data to the analyses. Panel numbers refer to the study number in the reference list below. Land-use types are: primary forest (PF), degraded forest (DF), plantation (PI), pasture (Pa) and cropland (Cr). Panels are ordered by the combination of land-use types for which data was available: (1-12) PF + DF; (13-15) PF + DF + PI; (16-18) DF + PI; (19-20) PF + Pa; (21) DF + Pa; (22-23) PF + Pa + Cr; and (24-25) DF + Cr. Shading of points indicates temperatures measured above-ground (orange) or below-ground (blue), and point symbol indicates temperatures measured during the dry season (circles) or wet season (triangles).

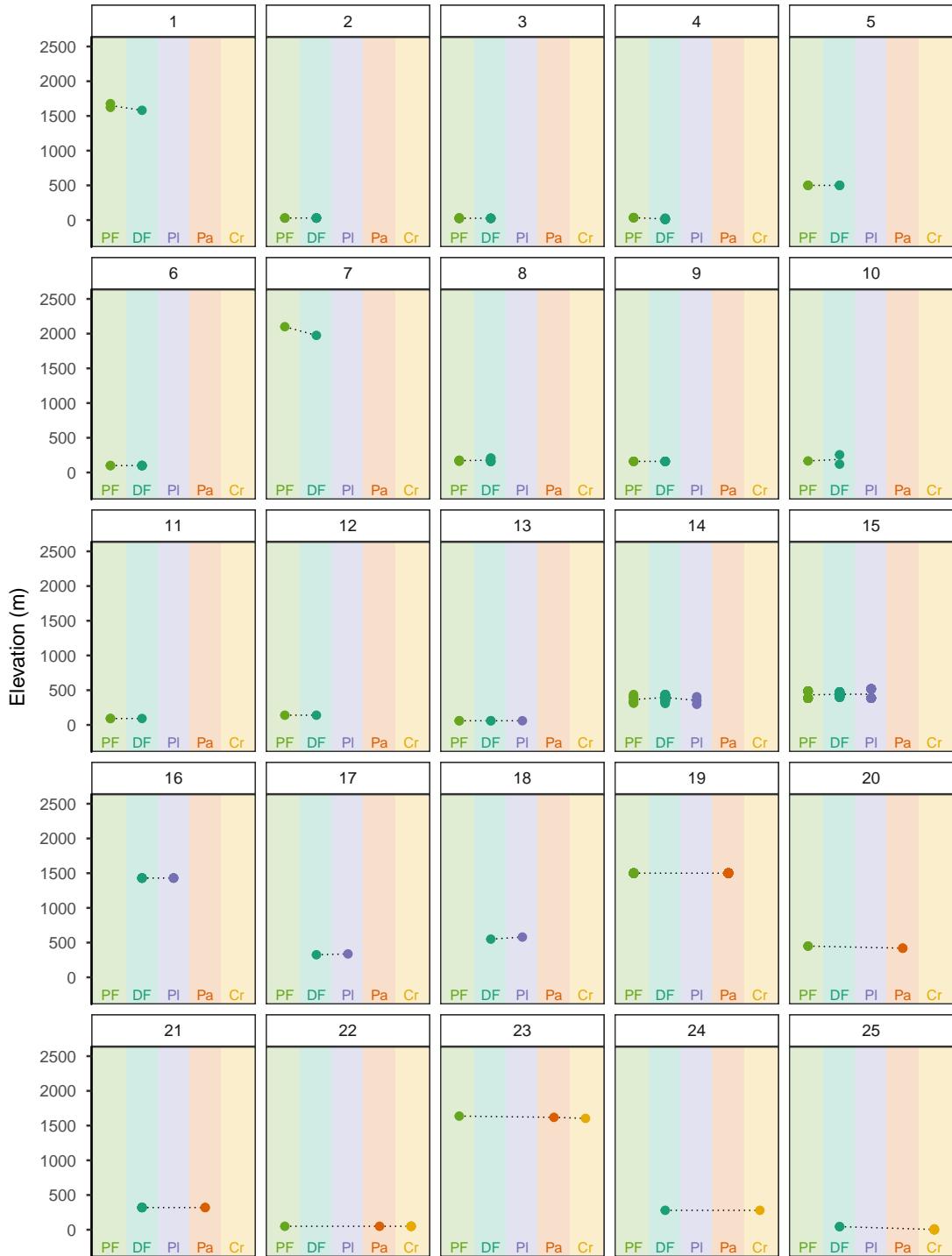


Figure A.5: Site elevation against land-use type for each study contributing data to the analyses. Panel numbers refer to the study number in the reference list below. Land-use types are: primary forest (PF), degraded forest (DF), plantation (PI), pasture (Pa) and cropland (Cr). Panels are ordered by 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.

## Appendix B

# Supporting information for Chapter 4

### B.1 Sampling methods for forest structure

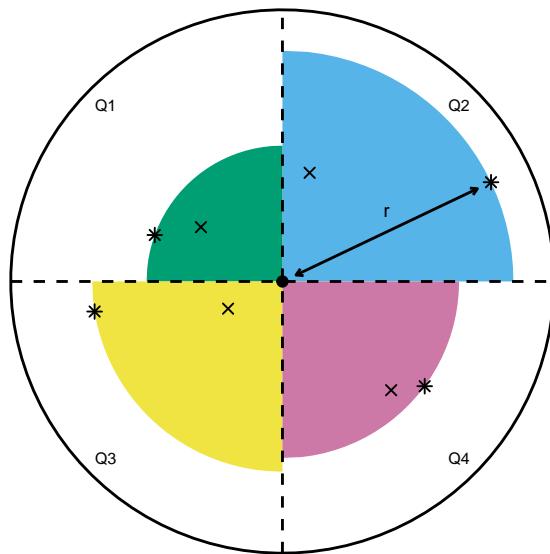


Figure B.1: Sampling design schematic.

Several different variables have been previously identified as efficiently capturing overall forest structure (Hamer et al., 2003; Lucey and Hill, 2012). Each plot (background circle in the schematic) was divided into quadrants (Q1-Q4). Within each quadrant we measured the distance to and circumference at breast height of the two nearest mature trees (circumference  $> 0.6$  m) and saplings (circumference 0.1-0.6 m). Stand basal area ( $m^2/ha$ ) was calculated separately for trees and for saplings. In the above schematic, tree/sapling individuals are depicted as points: there can be zero, one or two individuals in each quadrant; the nearest individual is represented by a cross, and the furthest individual as a star. To estimate

stand basal area, we calculated the basal area of each individual from its circumference at breast height, summed this across all observed individuals, divided by the true area of forest that was surveyed and multiplied by 10000 to convert units into the standard m<sup>2</sup>/ha. The true area surveyed is depicted by coloured quadrants; this was calculated for each quadrant individually and then summed together. Each true quadrant area was calculated using the equation:

$$A = \frac{1}{4}\pi r^2$$

Where A is the area (m<sup>2</sup>) and r is the distance to the furthest individual (tree or sapling; m).

To capture plot-level variation in basal area we calculated the coefficient of variation for trees and for saplings, and we also noted the proportion of observed tree individuals that were in the family Dipterocarpaceae, given the association of these species with mature, complex forest.

Finally, to capture the overall density of vegetation at the plot centre we measured percentage canopy cover using a spherical densiometer (Lemmon, 1956), and the same observer estimated percentage vegetation cover at three distinct forest strata: ground (1.5 m above ground), understorey (15 m above ground) and canopy (the main mat of leaf cover > 15 m above ground). Visual estimates of vegetation cover were made by imagining a horizontal gridded plane intersecting vegetation at the three different heights, and then estimating the percentage of grid cells occupied by vegetation.

## B.2 Extracting and processing data from thermal images

Using infrared cameras to sample microclimates in the terrestrial realm is a relatively novel methodology (Scheffers et al., 2017; but see: Caillon et al., 2014; Faye et al., 2016). There is, as yet, no standardised protocol, and there are numerous different choices of hardware. In this study, we used a FLIR Systems, model E40 camera. A single thermal image comprised 19200 distinct measurements from the infrared sensor (one per pixel). These raw data can be extracted and converted to temperature in °C using the freely available software FLIR Tools (cf. Scheffers et al., 2017). However, it is easier, faster and more thorough to use the R package *Thermimage* (Tattersall, 2017).

Raw data were first extracted from thermal images using the function `readflirJPG`, which produces a numeric matrix of the same dimensions as the original jpeg (160 x 120). The function `raw2temp` was then used to convert raw data into temperature using standard equations from infrared thermography (see `?Thermimage::raw2temp` for more details). At this point it is possible to specify various parameters that likely differ from the default settings. For emissivity we used a value of 0.986, which represents the mean of the range (0.982 to 0.990) for bare soil, leaf litter, live tree leaves and the bark of tree trunks in green broadleaf forests (Snyder et al., 1998). For atmospheric temperature and relative humidity, we used measurements taken using a whirling hygrometer immediately prior to each sampling event at each plot. We defined the distance between the camera and the surface as the hypotenuse of an isosceles right triangle with its vertical length equal to breast height:  $1.3 \times \sqrt{2} = 1.84$  m. Finally, there are five different calibration constants (`PlanckR1`, `PlanckB`, `PlanckF`, `PlanckO` and `PlanckR2`) that are specific to each camera, and we retrieved these from thermal images using the function `flirsettings`.

### B.3 Sampling methods for microhabitat volume

We measured the volume of leaf litter in five 1 x 1 m quadrats, centred 2 m to the left of the transect edge, at 0, 10 and 20 m from the plot centre. Leaf litter was compressed inside a purpose-built compression cylinder with a plunger, and the volume read directly from a graduated scale on the cylinder (Parsons et al., 2009).

Within the subplot we measured the length and circumference at both ends of all intact deadwood (> 10 cm diameter). If only a portion of the deadwood was contained within the subplot, we measured that portion only. We calculated volume using Smalian's volume formula (Waddell, 2002):

$$V = \frac{l \cdot (\frac{\pi}{8}) \cdot (D_S^2 + D_L^2)}{10000}$$

Where V is volume ( $\text{m}^3$ ), l is the length (m),  $D_S$  is the small-end diameter (cm),  $D_L$  the large-end diameter (cm). We also measured the maximum and minimum diameter of entrances to all tree holes (maximum entrance diameter > 2 cm and < 2 m high), and their internal volume. Approximating the entrance to an ellipse shape, we calculated entrance area using the standard equation for area of an ellipse:

$$A = \pi \times a \times b$$

Where A is entrance area ( $\text{cm}^2$ ), a is the maximum diameter of the entrance (cm) and b is the minimum diameter (cm). Internal volume could not be adequately measured for one very large tree hole, hence the plot in which it was located was excluded from analyses.

## B.4 Impact of logging on macroclimate

### B.4.1 Methods

To interpret the impact of selective logging on thermal buffering by microclimates in a meaningful way it is also necessary to know whether macroclimate conditions are affected by selective logging. As discussed in the Materials and Methods, macroclimate temperature was measured prior to thermal image collection using a whirling hygrometer, and also by a temperature datalogger suspended at the centre of each plot (HOBO pendant datalogger, Onset, model UA-001-64K or model UA-002-64K).

The necessity for thermoregulation, however, is dependent not only on temperature, but also on water availability. Vapour pressure deficit (VPD) encompasses both temperature and relative humidity. We measured VPD in two ways. First, using dry-bulb (i.e. macroclimate temperature) and wet-bulb temperature from the whirling hygrometer. We also suspended one hygrochron iButton datalogger (Maxim, model DS1923) 1.5 m above the ground in the plot centre of a subset of plots, alongside the HOBO dataloggers measuring macroclimate temperature. We attempted to distribute our limited number of hygrochrons as evenly as possible; ultimately we collected data from 15 plots across all six sites in primary forest, and from 13 plots across five sites in logged forest. As there were five plots in each site (Fig. 1), we placed dataloggers either in plots one, three and five, or plots one and five, depending on the number of hygrochrons available. Uneven sample sizes resulted because several hygrochrons were lost or broken. Hygrochrons measured relative humidity every 20 minutes for six days and, as in the main text (see Materials and Methods), a unique datapoint was the median value across each two-hourly increment from 04:40-14:40 hrs, on each day of recording for each of the 60 total plots.

Macroclimate VPD was calculated from saturated vapour pressure and relative humidity using the formula:

$$VPD = \frac{100 - RH}{100} \times SVP$$

Where VPD is vapour pressure deficit (Pa), RH is relative humidity (%) and SVP is saturated vapour pressure (Pa). SVP was calculated from temperature:

$$SVP = 610.7 \times 10^{\frac{7.5 \times T_d}{237.3 + T_d}}$$

Where  $T_d$  is macroclimate (dry-bulb) temperature ( $^{\circ}\text{C}$ ). Relative humidity can be estimated directly from a whirling hygrometer, but to reduce human error we calculated relative humidity using the equation:

$$RH = \frac{p}{SVP}$$

Where  $p$  is partial vapour pressure (Pa), estimated assuming ambient pressure of 1 atm:

$$p = SVR_w - 66.86 \cdot (1 + 0.00115 \cdot (T_w)) \cdot (T_d - T_w)$$

Where  $T_d$  is dry-bulb temperature ( $^{\circ}\text{C}$ ),  $T_w$  is wet-bulb temperature and  $SVP_w$  is saturated vapour pressure at the wet-bulb temperature, calculated in the same way as SVP, but substituting in  $T_w$  for  $T_d$ .

#### B.4.2 Statistical analysis

All supplementary analyses were carried out in an analogous way to the main analyses of microclimate temperature (see Statistical analyses). The response variables (macroclimate temperature or VPD, from either the hygrometer or dataloggers) were modelled against the fixed effects forest quality (measured as tree stand basal area;  $\text{m}^2/\text{ha}$ ) and forest type (categorical: primary forest or logged forest), using linear mixed effects models implemented in the `nlme` package (Pinheiro et al., 2017) in R (R Core Team, 2017). Plot nested in site was included as a random intercept term, to account for spatial pseudoreplication. Temporal autocorrelation of residuals was evident (function `acf`), and we therefore included date and time in a correlation structure, with the best structure determined using AIC (Zuur, 2009). Statistical significance was inspected using likelihood ratio tests (see Materials and Methods; Zuur, 2009), and diagnostic plots were assessed to confirm model fit.

#### B.4.3 Results

Macroclimate temperature was comparable between primary and logged forest whether measured using a whirling hygrometer ( $\text{LR} = 0.081, P = 0.776$ ; Fig. S2a) or suspended datalogger ( $\text{LR} = 0, P = 0.983$ ; Fig. S2b), and was also unaffected by forest quality for both the hygrometer ( $\text{LR} = 0.022, P = 0.883$ ; Fig. S2a) and datalogger measurements ( $\text{LR} = 0.527, P = 0.468$ ; Fig. S2b). Similarly, macroclimate VPD did not differ according to forest type for either method of VPD measurement: hygrometer ( $\text{LR} = 1.344, P = 0.246$ ; Fig. S2c) and suspended datalogger ( $\text{LR} = 3.489, P = 0.062$ ; Fig. S2d). Neither did the two measures of macroclimate VPD vary with forest quality ( $P > 0.05$ ; Fig. S2c-d). Thus, we found no evidence that selective logging impacted macroclimate temperature or macroclimate VPD.

## B.5 Impact of logging on microclimate over 24 hours

### B.5.1 Introduction

We were primarily interested in the impact of selective logging on thermal buffering at times when buffering from extremes of heat is most necessary. In the main analyses, therefore, we limited our study to temperatures recorded between the coolest part of the day (around sunrise) and the hottest part of the day (around noon; cf. Scheffers et al., 2017). However, the wealth of data recorded by dataloggers also enables us to investigate how thermal buffering varies over the full 24-hour period, and particularly during the day versus during the night. In the same way that we would expect logged forests to receive more incoming solar radiation during the day – because of reduced structural complexity and canopy cover (Okuda et al., 2003; Kumar and Shahabuddin, 2005) – we would also expect these forests to radiate heat more freely at night (Chen et al., 1995). Night-time conditions, although less thermally challenging, are still important biologically because nocturnal species can be inactive inside refugia during the heat of the day, but they must forage and seek mates at night if they are to survive and reproduce in the long-term.

### B.5.2 Statistical analysis

We assessed the impact of selective logging on microclimate temperature in the same way as in the main text (see Materials and Methods), but using the full datalogger dataset. Each unique datapoint was the median of six repeated measures taken every 20 minutes for each two-hourly interval, for each of six sequential days and in each of the 60 total plots (5 plots x 12 sites). As these analyses were not compared alongside results from thermal images, the two-hourly intervals began from 00:00 hrs (rather than 04:40 hrs). For simplicity, data recorded between 06:00-18:00 hrs were defined as being during the day, and 18:00-06:00 as during the night. Analyses were carried out separately for day and night and for each microhabitat: deadwood, tree holes and leaf litter. Thus, for each analysis (out of six), there was a maximum of 4320 unique datapoints: 12 time intervals x 6 days x 5 plots x 12 sites.

As in the main text, we used mixed effects models to analyse microclimate temperature as a function of forest quality (measured as tree stand basal area;  $m^2/ha$ ), forest type (primary or logged forest) and macroclimate temperature, with an interaction between the latter two variables. Models were implemented in the `nlme` package (Pinheiro et al., 2017) in R (R Core Team, 2017). We included plot nested within site as a random intercept to account for spatial pseudoreplication, and both date and time in a correlation structure to account for temporal autocorrelation (the best structure was determined using AIC; Zuur, 2009). Statistical signifi-

cance was inspected using likelihood ratio tests, first dropping the interaction and comparing to the full model, and then dropping main effects in turn and comparing to a model without the interaction term (Zuur, 2009).

### B.5.3 Results

We found no effect of either forest quality or forest type on microclimates at the surface or inside deadwood and leaf litter ( $P > 0.05$ ; Fig. S3). We found a very small effect of both variables on the absolute temperature of microclimates inside tree holes, during the day. At the median value of tree basal area, tree hole temperature in primary forest was 24.8°C compared to 24.9°C in logged forest ( $\text{LR} = 58.202, P < 0.001$ ; Fig. S3b), and with an increase in forest quality (i.e. tree stand basal area) of 1 m<sup>2</sup>/ha, tree hole temperature increased by 0.00504°C ( $\text{LR} = 57.814, P < 0.001$ ). Evidently, these effects were extremely small, and therefore unlikely to be relevant to the majority of organisms.

Similarly, any effects of forest type on the relationship between microclimate and macroclimate temperature, while statistically significant, were small in real terms. During the day, 1°C of warming in the macroclimate (from its median temperature) corresponded to more warming in primary forest than in logged forest for tree holes ( $\text{LR} = 18.214, P < 0.001$ ; Fig. S3b) and leaf litter ( $\text{LR} = 40.957, P < 0.001$ ; Fig. S3c), but there was no difference for microclimates inside deadwood ( $\text{LR} = 0.254, P = 0.614$ ; Fig. S3a). At night, 1°C of cooling in the macroclimate corresponded to more cooling in primary forest than in logged forest for microclimates inside deadwood ( $\text{LR} = 8.589, P < 0.01$ ; Fig. S3d) and leaf litter ( $\text{LR} = 861.623, P < 0.001$ ; Fig. S3f), but there was no longer any observed difference for microclimates inside tree holes ( $\text{LR} = 1.359, P = 0.244$ ; Fig. S3e).

Overall, there is some evidence that thermal buffering from warming and cooling is slightly enhanced for microclimates in logged forest compared to primary forest, but in reality the size of these effects was so small that they are unlikely to have much biological relevance. This is also evident from the large confidence intervals of Fig. S4, which demonstrate that for most values of macroclimate temperature, primary and logged forests did not differ in microclimate temperature.

## B.6 Supplementary figures

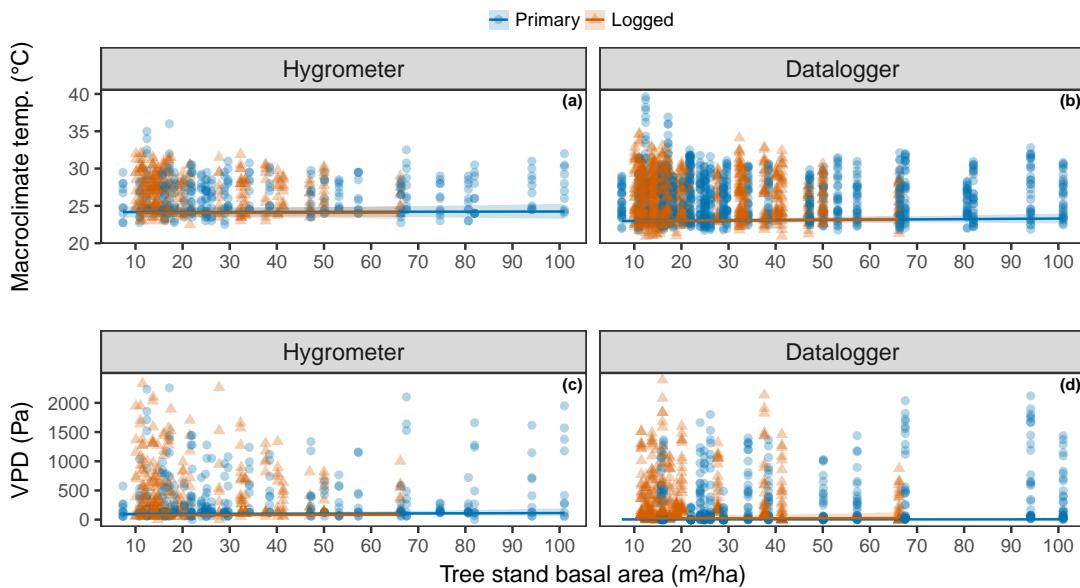


Figure B.2: The influence of forest type (primary or logged forest) and forest quality (measured as tree stand basal area;  $\text{m}^2/\text{ha}$ ) on macroclimate temperature (top row) and macroclimate vapour pressure deficit (VPD; bottom row). Macroclimate measurements collected using a whirling hygrometer are shown in the left column, and from dataloggers in the right column. Datapoints from primary forest points are depicted as blue circles, and from logged forest as orange triangles. Shaded bands are 95% confidence intervals.

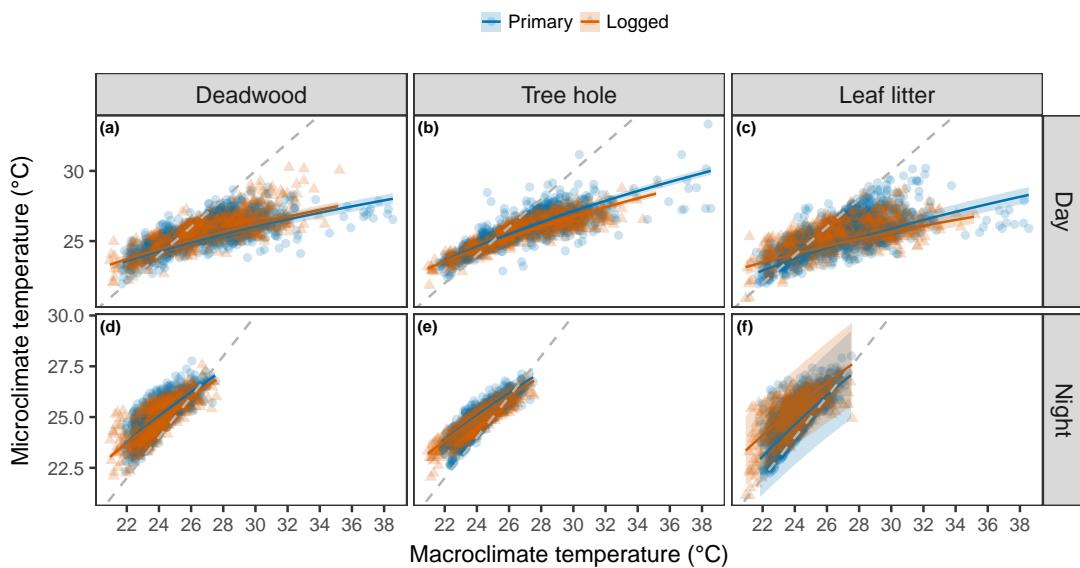


Figure B.3: Comparison of the relationship between microclimate temperature and macroclimate temperature within primary forest (blue circles) and logged forest (orange triangles), during the day (top row) and night (bottom row), and for three microhabitats: deadwood (left column), tree holes (centre column) and leaf litter (right column). The grey dashed line indicates zero temperature buffering, where the microclimate temperature is equal to the macroclimate temperature. Shaded bands are 95% confidence intervals.

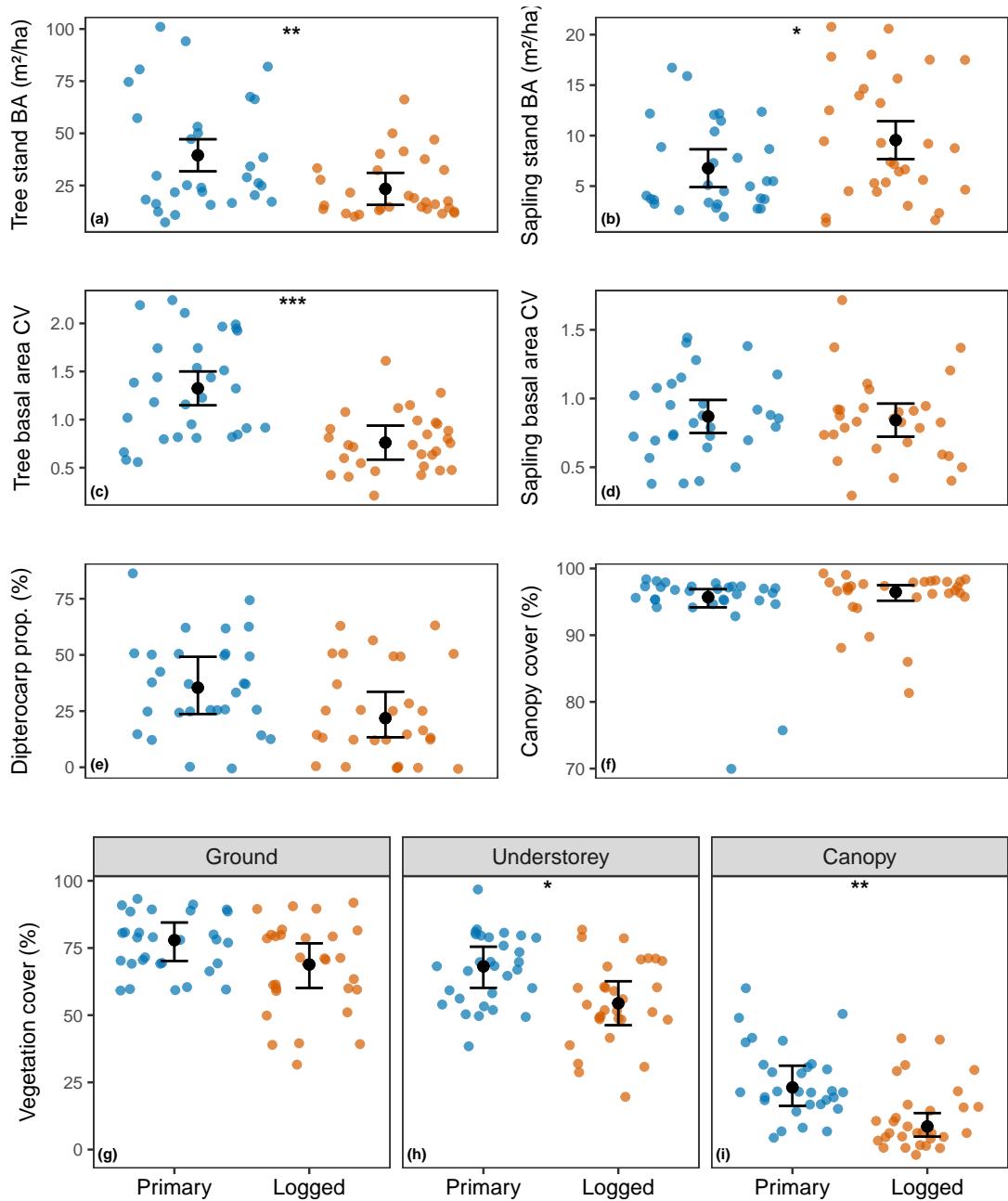


Figure B.4: Comparison between primary forest (blue) and logged forest (orange) for the nine forest structure measures: the stand basal area of trees (a) and saplings (b); the coefficient of variation for tree basal area (c) and sapling basal area (d); the proportion of trees that were in the family Dipterocarpaceae (e); the percentage canopy cover (f); and visual estimates of percentage vegetation at 1.5 m above ground (g), 15 m above ground (h) and  $> 15$  m above ground (i). Statistically significant differences are indicated by asterisks, differentiating between:  $0.01 < P < 0.05$  (\*);  $0.001 < P < 0.01$  (\*\*); and  $P < 0.0001$  (\*\*\*). Error bars are 95% confidence intervals.

# Bibliography

- Adachi, M., Bekku, Y. S., Rashidah, W., Okuda, T., and Koizumi, H. (2006). Differences in soil respiration between different tropical ecosystems. *Applied Soil Ecology*, 34(2–3):258–265.
- Asner, G. P., Keller, M., Pereira, Rodrigo, J., Zweede, J. C., and Silva, J. N. M. (2004). Canopy Damage and Recovery After Selective Logging in Amazonia: Field and Satellite Studies. *Eco-logical Applications*, 14(sp4):280–298.
- 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.
- Badejo, M. A. (1990). Seasonal abundance of soil mites (Acarina) in two contrasting environments. *Biotropica*, 22(4):382–390.
- Badejo, M. A., De Aquino, A. M., De-Polli, H., and Correia, M. E. F. (2004). Response of soil mites to organic cultivation in an ultisol in southeast Brazil. *Experimental & applied acarology*, 34(3-4):345–364.
- 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.
- Ball, I. R., Lindenmayer, D. B., and Possingham, H. P. (1999). A tree hollow dynamics simulation model. *Forest Ecology and Management*, 123(2–3):179–194.
- Barlow, J., Lennox, G. D., Ferreira, J., Berenguer, E., Lees, A. C., Nally, R. M., Thomson, J. R., Ferraz, S. F. d. B., Louzada, J., Oliveira, V. H. F., Parry, L., Ribeiro de Castro Solar, R., Vieira, I. C. G., Aragão, L. E. O. C., Begotti, R. A., Braga, R. F., Cardoso, T. M., Jr, R. C. d. O., Souza Jr, C. M., Moura, N. G., Nunes, S. S., Siqueira, J. V., Pardini, R., Silveira, J. M., Vaz-de Mello, F. Z., Veiga, R. C. S., Venturieri, A., and Gardner, T. A. (2016). Anthropogenic disturbance in tropical forests can double biodiversity loss from deforestation. *Nature*, 535(7610):144–147.
- 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.
- Berry, N. J., Phillips, O. L., Ong, R. C., and Hamer, K. C. (2008). Impacts of selective logging on tree diversity across a rainforest landscape: the importance of spatial scale. *Landscape Ecology*, 23(8):915–929.
- Bivand, R. and Piras, G. (2015). Comparing Implementations of Estimation Methods for Spatial Econometrics. *Journal of Statistical Software*, 63:1–36.
- Blakely, T. J. and Didham, R. K. (2008). Tree holes in a mixed broad-leaf–podocarp rain forest, New Zealand. *New Zealand Journal of Ecology*, 32(2):197–208.
- 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 and Evolution*, 27(3):145–150.
- Brodie, J. F., Giordano, A. J., Dickson, B., Hebblewhite, M., Bernard, H., Mohd-Azlan, J., Anderson, J., and Ambu, L. (2015). Evaluating multispecies landscape connectivity in a threatened tropical mammal community. *Conservation Biology*, 29(1):122–132.
- 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.
- Calabrese, J. M. and Fagan, W. F. (2004). A comparison-shopper’s guide to connectivity metrics. *Frontiers in Ecology and the Environment*, 2(10):529–536.
- Campos, C. (2006). Response of soil surface CO<sub>2</sub>-C flux to land use changes in a tropical cloud forest (Mexico). *Forest Ecology and Management*, 234(1–3):305–312.
- Carlson, B. S., Koerner, S. E., Medjibe, V. P., White, L. J. T., and Poulsen, J. R. (2017). Deadwood stocks increase with selective logging and large tree frequency in Gabon. *Global Change Biology*, 23(4):1648–1660.

- 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., Chiang, J. C. H., Lan, C.-W., Chung, C.-H., Liao, Y.-C., and Lee, C.-J. (2013). Increase in the range between wet and dry season precipitation. *Nature Geoscience*, 6(4):263–267.
- 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.
- Corlett, R. T. (2012). Climate change in the tropics: The end of the world as we know it? *Biological Conservation*, 151(1):22–25.
- Cosgrove, A. J., McWhorter, T. J., and Maron, M. (2017). Consequences of impediments to animal movements at different scales: A conceptual framework and review. *Diversity and Distributions*, page 1–12.
- 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.
- Davis, M. B. and Shaw, R. G. (2001). Range Shifts and Adaptive Responses to Quaternary Climate Change. *Science*, 292(5517):673–679.
- 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.
- Duellman, W. E. and Trueb, L. (1986). *Biology of Amphibians*. McGraw-Hill, New York.
- 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. and Laurance, W. F. (2013). Biodiversity Despite Selective Logging. *Science*, 339(6120):646–647.
- Edwards, D. P., Magrach, A., Woodcock, P., Ji, Y., Lim, N. T.-L., Edwards, F. A., Larsen, T. H., Hsu, W. W., Benedick, S., Khen, C. V., Chung, A. Y. C., Reynolds, G., Fisher, B., Laurance, W. F., Wilcove, D. S., Hamer, K. C., and Yu, D. W. (2014a). Selective-logging and oil palm: multitaxon impacts, biodiversity indicators, and trade-offs for conservation planning. *Ecological Applications*, 24(8):2029–2049.
- Edwards, D. P., Tobias, J. A., Sheil, D., Meijaard, E., and Laurance, W. F. (2014b). Maintaining ecosystem function and services in logged tropical forests. *Trends in Ecology & Evolution*, 29(9):511–520.
- ESRI (2011). ArcGIS Desktop: Release 10.
- Ewers, R. M. and Banks-Leite, C. (2013). Fragmentation Impairs the Microclimate Buffering Effect of Tropical Forests. *PLOS ONE*, 8(3):e58093.
- Ewers, R. M., Boyle, M. J. W., Gleave, R. A., Plowman, N. S., Benedick, S., Bernard, H., Bishop, T. R., Bakhtiar, E. Y., Chey, V. K., Chung, A. Y. C., Davies, R. G., Edwards, D. P., Eggleton, P., Fayle, T. M., Hardwick, S. R., Homathevi, R., Kitching, R. L., Khoo, M. S., Luke, S. H., March, J. J., Nilus, R., Pfeifer, M., Rao, S. V., Sharp, A. C., Snaddon, J. L., Stork, N. E., Struebig, M. J., Wearn, O. R., Yusah, K. M., and Turner, E. C. (2015). Logging cuts the functional importance of invertebrates in tropical rainforest. *Nature Communications*, 6:6836.
- Faye, E., Rebaudo, F., Yáñez-Cajo, D., Cauvy-Fraunié, S., and Dangles, O. (2016). A toolbox for studying thermal heterogeneity across spatial scales: from unmanned aerial vehicle imagery to landscape metrics. *Methods in Ecology and Evolution*, 7(4):437–446.
- 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.
- Fisher, B., Edwards, D. P., Larsen, T. H., Ansell, F. A., Hsu, W. W., Roberts, C. S., and Wilcove, D. S. (2011). Cost-effective conservation: calculating biodiversity and logging trade-offs in Southeast Asia. *Conservation Letters*, 4(6):443–450.
- 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.
- Furukawa, Y., Inubushi, K., Ali, M., Itang, A. M., and Tsuruta, H. (2005). Effect of changing groundwater levels caused by land-use changes on greenhouse gas fluxes from tropical peat lands. *Nutrient Cycling in Agroecosystems*, 71(1):81–91.
- Getis, A. and Ord, J. K. (1996). Local spatial statistics: an overview. *Spatial analysis: modelling in a GIS environment*, 374:261–277.
- 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. (n.d.). Unpublished data.
- 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.
- González-Dí Pierro, A. M., Benítez-Malvido, J., Méndez-Toribio, M., Zermeño, I., Arroyo-Rodríguez, V., Stoner, K. E., and Estrada, A. (2011). Effects of the physical environment and primate gut passage on the early establishment of Ampelocera hottlei Standley in rain forest fragments. *Biotropica*, 43(4):459–466.
- Goode, L. K. (n.d.). Unpublished data.
- Goode, L. K. and Allen, M. F. (2009). Seed germination conditions and implications for establishment of an epiphyte, Aechmea bracteata (Bromeliaceae). *Plant Ecology*, 204(2):179–188.
- 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.
- Hamer, K. C., Hill, J. K., Benedick, S., Mustaffa, N., Sherratt, T. N., Maryati, M., and K., C. V. (2003). Ecology of butterflies in natural and selectively logged forests of northern Borneo: the importance of habitat heterogeneity. *Journal of Applied Ecology*, 40(1):150–162.
- 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. and Orme, D. (2016). Aboveground microclimate at SAFE 2013 - 2015. *Zenodo*.
- 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.
- Hassall, M., Edwards, D. P., Carmenta, R., Derhé, M. A., and Moss, A. (2010). Predicting the effect of climate change on aggregation behaviour in four species of terrestrial isopods. *Behaviour*, 147(2):151–164.
- He, H. S., DeZonia, B. E., and Mladenoff, D. J. (2000). An aggregation index (AI) to quantify spatial patterns of landscapes. *Landscape Ecology*, 15(7):591–601.
- Heller, N. E. and Zavaleta, E. S. (2009). Biodiversity management in the face of climate change: A review of 22 years of recommendations. *Biological Conservation*, 142(1):14–32.
- 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.
- Hijmans, R. J., Cameron, S. E., Parra, J. L., Jones, P. G., and Jarvis, A. (2005). Very high resolution interpolated climate surfaces for global land areas. *International Journal of Climatology*, 25(15):1965–1978.
- Hijmans, R. J. and Graham, C. H. (2006). The ability of climate envelope models to predict the effect of climate change on species distributions. *Global Change Biology*, 12(12):2272–2281.
- 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.

- Hobbs, R. J., Valentine, L. E., Standish, R. J., and Jackson, S. T. (2018). Movers and Stayers: Novel Assemblages in Changing Environments. *Trends in Ecology & Evolution*, 33(2):116–128.
- Holl, K. D. (1999). Factors limiting tropical rain forest regeneration in abandoned pasture: seed rain, seed germination, microclimate, and soil. *Biotropica*, 31(2):229–242.
- Héault, B., Beauchêne, J., Muller, F., Wagner, F., Baraloto, C., Blanc, L., and Martin, J.-M. (2010). Modeling decay rates of dead wood in a neotropical forest. *Oecologia*, 164(1):243–251.
- 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.
- Ibanez, T., Hély, C., and Gaucherel, C. (2013). Sharp transitions in microclimatic conditions between savanna and forest in New Caledonia: Insights into the vulnerability of forest edges to fire. *Austral Ecology*, 38(6):680–687.
- 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 (2013). *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.
- Jarvis, A., Reuter, H., Nelson, A., and E., G. (2008). Hole-filled SRTM for the globe Version 4, available from the CGIAR-CSI SRTM 90m Database (<http://srtm.csi.cgiar.org/>).
- Jenkins, C. N., Pimm, S. L., and Joppa, L. N. (2013). Global patterns of terrestrial vertebrate diversity and conservation. *Proceedings of the National Academy of Sciences*, 110(28):E2602–E2610.
- Kaspari, M., Clay, N. A., Lucas, J., Yanoviak, S. P., and Kay, A. (2015). Thermal adaptation generates a diversity of thermal limits in a rainforest ant community. *Global Change Biology*, 21(3):1092–1102.

- 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.
- Khaliq, I., Hof, C., Prinzing, R., Böhning-Gaese, K., and Pfenninger, M. (2014). Global variation in thermal tolerances and vulnerability of endotherms to climate change. *Proceedings of the Royal Society of London B: Biological Sciences*, 281(1789):20141097.
- King, J. R., Andersen, A. N., and Cutter, A. D. (1998). Ants as bioindicators of habitat disturbance: validation of the functional group model for Australia’s humid tropics. *Biodiversity & Conservation*, 7(12):1627–1638.
- Kingsolver, J. G. (2009). The well-temperated biologist. *The American Naturalist*, 174(6):755–768.
- Klein, A.-M., Steffan-Dewenter, I., and Tscharntke, T. (2002). Predator–prey ratios on cocoa along a land-use gradient in Indonesia. *Biodiversity & Conservation*, 11(4):683–693.
- 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.
- Lebrija-Trejos, E., Pérez-García, E. A., Meave, J. A., Poorter, L., and Bongers, F. (2011). Environmental changes during secondary succession in a tropical dry forest in Mexico. *Journal of Tropical Ecology*, 27(05):477–489.
- Lemmon, P. E. (1956). A spherical densiometer for estimating forest overstory density. *Forest Science*, 2(4):314–320.
- 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.
- Lindenmayer, D. B., Cunningham, R. B., Pope, M. L., Gibbons, P., and Donnelly, C. F. (2000). Cavity sizes and types in Australian eucalypts from wet and dry forest types—a simple rule of thumb for estimating size and number of cavities. *Forest Ecology and Management*, 137(1–3):139–150.
- Littlefield, C. E., McRae, B. H., Michalak, J., Lawler, J. J., and Carroll, C. (2017). Connecting today's climates to future analogs to facilitate species movement under climate change. *Conservation Biology*, pages n/a–n/a.
- Liu, Z. G. and Zou, X. M. (2002). Exotic earthworms accelerate plant litter decomposition in a Puerto Rican pasture and a wet forest. *Ecological Applications*, 12(5):1406–1417.
- 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.
- Lucey, J. M. and Hill, J. K. (2012). Spillover of Insects from Rain Forest into Adjacent Oil Palm Plantations. *Biotropica*, 44(3):368–377.
- 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.
- Martensen, A. C., Saura, S., and Fortin, M.-J. (2017). Spatio-temporal connectivity: assessing the amount of reachable habitat in dynamic landscapes. *Methods in Ecology and Evolution*, pages n/a–n/a.
- 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.
- Maxwell, S. L., Fuller, R. A., Brooks, T. M., and Watson, J. E. M. (2016). Biodiversity: The ravages of guns, nets and bulldozers. *Nature News*, 536(7615):143.
- McGuire, J. L., Lawler, J. J., McRae, B. H., and Theobald, D. M. (2016). Achieving climate connectivity in a fragmented landscape. *Proceedings of the National Academy of Sciences*, 113(26):7195–7200.
- McLaughlin, B. C., Ackerly, D. D., Klos, P. Z., Natali, J., Dawson, T. E., and Thompson, S. E. (2017). Hydrologic refugia, plants, and climate change. *Global Change Biology*, 23(8):2941–2961.

- 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.
- Nadeau, C. P., Urban, M. C., and Bridle, J. R. (2017). Coarse climate change projections for species living in a fine-scaled world. *Global Change Biology*, 23(1):12–24.
- Negrete-Yankelevich, S., Fragoso, C., Newton, A. C., and Heal, O. W. (2007). Successional changes in soil, litter and macroinvertebrate parameters following selective logging in a Mexican Cloud Forest. *Applied Soil Ecology*, 35(2):340–355.
- 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., Echeverria-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 (n.d.). Solar Calculations. Available at: <https://www.esrl.noaa.gov/gmd/grad/solcalc/calcdetails.html>.
- NOAA Climate Prediction Center (2015). Available at: [http://www.cpc.noaa.gov/products/analysis\\_monitoring/ensostuff/ensoyears.shtml](http://www.cpc.noaa.gov/products/analysis_monitoring/ensostuff/ensoyears.shtml).
- Nuñez, T. A., Lawler, J. J., Mcrae, B. H., Pierce, D. J., Crosby, M. B., Kavanagh, D. M., Singleton, P. H., and Tewksbury, J. J. (2013). Connectivity Planning to Address Climate Change. *Conservation Biology*, 27(2):407–416.

- 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.
- Parmesan, C. and Yohe, G. (2003). A globally coherent fingerprint of climate change impacts across natural systems. *Nature*, 421(6918):37–42.
- Parsons, S. A., Shoo, L. P., and Williams, S. E. (2009). Volume measurements for quicker determination of forest litter standing crop. *Journal of Tropical Ecology*, 25(06):665–669.
- 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.
- Peh, K. S. H. (2007). Potential Effects of Climate Change on Elevational Distributions of Tropical Birds in Southeast Asia. *The Condor*, 109(2):437–441.
- 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. ArticleType: research-article / Full publication date: Jul. 21, 1995 / Copyright © 1995 American Association for the Advancement of Science.
- Pinheiro, J., Bates, D., DebRoy, S., Sarkar, D., and R Core Team (2017). nlme: Linear and Nonlinear Mixed Effects Models.
- Potter, K. A., Arthur Woods, H., and Pincebourde, S. (2013). Microclimatic challenges in global change biology. *Global Change Biology*, 19(10):2932–2939.
- 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., Fredericksen, 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. Available at: <https://www.R-project.org/>.
- 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.
- Raxworthy, C. J., Pearson, R. G., Rabibisoa, N., Rakotondrazafy, A. M., Ramanamanjato, J.-B., Raselimanana, A. P., Wu, S., Nussbaum, R. A., and Stone, D. A. (2008). Extinction vulnerability of tropical montane endemism from warming and upslope displacement: a preliminary appraisal for the highest massif in Madagascar. *Global Change Biology*, 14(8):1703–1720.
- Reynolds, G., Payne, J., Sinun, W., Mosigil, G., and Walsh, R. P. D. (2011). Changes in forest land use and management in Sabah, Malaysian Borneo, 1990–2010, with a focus on the Danum Valley region. *Philosophical Transactions of the Royal Society B: Biological Sciences*, 366(1582):3168–3176.
- 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.
- Sanchez-Azofeifa, A., Antonio Guzmán, J., Campos, C. A., Castro, S., Garcia-Millan, V., Nightingale, J., and Rankine, C. (2017). Twenty-first century remote sensing technologies are revolutionizing the study of tropical forests. *Biotropica*, pages 1–16.
- 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.
- Santos, B. A. (2011). *La interacción de heliconia con sus insectos herbívoros y hongos patógenos foliares en selvas tropicales fragmentadas*. PhD thesis, Universidad Nacional Autónoma de México, Centro de Investigaciones en Ecosistemas.
- Santos, B. A. and Benítez-Malvido, J. (2012). Insect herbivory and leaf disease in natural and human disturbed habitats: lessons from early-successional Heliconia herbs. *Biotropica*, 44(1):53–62.
- 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., Edwards, D. P., Macdonald, S. L., Senior, R. A., Andriamahohatra, L. R., Roslan, N., Rogers, A. M., Haugaasen, T., Wright, P., and Williams, S. E. (2017). Extreme thermal heterogeneity in structurally complex tropical rain forests. *Biotropica*, 49(1):35–44.
- 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.
- Scheffers, B. R., Phillips, B. L., Laurance, W. F., Sodhi, N. S., Diesmos, A., and Williams, S. E. (2013). Increasing arboreality with altitude: a novel biogeographic dimension. *Proceedings of the Royal Society B: Biological Sciences*, 280(1770):20131581–20131581.
- 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.
- Sciven, 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.

- Sears, M. W., Angilletta, M. J., Schuler, M. S., Borchert, J., Dilliplane, K. F., Stegman, M., Rusch, T. W., and Mitchell, W. A. (2016). Configuration of the thermal landscape determines thermoregulatory performance of ectotherms. *Proceedings of the National Academy of Sciences*, 113(38):10595–10600.
- Sears, M. W., Raskin, E., and Angilletta, M. J. (2011). The world is not flat: defining relevant thermal landscapes in the context of climate change. *Integrative and Comparative Biology*, 51(5):666–675.
- Senior, R. A., Hill, J. K., González del Pliego, P., Goode, L. K., and Edwards, D. P. (2017). A pantropical analysis of the impacts of forest degradation and conversion on local temperature. *Ecology and Evolution*, 7(19):7897–7908.
- Shi, H., Wen, Z., Paull, D., and Guo, M. (2016). A framework for quantifying the thermal buffering effect of microhabitats. *Biological Conservation*, 204:175–180.
- Shoo, L. P., Storlie, C., Williams, Y. M., and Williams, S. E. (2010). Potential for mountaintop boulder fields to buffer species against extreme heat stress under climate change. *International Journal of Biometeorology*, 54(4):475–478.
- Sirami, C., Caplat, P., Popy, S., Clamens, A., Arlettaz, R., Jiguet, F., Brotons, L., and Martin, J.-L. (2017). Impacts of global change on species distributions: obstacles and solutions to integrate climate and land use. *Global Ecology and Biogeography*, 26(4):385–394.
- 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.
- Snyder, W. C., Wan, Z., Zhang, Y., and Feng, Y.-Z. (1998). Classification-based emissivity for land surface temperature measurement from space. *International Journal of Remote Sensing*, 19(14):2753–2774.
- Sonnleitner, M., Dullinger, S., Wanek, W., and Zechmeister, H. (2009). Microclimatic patterns correlate with the distribution of epiphyllous bryophytes in a tropical lowland rain forest in Costa Rica. *Journal of Tropical Ecology*, 25(03):321–330.
- 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.
- Tattersall, G. J. (2017). Thermimage: Thermal Image Analysis. Available at: <https://CRAN.R-project.org/package=Thermimage>.
- 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.
- Titeux, N., Henle, K., Mihoub, J.-B., Regos, A., Geijzendorffer, I. R., Cramer, W., Verburg, P. H., and Brotons, L. (2017). Global scenarios for biodiversity need to better integrate climate and land use change. *Diversity and Distributions*, 23(11):1231–1234.
- Tucker, M. A., Böhning-Gaese, K., Fagan, W. F., Fryxell, J. M., Moorter, B. V., Alberts, S. C., Ali, A. H., Allen, A. M., Attias, N., Avgar, T., Bartlam-Brooks, H., Bayarbaatar, B., Belant, J. L., Bertassoni, A., Beyer, D., Bidner, L., Beest, F. M. v., Blake, S., Blaum, N., Bracis, C., Brown, D., Bruyn, P. J. N. d., Cagnacci, F., Calabrese, J. M., Camilo-Alves, C., Chamaillé-Jammes, S., Chiaradia, A., Davidson, S. C., Dennis, T., DeStefano, S., Diefenbach, D., Douglas-Hamilton, I., Fennessy, J., Fichtel, C., Fiedler, W., Fischer, C., Fischhoff, I., Fleming, C. H., Ford, A. T., Fritz, S. A., Gehr, B., Goheen, J. R., Gurarie, E., Hebblewhite, M., Heurich, M., Hewison, A. J. M., Hof, C., Hurme, E., Isbell, L. A., Janssen, R., Jeltsch, F., Kaczensky, P., Kane, A., Kappeler, P. M., Kauffman, M., Kays, R., Kimuyu, D., Koch, F., Kranstauber, B., LaPoint, S., Leimgruber, P., Linnell, J. D. C., López-López, P., Markham, A. C., Mattisson, J., Medici, E. P., Mellone, U., Merrill, E., Mourão, G. d. M., Morato, R. G., Morellet, N., Morrison, T. A., Díaz-Muñoz, S. L., Mysterud, A., Nandintsetseg, D., Nathan, R., Niamir, A., Odden, J., O'Hara, R. B., Oliveira-Santos, L. G. R., Olson, K. A., Patterson, B. D., Paula, R. C. d., Pedrotti, L., Reineking, B.,

- Rimmler, M., Rogers, T. L., Rolandsen, C. M., Rosenberry, C. S., Rubenstein, D. I., Safi, K., Saïd, S., Sapir, N., Sawyer, H., Schmidt, N. M., Selva, N., Sergiel, A., Shiilegdamba, E., Silva, J. P., Singh, N., Solberg, E. J., Spiegel, O., Strand, O., Sundaresan, S., Ullmann, W., Voigt, U., Wall, J., Wattles, D., Wikelski, M., Wilmers, C. C., Wilson, J. W., Wittemyer, G., Zięba, F., Zwijacz-Kozica, T., and Mueller, T. (2018). Moving in the Anthropocene: Global reductions in terrestrial mammalian movements. *Science*, 359(6374):466–469.
- 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.
- Waddell, K. L. (2002). Sampling coarse woody debris for multiple attributes in extensive resource inventories. *Ecological Indicators*, 1(3):139–153.
- 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.
- Wangluk, S., Boonyawat, S., Diloksumpun, S., and Tongdeenok, P. (2013). Role of soil temperature and moisture on soil respiration in a teak plantation and mixed deciduous forest in Thailand. *Journal of Tropical Forest Science*, 25:339–349.
- Warton, D. I. and Hui, F. K. C. (2011). The arcsine is asinine: the analysis of proportions in ecology. *Ecology*, 92(1):3–10.
- Werner, C., Zheng, X., Tang, J., Xie, B., Liu, C., Kiese, R., and Butterbach-Bahl, K. (2006). N<sub>2</sub>O, CH<sub>4</sub> and CO<sub>2</sub> emissions from seasonal tropical rainforests and a rubber plantation in Southwest China. *Plant and Soil*, 289(1-2):335–353.
- 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.
- Wood, T. E. and Lawrence, D. (2008). No short-term change in soil properties following four-fold litter addition in a Costa Rican rain forest. *Plant and Soil*, 307(1-2):113–122.
- World, T. (2015). Tree plantations. Available at: [www.globalforestwatch.org](http://www.globalforestwatch.org).

- Xu, M., Qi, Y., Chen, J., and Song, B. (2004). Scale-dependent relationships between landscape structure and microclimate. *Plant Ecology*, 173(1):39–57.
- Yashiro, Y., Kadir, W. R., Okuda, T., and Koizumi, H. (2008). The effects of logging on soil greenhouse gas (CO<sub>2</sub>, CH<sub>4</sub>, N<sub>2</sub>O) flux in a tropical rain forest, Peninsular Malaysia. *Agricultural and Forest Meteorology*, 148(5):799–806.
- Yeong, K. L., Reynolds, G., and Hill, J. K. (2016). Leaf litter decomposition rates in degraded and fragmented tropical rain forests of Borneo. *Biotropica*, 48(4):443–452.
- Zuur, A. F. (2009). *Mixed effects models and extensions in ecology with R*. Statistics for biology and health. Springer, New York, NY.