

# Dragons Feel the Heat

## The Ecology of Tropical Agamid Lizards During Land Use and Climatic Change

James John Hicks, MZoology with Herpetology

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## **Contributions**

The research contained in this PhD thesis was mostly carried out by myself however, as with any large body of work, it would not have succeeded without key contributions from various sources along the way. Detailed below are where and how other researchers contributed to my work.

### **Chapter 2: Biodiversity in plantations**

The transects were ground-tested with help from Max Jones, Alicia Solana. Transects were carried out with help primarily from Max Jones but we were also accompanied by the Management and Ecology of Malaysian Elephants (MEME) field team: Param, Ridzuan, Hussain, Cherang and Alicia Solana Mena on various occasions (their observations were excluded from the dataset). Adam Algar and Joe Bailey helped with the spatial statistics in ARCMAP.

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# 1 Introduction and literature review

## 1.1 Background

Climate change and its effects on biodiversity are currently recognised as an area of great importance for biodiversity and ecological research. Global warming has already caused widespread ecological impacts in both marine and terrestrial ecosystems (Walther *et al.* 2002, Parmesan 2006, Burrows *et al.* 2011) and these impacts are predicted to continue into the future. Climate change is of particular importance to terrestrial ectothermic organisms due to their reliance on environmental temperatures for biological processes (Deutsch *et al.*, 2008). Climate change has been predicted to negatively affect almost every species studied thus far (Sinervo *et al.* 2010, although see Logan *et al.* 2013) and has already been implicated in the extinctions of a diverse range of taxa (for example McLaughlin *et al.* 2002; Franco *et al.* 2006; Sinervo *et al.* 2010; Glynn 2012) at both global (Malcolm *et al.* 2006, Szabo *et al.* 2012) and local scales (Rutherford *et al.* 1999, Ochoa-Ochoa *et al.* 2012) although the exact causes in each case are often variable and poorly understood (Cahill *et al.* 2013). Malcolm *et al.* (2006) predicted climate change to exceed deforestation by 2106 as the leading cause of plant extinctions in tropical biodiversity 'hotspots', which, consequently, could have substantial impact on the associated faunal assemblages.

Despite this recent (and justified) focus of the literature on climate change as a driver of adaptation or extinction, land cover change (and land use change) remains the current largest risk to biodiversity on a global scale (Pereira *et al.* 2010) and will likely only be compounded by climate change (Yang *et al.* 2009). Land use change also contributes to climate change (Dale 1997, Hua and Chen 2013) and is a leading source of CO<sub>2</sub> emissions, after fossil fuels (Le Quere *et al.* 2009), creating a positive feedback cycle between the two. However, land use change is often considered inevitable due to the growing demand placed upon the planet to support the ever increasing human population despite current practices already impacting future viability and productivity of the ecosystems they are supported by (Foley *et al.* 2005).

## 1.2 Land use change

Land use change is the result of an interaction between a country's historical land use, its economy, technological prowess and population and biological factors such as climatic region and soil composition (Lambin *et al.* 2001, 2003, Meiyappan *et al.* 2014). It is especially prevalent and destructive in the tropics, notably the Amazon basin and Southeast Asia and over 80% of global agricultural land created since 1980 has been a result of forest conversion (Gibbs *et al.* 2010). The Amazon basin and Southeast Asia are also the two most significant contributors to CO<sub>2</sub> emissions from land use change through the deforestation process and subsequent cultivation of the remaining soil (Le Quere *et al.* 2009). With land cover change progressing at such a rate, current reserve areas are insufficient to conserve extant biodiversity and organisms will be forced to alter their behaviours to persist (Corlett 2013). Even organisms within protected areas are not immune; protected areas are also at risk of shifts in floral composition as a result of climate change (Holmes *et al.* 2013).

A species' 'suitable' and 'unsuitable' habitat can be estimated and predicted, as can suitable microclimates using correlative and/or mechanistic niche modelling. However, both of these methods generally rely on broad-scale climate data (mechanistic models generally model microclimate from macroclimate), ignore non-climatic niche axes (but see Algar *et al.* 2013), and assume strong niche conservatism, i.e. prohibit niche evolution (but see Buckley *et al.* 2015). Moreover, these models do not consider land-use change when projecting future species responses. As novel thermal environments are created by land use change much more rapidly than by climate change, identifying the specific physiological challenges, e.g. thermal stress, as well as non-thermal pressures, that organisms face in these environments is paramount. Species may be unable to evolve along the relevant niche axes quickly enough to utilize the novel conditions to which land-cover change is rapidly exposing them. Moreover, the immediate potential thermal threat to organisms from land use change has been overlooked relative to the more gradual threat posed by global warming which will only compound, in the longer-term, the challenges organisms face in utilising the rapidly created, novel, thermal environments after land use change.

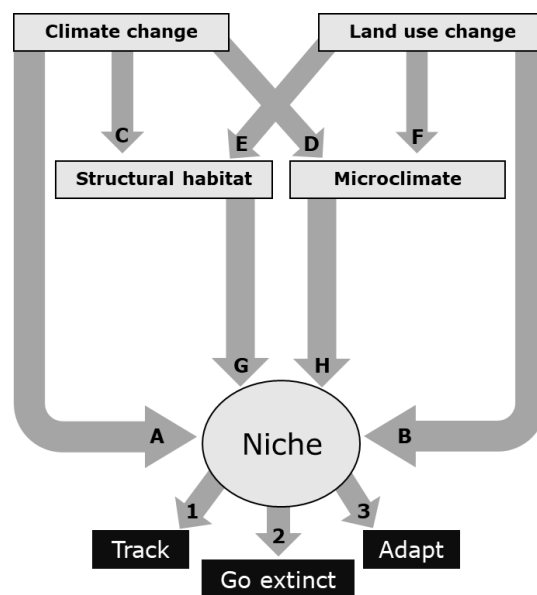
The principal crops responsible for land use change are oil palm and soy bean, especially in Southeast Asia. In Southeast Asia, rubber plantations are another



major source of habitat modification (Warren-Thomas *et al.* 2015). Oil palm and soybean monocultures account for over 60% of global vegetable oil production but only around 10% of research in agriculture is centred on them and of this, less than 1% focuses on biodiversity/conservation (Turner *et al.* 2008). This statistic highlights an important lack of knowledge on the ecological effects of these monocultures. Oil palm plantations cover over 14.5 million hectares globally, with Malaysia and Indonesia producing the largest quantities (Turner *et al.* 2008). Between 1990 and 2005 over 50% of all oil palm crops planted in Malaysia and Indonesia were done so by the conversion of primary and secondary forests (Koh and Wilcove 2008). Due to the favourable climate, the crop is grown in the tropics, where most of the planet's biodiversity is concentrated, along with high levels of endemism (Myers *et al.* 2000, Sodhi *et al.* 2004, 2010, Koh and Wilcove 2008). The relatively few biodiversity orientated studies that have examined oil palm have found that species diversity and abundance decline in plantations compared to untouched habitat in comparable regions (Foster *et al.* 2011). The changes in species diversity and composition arise from initial extinctions at the clearance stage where the land is cleared and terraced for the oil palms to be planted. Diversity then accumulates through colonisation from neighbouring habitats of species which can tolerate these plantations during their relatively long lifespan (25-30 years) (Snaddon *et al.* 2013), therefore older plantations are expected to have higher diversity than younger plots. However this, in turn, can cause additional biodiversity loss when the crops are destroyed and replanted. These results are concordant with those from other agricultural landscapes e.g., in the Caribbean where *Anolis* diversity is inversely proportional to the level of disturbance and harvesting (Glor *et al.* 2001).

Few studies have gathered data on the mechanistic reasons organisms fail to fully utilise oil palms. However, such failures seem likely to arise from changes along two main ecological niche axes: microclimate and structural habitat (Fig. 1.1) although predators, prey availability and pathogens also contribute. Habitat simplification is suggested as one reason by Foster *et al.* (2011) and there is evidence that greater plant diversity automatically results in greater animal diversity (Novotny *et al.* 2006, Dyer *et al.* 2007, Condon *et al.* 2008) and thus the far fewer plant species within oil palm plantations should result in correspondingly low faunal diversity. Mariau (2001) suggests, on the other hand, that as the lifespan of the crops is relatively long, substantial heterogeneity may accumulate and fairly rich species assemblages may form.

For example, half of all lowland epiphyte species in Malaysia may be found in oil-palm monocultures (Foster *et al.* 2011). In addition to habitat simplification, microclimatic effects of forest conversion on organisms have been documented, mainly in arthropods. The lower, simplified canopy and more open nature of oil palm monocultures causes greater daily temperature fluctuations and a higher maximum temperature and lower minimum humidity (Turner and Foster 2006, Koh *et al.* 2009). Research has been undertaken to predict climatic patterns within the increasing land use change at both local (Troy *et al.* 2007, Othman *et al.* 2009) and, more rarely, global scales (Meiyappan *et al.* 2014). The relative strengths and weaknesses of each approach are reviewed in Heistermann *et al.* (2006).



**Figure 1.1:** A highly simplified diagrammatic representation of the effects of climate and land use change on the niche of herpetofauna. Most studies have focused on broad scale interactions, especially processes A and B using niche modelling. Climate changes' effects on structural habitat is fairly poorly studied whereas its effect on microclimate has been a focus for many studies, the reverse is true of land use change. In lizards, interaction G is especially well-studied in *Anolis* (Reviewed by Losos, 2009) but data is relatively poor for other taxa. Detailed research on microclimates' effect on the realised niches of reptiles is fairly sparse. Examples have been studied of all 3 responses to changes to the niches of herpetofauna (Araujo *et al.*, 2006, Stuart *et al.*, 2014), with extinction being a particularly significant risk to amphibian species globally (Duart *et al.*, 2012). Not included here are predators, prey or pathogens which also affect the niche space of an organism and may feasibly be altered by plantations.

### 1.3 Introduction to thermal performance

Organisms' ecological 'performance' is their ability to carry out ecologically relevant activities (such as sprinting to capture prey or avoid predation) and is a proxy of overall fitness and probability of survival. Organismal performance varies with temperature, and responds quickly to changes in body temperature

(Angilletta 2009). Commonly measured proxies of whole-organism performance include endurance (Angilletta *et al.* 2002a, Clemente *et al.* 2009) and digestion (Avery *et al.* 1993, Qu *et al.* 2011) but in reptiles, sprint speed is most commonly used (Angilletta 2009).

The variation in performance over different temperatures follows a characteristic curve (Huey and Stevenson 1979) whereby performance rises past a critical thermal minimum ( $CT_{min}$ ) to reach the organism's optimum temperature ( $T_{opt}$ ) in ectotherms. Performance rapidly decreases past this point until the organism reaches its critical thermal maximum ( $CT_{max}$ ). Despite the thermal performance curve's (TPC) generality, its shape can vary substantially among organisms. For example, organisms may be thermal specialists (i.e., only performing well at a specific temperature) or thermal generalists (i.e., performs well across a range of temperatures) (Angilletta 2009). Organisms also have different strategies related to the extent to which they attempt to remain at  $T_{opt}$ . This ranges between hypothetical perfect thermoregulators (which maintain body temperature at an optimal value exactly, via behaviour or physiology) and perfect thermoconformers (their body temperature exactly matches their environment at all times). Species which are both thermal specialists and thermoconformers, i.e., many tropical forest lizards, are predicted to be most at risk from future climate change (Huey and Tewksbury 2009, Huey *et al.* 2009), at least in the absence of thermal adaptation (Buckley *et al.* 2015). Within terrestrial ectotherms, amphibians are predicted to be particularly at risk of climate change (Reading 2007, Duarte *et al.* 2012) with climate-driven local declines already reported (D'Amen and Bombi 2009) but even more so to short term climatic events (Neveu 2009). Climatic changes in East Asia have already affected the breeding cycles of some species (Kusano and Inoue 2008). Species in other areas may already be experiencing sub-optimal temperatures (Huey *et al.* 2009, Scheffers *et al.* 2014) potentially putting species at risk of reduced performance, increasing predation risk (Knowles and Weigl 1990, McMillan *et al.* 2009, Rempel 2011, Ewald *et al.* 2013) and reducing their reproductive output (Bell *et al.* 2013).

How the thermal vulnerability of ectothermic organisms will change as the microclimates they occupy become warmer is a subject that hasn't been as broadly studied as climate changes' predicted direct impacts on broad-scale environmental niches. Organisms are generally predicted to be negatively affected in the long term but may temporarily benefit from increased

performance from global warming e.g., some Honduran *Anolis* species (Logan *et al.* 2013). Microhabitats have been shown to buffer climatic increases effectively in tropical forests (Scheffers *et al.* 2014) however temperatures outside these microhabitats are already above the  $CT_{max}$  of many of the native species (Sunday *et al.* 2014) and temperature increases within these microhabitats could still endanger these species.

#### **1.4 Thermal tolerance of ectotherms**

The critical thermal maxima and minima are the temperature limits an organism can tolerate, assuming no other hazards are present (Santos *et al.* 2011). Heritability of these traits is crucial to the ability of organisms to survive changes in their extant thermal niches (e.g., climate change) or utilise novel ones (e.g., those created by land use change). Two theoretical evolutionary responses to an increase in lizard body temperature due to climate change are illustrated in Huey and Kingsolver (1993): a linear shift towards higher performance at higher temperatures (assuming  $CT_{min}$  and  $CT_{max}$  are not genetically linked), or a broadening of the thermal performance curve with a slight loss of peak performance if thermal tolerance limits are linked.

Thermal tolerances in reptiles are usually measured by artificially warming or cooling individuals in controlled conditions for  $CT_{max}$  and  $CT_{min}$ , respectively (e.g., Qu *et al.* 2011; Kolbe *et al.* 2012; Leal and Gunderson 2012; Munoz *et al.* 2014). The  $CT_{max}$  or  $CT_{min}$  differ from lethal temperatures. Rather they are reached when an organism experiences a steep decline in its motor response, usually measured in lizards as the animal's inability to right itself (Angilletta 2009). Critical thermal temperatures are sometimes estimated from thermal performance curves based on less extreme temperatures (Logan *et al.* 2013), but these involve extrapolation beyond the range of the predictor variables and thus must be used carefully.

Overall, the thermal tolerances (i.e.,  $CT_{min}$  and  $CT_{max}$ ) of reptiles are highly variable (reviewed by Clusella-Trullas and Chown 2014). However,  $CT_{min}$  is far more variable than  $CT_{max}$  (Araujo *et al.* 2013). While variations in  $CT_{min}$  have been shown to evolve relatively quickly in ectotherms at interspecific (Grigg and Buckley 2013, Muñoz *et al.* 2014) and intraspecific (Kolbe *et al.* 2012, 2014, Leal and Gunderson 2012) scales (from  $<1$  to  $>10^{\circ}C$ , Qu *et al.*, 2011),  $CT_{max}$  is more conserved (Muñoz *et al.* 2014), usually near  $40^{\circ}C$  (although some

more extreme examples are known from lizards, see Qu *et al.*, 2011 for a review of  $CT_{min}$  and  $CT_{max}$  values), a pattern reflected in many other organisms as well, including endotherms (Araujo *et al.* 2013). It has been shown that critical thermal maxima and minima are not strongly linked at a genetic or physiological level (Brown 1996) and thus, they evolve independently. However, single, brief exposures to particular temperatures are not entirely representative of an organisms' thermal limit, which also depend on the duration and severity of the thermal stress imposed upon the animal (Rezende *et al.* 2014).

Van Berkum (1988) proposed that reptile thermal tolerances follow a latitudinal cline, with low latitude, tropical species having narrower thermal ranges ( $CT_{max} - CT_{min}$ ), than their temperate counterparts. Elevation has been shown to have a similar effect on  $CT_{min}$ : higher altitude species/populations have correspondingly lower critical thermal thresholds, but without a consistent decrease in  $CT_{max}$  (Brown 1996, Muñoz *et al.* 2014). For diurnal *Anolis* species, the relatively rapid rate of  $CT_{min}$  evolution likely reflects selection upon this trait during cool nights (Muñoz *et al.* 2014). In contrast, lizards could behaviourally thermoregulate during the day to avoid the hottest temperatures, thus avoiding selection for higher  $CT_{max}$  (the Bogert effect, Huey *et al.* 2003a); opportunities for effective behavioural thermoregulation are less available at night, thus exposing lizards to selection on  $CT_{min}$  (Muñoz *et al.* 2014). Extensive thermoregulation exposes ectotherms to increased risk from predation and lessens their ability to forage, reproduce and defend territory (Huey 1974, Grant and Dunham 1988, Adolph and Porter 1993) and reduces growth rates (Brewster *et al.* 2013). Despite this, there are many physiological and biochemical benefits to maintaining a relatively high body temperature (Bennett 1987, Huey and Kingsolver 1989, Savage *et al.* 2004, Huey *et al.* 2009, Angilletta *et al.* 2010). To evolve to thermoregulate to a higher body temperature rather than physiologically operate at lower body temperatures presumably involves far less genetic change (Blomberg *et al.* 2003) as thermoregulation already varies seasonally within species (Christian and Bedford 1995, Muñoz *et al.* 2014), i.e., "evolution along a genetic line of least resistance" (Schluter 1996). However this does not explain the lack of adaptation to even higher temperatures by the low altitude species studied by Muñoz *et al.* (2014). This apparently slow rate of evolution for  $CT_{max}$  in diurnal lizards is a cause for great concern as many lizards live in areas where environmental temperatures are regularly already greater than their  $CT_{max}$  and

rely on microhabitats to survive (Scheffers *et al.* 2014). If these microhabitats become warmer the lizards that rely on behavioural mechanisms to account for lethally high environmental temperatures may be unable to evolve higher  $CT_{max}$  quickly enough to outpace selection on them.

Sorte *et al.* (2011) found that some marine invertebrates show adjustment to higher temperatures via acclimation across their current distribution, although the potential for higher thermal tolerances were not uniform even within a species; some populations had higher limits than others. This is also found in groups of lizards where considerably different patterns of adaptation have been suggested. In the nocturnal Gran Canaria gecko *Tarentola boettgeri* both  $CT_{min}$  and  $CT_{max}$  varied between populations and were negatively correlated with elevation Brown (1996). Brown (1996) also suggested that  $CT_{min}$  may be able to evolve at a faster rate in nocturnal species than in diurnal lizards. Initial differences in thermal tolerance can be attributed to non-genetic processes and acclimatisation to source environments (Garland and Adolph 1991). However, in *Tarentola boettgeri*, variance in  $CT_{min}$  remained even after a lengthy acclimation period in the laboratory, suggesting an underlying genetic basis and therefore, the potential for heritability of varying thermal tolerance at the intraspecific level (Brown 1996). Another example of capacity to evolve higher  $CT_{max}$  is found in two closely related, sympatric *Phrynocephalus* species (*P.frontalis*, *P.versicolor*: Agamidae) with similar  $CT_{min}$  but divergent  $CT_{max}$  (Qu *et al.* 2011). The higher  $CT_{max}$  in *P.versicolor* is thought to be an adaptation to reduce competition between these species for resources in the same structural habitat, leading to thermal niche partitioning.

On a broader phylogenetic scale, differences between thermal tolerances (both  $CT_{min}$  and  $CT_{max}$ ) have been found in Iguanidae (Huey and Kingsolver 1993) and Scincidae (Garland *et al.* 1991). These studies also found positive correlations between measured body temperatures in the field and  $T_{opt}$ , measured from sprint speed data obtained using experimental racetracks. Additionally,  $CT_{max}$  was positively correlated with  $T_{opt}$  but not with  $CT_{min}$ . These results suggest numerous evolutionary scenarios: firstly,  $CT_{max}$  seemingly evolves alongside optimum temperatures, in the same direction, whether by a genetic link or environmental selection on both traits acting independently of one another (Felsenstein 1988, Huey *et al.* 1991, Martins and Garland 1991). Secondly, there is no apparent genetic link or co-adaptive potential between

CT<sub>max</sub> and CT<sub>min</sub>. Iguanids were shown to obviously be capable of evolving varying interspecific differences in CT<sub>max</sub> values (Huey and Kingsolver 1993).

On a wider scale, thermal tolerances and preferences are highly variable in lizards depending on phylogenetic affinities, biotope and more fine scale environmental factors. Qu *et al.* (2011) present a synthesis of previous data gathered for lizard thermal tolerances and preferred temperatures (T<sub>sel</sub>). Their results suggest no correlation between CT<sub>min</sub> and T<sub>sel</sub> but report a significant correlation between CT<sub>max</sub> and T<sub>sel</sub>, in concordance with Huey and Kingsolver's (1993) data for Iguanidae and also previous results for Scincidae by Garland *et al.* (1991). Qu *et al.* (2011) classified species as "Cold", "Temperate" or "Warm" climate types and additionally by activity period (diurnal or nocturnal) and microhabitat preference (sun exposed or shady). Results suggest "Warm" and "Temperate" species show similar CT<sub>min</sub>, CT<sub>max</sub> and T<sub>sel</sub> whereas lizards from "Cold" climates can withstand higher and lower temperatures. Within temperate and warm climate types, lizards did not possess significantly different CT<sub>max</sub> or CT<sub>min</sub> based on activity period, however diurnal lizards showed higher T<sub>sel</sub>. Lizards occupying sunny microhabitats had higher T<sub>sel</sub> and CT<sub>max</sub> while shade dwelling species had lower CT<sub>min</sub>. Selected body temperatures were highest in "Cold" climate lizards, lowest in "Warm" climate species and intermediate in "Temperate" species (Qu *et al.* 2011). Despite the apparent value of such a comprehensive review of thermal data for lizards, the authors unfortunately fail to provide detailed parameters used to classify the climatic origins of the lizard species included in this synthesis and also for the further classification of activity period and microhabitat types, casting doubt over the reproducibility of these results and inhibiting the inclusion of additional data from other lizard groups and lowering the rigor of the results obtained.

If organisms are capable of adapting to rising temperatures, the heritability of elevated thermal tolerance will probably be vital. Results in reptiles are scarce and the heritability of CT<sub>max</sub> has been studied most extensively in *Drosophila* species, however, results are mixed. Studies using 'realistic', slow rates of heating to mimic climate change traditionally show little heritability or genetic variance in the CT<sub>max</sub> for the majority of species or even negative effects (discussed in Santos *et al.* 2011) and have more recently been contradicted by Santos *et al.* (2012), showing that flawed methodologies could underestimate the true heritability of CT<sub>max</sub> in *Drosophila*. Additionally, Santos *et al.* (2012) found no interaction between warming rate and heritability, indicating that in

a natural scenario seasonal or daily variations in the rate of temperature increase would not greatly affect the evolutionary response of  $CT_{max}$ . This study gives some hope for organisms' genetic ability to adapt to long-term gradual thermal change, however it is merely a simulation and on one of the most adaptable species of *Drosophila* (Powell 1997) and may not hold true for vertebrates, with far longer generation times. Additionally a later study by Paaijmans *et al.* (2013) found results to the contrary in their chosen model organism, a mosquito (*Anopheles stephensi*), whereby adding daily temperature fluctuations decreased the  $CT_{max}$ , thus increasing susceptibility to climate change.

Plasticity has been shown to provide insects with a limited capability (2-4°C) of withstanding short term heat stress (Hoffmann *et al.* 2003, Chown *et al.* 2009, Allen *et al.* 2012). While this may allow species at some latitudes/elevations to survive in the short term it may result in species in the mid latitudes being at risk of extinction (Hoffmann *et al.* 2013). It is however, currently unknown if these capabilities are shared by vertebrate ectotherms.

While the proven ability of some ectotherm groups to adapt to differing microclimatic niches over relatively large periods of evolutionary time (Huey and Kingsolver 1993) will be important for species to persist under ongoing, relatively gradual climate change, their ability to adapt to the abrupt, short term shifts, specifically, in climate that land use change can cause is arguably as important but has been the subject of considerably less, if any, research.

## **1.5 Modelling the impacts of change on ectotherms**

Predictions of how climate and land use change will affect species geographical distribution at various temporal scales often rely on environmental niche models, based on climate data from species' current ranges (Barrows 2011, Kolbe *et al.* 2012, Barlow *et al.* 2013, Sow *et al.* 2014). Modelling approaches can be roughly divided into two broad categories: mechanistic and correlative. Correlative modelling link geo-referenced species occurrences to environmental conditions, usually climate, at particular locations. Maximum entropy modelling (MaxEnt) is a powerful and popular (Harte and Newman 2014) example of correlative modelling, with good performance (Elith and Graham 2009) especially in predicting putative range losses resulting from climate change, as it allows distribution to be predicted under both future and



past climatic conditions. This methodology has however been problematic, especially using the default settings (Rodda *et al.* 2011) due to its' fairly coarse scale which ignores subtle local variations in climate, which are important for small vertebrates like reptiles and due to realised niches i.e., organisms only occupying a portion of their potential niche space due to external, locally variable confounding factors. Regardless of this, the model is of limited use in planning and introducing population-scale conservation actions when used at the most typical scale (Renwick *et al.* 2012).

Mechanistic niche models focus solely on real relationships between the performance of an organism and its environment and infer distribution changes from these relationships and in theory, should be more accurate than correlative models (Buckley *et al.* 2010). The most robust predictions are made from methodologies that incorporate both modelling approaches (Kearney *et al.* 2010) and this combined modelling approach should form the basis for future species distribution predictions.

Several studies have focused on using niche modelling to predict how land use change and climate change may affect species' distributions. Loiselle *et al.* (2010) predicted deforestation to be the more destructive of the two processes but conceded that the novel thermal habitats that climate change will create in the future will force species to adapt to the warmer microhabitats or go extinct. The authors assumed that change has already taken place in response to these novel thermal habitats, but did not measure these changes. Similarly, Gadsden *et al.* (2012) examined how climate and land use change would affect the distributions of *Crotaphytus antiquus* and *Sceloporus cyanostictus* in Mexico. Using MaxENT, they found *C. antiquus* to lose a significant amount of habitat by 2050 to anthropogenic land use change and in contrast, the future range of *S. cyanostictus* would be constrained by climate change. A study by Steen *et al.* (2010) examined the effect of both on game fish populations in the Muskegon River Watershed. While a few species' distributions were affected (e.g., a predicted 276% gain for *Esox lucius* and a 90% loss for *Salvelinus fontinalis*) the overall species composition in the study area wasn't affected. This study used an *in situ* modelling system that was already in place for the watershed, and so the methods cannot be replicated easily for other habitats.

While studies modelling distribution changes are numerous, relatively few attempt to show changes in population density and abundance within these

hypothetical ranges, which is more valuable for conservation actions. Renwick *et al.* (2012) addressed this using generalized linear models (Shedden 2010) applied to data obtained from the Breeding Birds Survey in 1997 to predict abundance in 2012. Abundances in 2050 and 2080 were modelled under the two most extreme climatic scenarios (B1 & A1F1: UK Climate Impacts Programme, 2002) for two species of bird in the North of the UK and two in the South. Differing land use was accounted for using a national scale map of land cover (Haines-Young *et al.* 2000) to check for correlations with climate to avoid misleading results i.e., to ensure range shifts were due to climate change and not to inherent differences between climates in different land use types. In this study the more southerly species were predicted to gain from climate change and the northerly ones' abundances were predicted to decline. Harris *et al.* (2014) found a similar disparity in tropical birds, but between mid and high altitude assemblages. Specifically, Harris *et al.* (2014) reported that, on Sulawesi, a high altitude bird species was buffered from the effects of deforestation due to its distribution, far from human settlements, and thus was not as significantly affected by the 11.8% loss of forest cover in the study area between 2000-2010 as it may be by climate change (61% predicted population decline). The mid-elevation species, while being affected by climate change (8-11% loss), had suffered a greater population loss from land use change and the associated loss of suitable habitat.

## **1.6 Functional morphology and structural habitat**

Land cover change will affect multiple ecological niche axes. In addition to altering thermal environments, it will also change the available structural habitat. In addition to producing novel structural habitat for species to utilise, it will also simplify the range of existing ones (Foster *et al.* 2011). Structural habitat in lizards generally correlates with morphological trait measurements including toe/toepad size (Stuart *et al.* 2014), limb length (Ord and Klomp 2014) and scalation (Wegener *et al.* 2014) although see Vanhooydonck and Van Damme (1999) for an example of a relatively unspecialised clade (Lacertidae). These differences in morphological characters have been suggested in many cases to be adaptive for improved whole-organism performance in the given environment (Irschick 2002, Da Silva *et al.* 2014) and animals avoid habitats where they would not perform optimally (Irschick and Losos 1999). For example, in terrestrial species, limb and toe length is a commonly measured trait and generally correlates closely with sprint speed on

specific substrate types, a relationship that has been shown in multiple lizard clades (Kohlsdorf *et al.* 2001, Goodman *et al.* 2008). In arboreal species however there is an increased focus on the proposed trade-off between speed and stability on differing perch widths in these characters, with longer legs generally being found in species (or in some cases, populations within species) that utilise wider perches and vice versa (Irschick and Losos 1999, Irschick 2002, Calsbeek *et al.* 2007, Kuo *et al.* 2009). In some cases, however, morphological traits may instead correlate with behavioural traits rather than habitat types e.g., predator escape behaviour in *Liolaemus* (Schulte *et al.* 2004). Some members of the *Anolis* clade possess considerable plasticity in some morphological traits e.g., hindlimb length; whereby young raised on wider perches grow longer hindlimbs (Kolbe and Losos 2005). This would theoretically allow lizards to adjust, to some degree, to rapid structural habitat change without undergoing any genetic changes such as being forced to utilise novel perch types, however it has not been discovered in other groups thus far.

Diverse structural habitats can allow similar lizard species to evolve in sympatry by habitat partitioning and character displacement (Singh *et al.* 2002, Ord and Klomp 2014) and in some cases, to large-scale adaptive radiations as in *Anolis* lizards (Losos *et al.* 1998). Short generation times have allowed some species to evolve adaptations to novel environments rapidly (Stuart *et al.* 2014) and although this is traditionally driven by interspecific competition, leading to character displacement, the same adaptive pressure could plausibly be initiated by colonisation of a completely novel habitat as would have been the case in *Anolis* during founder events on the Greater Antillean islands, that eventually led to in-situ speciation (Losos 2009).

## **1.7 Adaptation to land use change**

If lizards are to utilise the novel thermal and structural habitats created by land use change they must either adapt to them *in situ* or possess prior pre-adaptations to the vacant niches they offer. Due to the short evolutionary timescale that land use change occurs over, the majority of species simply might not have time to adapt. Species that are 'pre-adapted' for the habitat or evolutionary 'generalists' may colonise and thrive (Pandit *et al.* 2009), for example, *Calotes versicolor* and *C. emma* in Malaysian cities and oil palm monocultures, respectively (Grismer 2011). The Southeast Asian Genus

*Calotes* has also adapted well to modified habitat in the Western Ghats (Venugopal 2010), more so than a sympatric *Draco* species. Lizards have, however, been shown to possess great potential for 'contemporary evolution' (Stockwell *et al.* 2003) where traits that are strongly selected upon by changes to structural habitat can evolve within a few years (20 generations) (Stuart *et al.* 2014). The relative impact of types of land use change are largely dependent on the new cover's similarity at an ecologically relevant scale to organisms e.g., for lizards; the perches afforded by rubber plantations more closely resemble those offered by forest than the perches offered by oil palm plantations do.

Land use change, for example the expansion of oil-palm monocultures, may favour particular characteristics across a broad range of species. Using data from 487 species of various bird, beetle and ant genera, Senior *et al.* (2013) detected patterns of traits that pre-adapted species to forest conversion and subsequent colonisation of the novel habitats it creates. They found small-bodied species from relatively low trophic levels to colonise the most efficiently; and species that did manage to colonise were often uncommon in the unaltered habitat, whereas the more common, large bodied forest species from higher trophic levels were the least able to colonise the altered habitat (Senior *et al.* 2013). The small-bodied species that were able to colonise were often extremely abundant, consistent with reports of lizard assemblages in oil-palm, prior to my research (Algar, pers. comm., Grismer 2011). Whether other, more specialised lizards are genetically capable of either evolving physiological measures to counteract the novel thermal microhabitats they will be forced to occupy or adapt their behaviour to buffer against this change remains to be studied. Also the long term implications of climate change have not been predicted in the species that are able to colonise and whether or not these species are operating nearer their  $CT_{max}$  in these realised niches could prove crucial to their long term survival. Future research needs to first examine the thermal preference and tolerances of those lizard species that have managed to colonise, estimate their thermal safety margins ( $CT_{max}$ - environmental temperatures) and then estimate the implications of predicted climate change on these species.

## **1.8 Amphibians and land use change**

Another group of ectotherms, the amphibians are also profoundly affected by land use change. This group's general reliance on water sources for spawning immediately limits their dispersal abilities in habitats with limited surface

water. More research has been conducted on amphibians' tolerance of plantation habitat than in reptiles and tends to indicate similar results. Faruk *et al.* (2013) found that oil palm plantations in Malaysia supported comparable amphibian species richness to forests, however community composition was greatly altered. In effect, plantations supported a wide variety of highly disturbance tolerant species that are already present in urban environments and so constitute an area of lower conservation value, despite their seemingly fairly diverse array of amphibian species. Faruk *et al.* (2013) also report similar overall amphibian abundance between plantations and forests although abundance in specific, comparable habitat features e.g., streams, often proved higher in forests. Wanger *et al.* (2010) however found that in Sulawesi, both amphibian alpha diversity and abundance decreased along a land use gradient from forest to plantation, signifying that results for amphibian plantation tolerance may not be generalizable across South East Asia.

### **1.9 Strategies to mitigate biodiversity loss**

While the species that successfully colonise oil palm plantations are often locally common (Senior *et al.* 2013), the biodiversity they contain is uniformly poorer than logged forests (which in some cases may be very suitable for some species, Clements *et al.* 2012) and primary forest (Wanger *et al.* 2010, Foster *et al.* 2011, Faruk *et al.* 2013, Azhar *et al.* 2014a). Increasing habitat heterogeneity within plantations has been shown to increase species richness (Foster *et al.* 2011, Azhar *et al.* 2014a, 2014b) and including areas of forest around and between plantations has also been shown to promote greater biodiversity in mammals in Peninsular Malaysia (Azhar *et al.* 2014a). The method of oil palm culture can also affect biodiversity. Azhar *et al.* (2014b) reported that monocultures actually supported greater species richness in birds, while polycultures supported higher abundance. Species richness increased with the height of ground vegetation and proximity to rivers but decreased with proximity to roads and vegetation cover. Species were mostly those that preferred open habitat, indicating forest species still failed to utilise this altered habitat.

Birds' inherently high dispersal abilities may enable them to withstand habitat change more than other, more dispersal-limited taxa like reptiles. However, despite their high dispersal ability, 48-60% of bird species are still lost through forest conversion, although as in reptiles, some species benefit greatly (Azhar *et al.* 2011). Additionally some of this loss can be mitigated by the structure of the plantation; if multiple age classes of crop are used, the resulting heterogeneity allows more species to be present (Azhar *et al.* 2011). Data on Caribbean *Anolis* lizards (Glor *et al.* 2001) suggests that relatively small areas

of suitable habitat within an agricultural and otherwise species-poor landscape allows greater overall species diversity in the region however these 'islands' of suitable habitat would need to be connected by habitat corridors to prevent inbreeding depression and allow gene flow across the less suitable agricultural land.

## **1.10 Conclusions**

Although independently, climate change and land use change are both recognised risks to biodiversity, study of their integrated impacts on reptiles in Asian oil-palm plantations has been neglected. This agricultural crop could provide some species (rare in forest habitat) with vast swathes of suitable, novel habitat to utilise and increase their overall abundance while being completely inhospitable to others (Azhar *et al.* 2014a). The thermal constraints of reptiles, particularly lizards, are fairly well understood (Angilletta 2009), however little data has been published for South East Asian species. Compared to the relatively gradual rate of climate change, the dramatic changes in thermal conditions created by palm oil plantations could create rapid evolutionary responses in the native lizard fauna or prove uninhabitable. This research scarcity must be addressed if tropical reptile species are to be conserved within these increasingly anthropocentric landscapes as the current protected habitat will not be sufficient to support their populations in the future (Corlett 2013). Increased research on this topic may also provide valuable insights into the rapid evolutionary responses lizards and other organisms can undergo when faced with environmental challenges created by human activity. In this thesis, I will attempt to address some of these identified shortcomings by focussing on secondary forests and two types of plantation (oil palm and rubber) in Northern Peninsular Malaysia, an area with a mosaic of land use types. I will initially quantify reptile and amphibian species richness in differing land use types before focussing on *Calotes emma*, an abundant species of small diurnal lizard found in all three habitat types, to examine differences between habitats in more detail along two major niche axes and how these may affect the lizards of the region.

Firstly, I will present results from reptile and amphibian species richness surveys in Chapter 2 comparing both types of plantation to forests, to test the hypothesis that plantations support fewer species of reptile and amphibian than the forests they replace. I will describe some conservation implications

regarding plantations for reptiles and amphibians and make suggestions for maintaining conservation value in these land use types.

In Chapter 3, I will focus in on the structural niche axis of reptiles in plantations. I analyse structural differences between the three habitats, a key stressor for lizard biomechanics and potentially a strong driver of lizard morphology over short time scales. I will then attempt to relate and compare these differences to predicted and observed patterns in the morphology of *C. emma* measured from each habitat type and discuss whether the patterns relate to previously studied lizard model systems

I will then compare the thermal environments of these habitats in Chapter 4 and analyse any effects on suitability this may have had on a lizard that occupies all three habitat types by quantifying its thermal tolerance and performance. I present results under current climatic scenarios and repeat them under the generalised prediction of a 3°C rise in air temperature to represent climate change and assess any changes in thermal suitability and/or thermal stress. I test whether any differences contribute to higher thermal stress and lower suitability in plantations and whether the observed trends continue under future climatic predictions.

During my research, a general lack of detailed information on the reptiles and amphibians of this region became apparent aside from a single, albeit comprehensive reference book. In Chapter 5, I present a collection of observations I made during my time conducting this research to add to the body of knowledge on the ecology of Malaysian reptiles. Initial observations are often the key to useful hypotheses and I hope this informal collection of notes may provide a useful basis for future research ideas.

To end the thesis I draw conclusions from all data chapters to form a coherent and more comprehensive report on the risks and opportunities plantations generate for ectotherms and identify extensive further research that needs to be conducted to solidify our understanding of the effects these rapidly expanding habitats have on this vulnerable group of vertebrates.

## 2 Winners and Losers Amongst Tropical Reptiles and Amphibians in the Oil Palm Boom

### 2.1 Introduction

Land use change is the largest current threat to terrestrial biodiversity worldwide (Sala *et al.* 2000, Newbold *et al.* 2015) and has already compromised the ecological functioning of the planet (Newbold *et al.* 2016). Forest loss is progressing at a high rate (ca. 2.3 million km<sup>2</sup> lost worldwide between 2000-2012, Hansen *et al.*, 2013), predominantly in the tropics, where the rate of loss is predicted to increase by 2101 km<sup>2</sup> annually (Hansen *et al.* 2013). This forest loss comes at the expense of the world's oldest and most biodiverse terrestrial habitats, and has been linked with biotic homogenization, where a small number of species capable of adapting to human activities replace forest biodiversity (Kormann *et al.* 2018). In areas where anthropogenic habitat conversion dominates the landscape, species' continued persistence will depend on their ability to successfully survive and reproduce in human-modified habitats (Daily *et al.* 2001, Frishkoff *et al.* 2014). Being able to predict which species can occupy these newly dominant, anthropogenic, environments is thus important for identifying those taxa most at risk from habitat modification and for assigning priorities in conservation efforts (Tomimatsu *et al.* 2013, Guilherme and Miguel Pereira 2013, Frishkoff *et al.* 2014).

Oil palm and rubber plantations in Southeast (SE) Asia are a central conservation concern. Plantations regularly replace the oldest, most structurally and botanically complex terrestrial habitats with greatly simplified landscapes, often leading to net losses of biodiversity (Savilaakso *et al.* 2014) and ecosystem function (Dislich *et al.* 2017). This replacement may be either direct or indirect via logging and other land uses (Vijay *et al.*, 2016). Plantations' capacities to support biodiversity vary across taxa, with some groups being more diverse in plantations (e.g. bees; Lee *et al.*, 2001), while the majority see a trade-off of overall species diversity for higher abundance of the few species that survive (Foster *et al.* 2011), greatly altering species composition and community structure. Different axes of biodiversity may also show differing responses to plantations. For birds, species richness and phylogenetic diversity decline in oil palm, while functional diversity is less



affected, though functional redundancy is greatly reduced (Chapman *et al.* 2018).

We still lack information on how plantations affect most taxa, including some vertebrate groups. We know little about reptiles' status in plantations, and there is even less information available on Southeast (SE) Asian reptiles specifically. Foster *et al.* (2011) provided an assessment of lizards in plantations, but their work was based on a single study by Glor *et al.* (2001) from the Neotropics. Glor *et al.* (2001) found that, in the Caribbean, the most disturbed, active areas of agriculture supported the fewest lizard species, abandoned agricultural areas supported intermediate levels and undisturbed habitat contained the greatest number of species. Since then, Gallmetzer and Schulze (2015) have also reported on the effects of oil palm in the Neotropics where plantations supported less than 50% of the diversity of reptiles and amphibians that forests did. However, such findings may vary greatly in areas with different biogeographical histories: in Sulawesi, cacao agroforestry can support higher reptile species richness than primary forest (Wanger *et al.* 2010).

Unlike reptiles, the effects of land use change in SE Asia on amphibian diversity have received more attention. In central Peninsular Malaysia, oil palm supports a considerable number of amphibian species (Faruk *et al.* 2013) and neither abundance or species richness differed significantly between forest and plantation habitat. However, Faruk *et al.* (2013) also found that community composition was greatly altered in plantations where the amphibian community was comprised of mostly disturbance tolerant species with high fecundity and large ranges. The authors proposed that if the presence of endemic forest species is used as a measure of the conservation value of a habitat then the species assemblage in oil palm plantations are of low worth as plantation species are also found in gardens and urban environments across Malaysia and Southeast Asia as a whole (Faruk *et al.* 2013).

The ability to predict, based on species' characteristics, which species can successfully occupy plantations could be a vital tool in projecting effects of plantation expansion on biodiversity and also point toward ways to mitigate the negative effects on biodiversity, typically associated with plantations. Faruk *et al.* (2013) suggested high fecundity is common in disturbance tolerant species, allowing them to populate an area quickly and take advantage of the

niche space left vacant by species displaced by the initial conversion process. This could theoretically result in the commonly observed trend in plantations of reduced species richness but equal, or greater abundance of the few species present. Body size may affect tolerance to disturbed habitats in different ways (Henle *et al.* 2004, Barbaro and Van Halder 2009); larger amphibian species may be less dependent on forest, but this may not be the case for reptiles (Mendenhall *et al.* 2014, Frishkoff *et al.* 2015). In the Neotropics, Frishkoff *et al.* (2015) found that reptile and amphibian species' thermal niches (thermal performance optima and critical thermal maxima) and/or climatic temperature niche (mean temperature of occurrence) were associated with occupation of disturbed habitats, which were also warmer. Similar conclusions were reached for amphibians by Nowakowski *et al.* (2017) where Neotropical amphibians restricted to forests displayed corresponding lower critical thermal maxima ( $CT_{max}$ ). Additionally, Frishkoff *et al.*, (2016) examined characteristics of more than 300 bird species and found that success in agricultural habitats was associated with lower precipitation niches, i.e. occupation of drier conditions at macroecological scales. Oil palm plantations are hotter and drier than forests in the same areas, with higher diel variability in these measures (Luskin and Potts 2011), further suggesting that climate niches could play a key role in determining whether species can successfully exploit these habitats.

In this study I seek to address the lack of knowledge on the effects plantations have on tropical reptiles in Southeast Asia by describing patterns of species and phylogenetic diversity of reptiles, as well as amphibians, in plantations and forest patches in Northern Peninsular Malaysia. I then test whether climate niches, or other species' characteristics including range size and body size are predictors of species' ability to utilise plantations habitats. Based on previous findings I hypothesise that warm and dry adapted, more widespread, species will be more likely to inhabit plantations and that forests will contain higher overall species richness than plantations.

## **2.2 Methods**

### **2.2.1 Study region**

I focussed on an area near the town of Gerik in Perak state, Northern Peninsular Malaysia. This area contains a patchwork of habitats with oil palm plantations and rubber plantations, both large and small holdings, being prominent features of the landscape. The area is well known for the Belum-Temenggor

forest complex, a large area of contiguous forest stretching into Thailand, bordering an artificial reservoir (Tasik Temenggor) near Gerik, with high biodiversity (Abdullah *et al.* 2011). I focussed on three land uses: oil palm plantation, rubber plantation and logged forest. I did not conduct transects in primary forest. Reliably identifiable remaining primary growth forest i.e., forest which has not been logged, is scarce in Peninsular Malaysia and often logistically difficult to access. Furthermore and as a result of this scarcity it is predominantly secondary growth forest that is now being lost to plantations (Koh & Wilcove, 2008). Secondary forests are usually found to support lower reptile and amphibian diversity than primary forests (Wanger *et al.*, 2010) thus making my results a conservative baseline for the true differences between plantations and any primary forests remaining.

### 2.2.2 Reptile and amphibian surveys

I identified and established 4x100m transects at a pair of sites per focal habitat type: oil palm plantation, rubber plantation and logged forest. Transects were established at least 50m from any neighbouring habitat types and 100m from each other to avoid edge effects and pseudo-replication (Carvajal-Cogollo and Urbina-Cardona 2015). Transects were chosen haphazardly from Google Earth at sites and were then evaluated by the team in terms of accessibility before six sites were chosen containing four transects each. Selection of random transect locations was unfeasible given the patchiness of the habitat and lack of accessibility.

Each transect was walked twice by myself and Max Jones during the morning and twice at night for a total of 96 transect walks across the six sites. Transects were walked at a pace of 100m/10mins, keeping the order of surveyors consistent. Surveys commenced at approximately 11am and then again at night at approximately 9pm. Night surveys were aided by high output LED headtorchs. JJH used a Cluson Clulite HL12FC Super Beam LED Head Torch and Xtar B20 Pilot II LED Torch, MDJ used a Petzl Tikka RXP. I limited my search area to 5m either side of the transect, individuals seen beyond this distance were not recorded. Animals were located by direct observation in most cases although some amphibians were found by following their calls (only individuals within 5m of the transect were recorded). Animals observed while walking between transects or while accessing sites were not recorded. Any debris or structures within 5m of the transect that were checked were subsequently

searched on every transect. I did not control for the presence of water sources (e.g. streams) although every site had a water course feature in at least one transect (Table 2.1 contains a summary of habitat features in each transect for each site).

**Table 2.1:** A summary of habitat features that each transect incorporated. Every site included at least one water source (defined as ponds, puddles, rivers) or artificial structure (barrels, buildings, rubbish piles) within 5m of one of the transects. Site abbreviations are assigned based on the habitat they represent (oil palm= OP, rubber= R, secondary forest= F).

Site	Site GPS	Transect	Water source	Artificial structure
OP1	N: 5.471175° E: 101.227585°	1	1	0
OP1		2	0	0
OP1		3	1	0
OP1		4	0	1
OP2	N: 5.476714° E: 101.177540°	1	1	0
OP2		2	0	0
OP2		3	0	0
OP2		4	0	1
R1	N: 5.391672° E: 101.125330°	1	1	0
R1		2	1	0
R1		3	0	1
R1		4	0	1
R2	N: 5.359140° E: 101.155563°	1	0	0
R2		2	1	1
R2		3	0	0
R2		4	1	0
F1	N: 5.376007° E: 101.120327°	1	1	0
F1		2	0	0
F1		3	0	0
F1		4	1	0
F2	N: 5.044446° E: 100.949335°	1	0	1
F2		2	1	1
F2		3	1	1
F2		4	1	1

### 2.2.3 Survey sites

#### Oil palm 1

This is a large, mature oil palm plantation on the outskirts of Gerik (Fig. 2.1). It is characterised by a relatively high canopy (3-4m+) and several streams that cross the site. My transects included riverside situations as well as plantation interior. The fallen frond piles characteristic of other oil palm plantations in the area were scarce at this site although there was an abundance of rocks and artificial cover that could feasibly be utilised by amphibians and reptiles. I saw evidence of dense livestock grazing around my transect area at this site.

### Oil palm 2

Surrounded by the Sungai Perak river, this plantation is an expansive, even-terrained oil palm plantation with adjoining rubber plantations. It was flooded after the first round of transects, subsequently the ground was covered by sediment and large puddles and ponds which were heavily utilised by amphibians during night surveys. Long, gathered piles of fallen fronds were present between most rows of palms.

### Rubber 1

This site is near Kampung Tawai and is situated on a hill bordered by secondary forest. The landscape is terraced with the rubber trees planted in distinct rows along these terraces. There is considerable amounts of undergrowth between these terraces but each row is clear of undergrowth. Pools of water were present on Transect 1 and metal barrels of water were situated along transects 3 and 4.

### Rubber 2

This site is located around 5km up the same road as Rubber 2. This site is more level than the previous rubber plantation with the topography featuring less prominent terracing. There is less undergrowth than in Rubber 2 but the rubber trees at both sites are of a similar age, planting density and height. Transect 4 passed near a small pond.

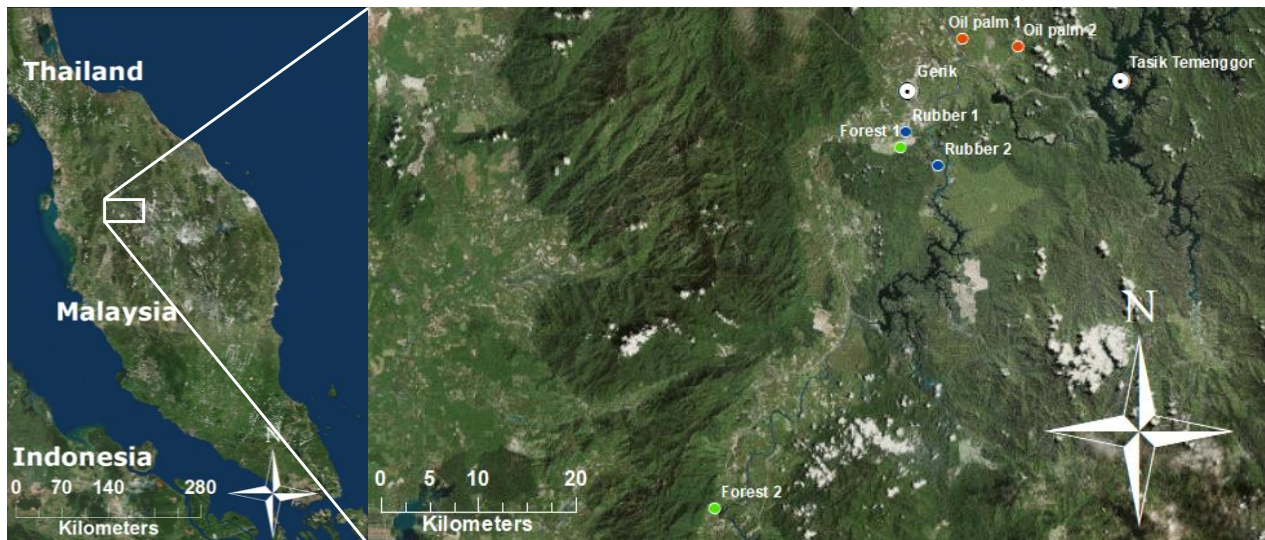
### Forest 1

This is a section of forest near Kampung Air Ganda that had recently had a logging operation established. Transects were conducted between 1-3km from the main road, either side of a logging road. Aside from ongoing logging the site was a mature forest with dipterocarps >10m high. Much of this forest lies on steep sided hills and is heavily vegetated.

### Forest 2

This is a recreational forest park (hutan lipur Lata Kekabu) near the town of Lenggong consisting of a valley of riparian forest bisected by a fast flowing river. All transects more or less followed the course of this river, aside from Transect 1 which covers paved ground between the river and car park. The vegetation at this site has been heavily altered around the paved recreation

areas either side of the river with little to no undergrowth here although many large trees >10m tall have been left. Numerous buildings, bridges and small rest shelters are present within 10m of the river. Mature forest and dense undergrowth survives largely unaltered around 20m from the river itself on the inaccessible valley slopes although my transects focussed on the disturbed areas near the river.



**Figure 2.1:** Transect localities with local points of reference (Gerik town centre and Tasik Temenggor reservoir) noted. The study area is contextualised in the left panel in terms of Peninsular Malaysia and neighbouring countries.

Imagery source: Esri, DigitalGlobe, GeoEye, Earthstar Geographics, CNES/Airbus DS, USDA, USGS, AEX, Getmapping, Aerogrid, IGN, IGP, swisstopo and the GIS user community.

#### 2.2.4 Species richness

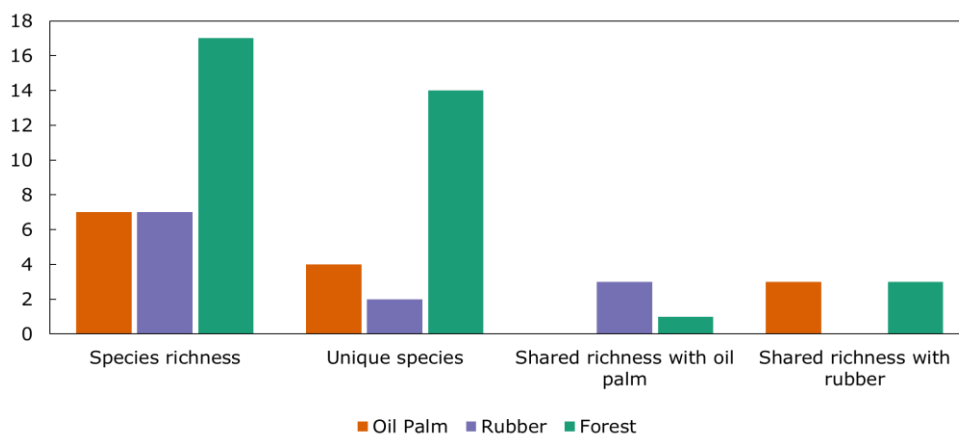
I compared species richness among habitat types by summing walks within each transect and comparing species richness among habitat types (four transects per site, two sites per habitat type) using a linear mixed effects model with habitat type as a fixed effect and site as a random effect. I generated species accumulation curves and confidence intervals using the `specaccum` function in the `vegan` package (Oksanen *et al.* 2018): in R v.3.4.4 (R core Development team, 2018). I used individual transect walks as sampling events to quantify surveying effort for species accumulation curves. Due to time and logistical constraints during fieldwork, relative abundance or mark-recapture data were not collected, limiting my analysis to species richness only, which nevertheless serves as a useful, conservative baseline for ectotherms in these habitats.

### 2.2.5 Covariates of plantation use

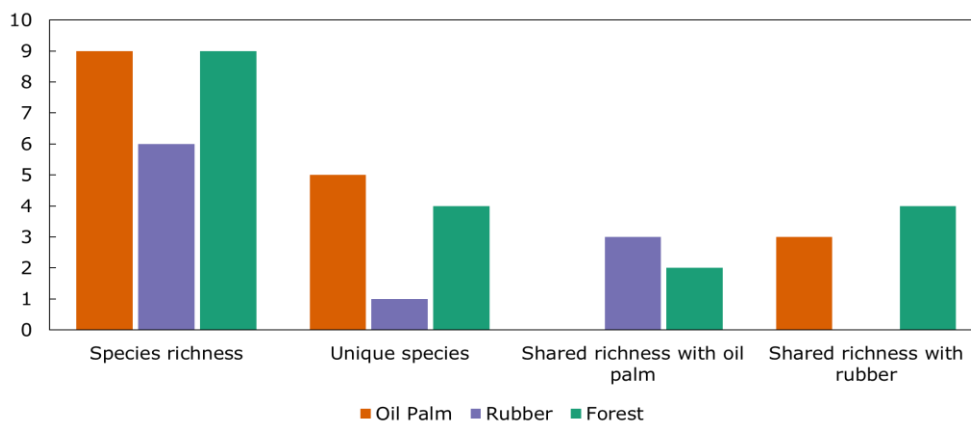
To identify species' characteristics associated with occupation of plantations, I gathered data on body size, range size, average annual mean temperature across the range, and average precipitation of the driest quarter across the range to represent aridity. Average precipitation of the driest quarter was selected as it represents some measure of how pronounced the dry season is (if any) throughout a species' range. To allow for comparisons of body sizes among groups with very different average sizes (e.g. snakes versus lizards) and differing body size measures (body length in amphibians from Oliveira *et al.* (2017), snout-vent length in lizards from Scharf *et al.* (2015), total length in snakes from Scharf *et al.* (2015)), I calculated body size Z-scores (number of standard deviations from the mean body size of the sub-class) following the equation:  $(\text{body size} - \text{mean class body size}) / \text{standard deviation of class body size}$  after the species had been sub-classed as either amphibian, lizard or snake. Range size (km<sup>2</sup>) was measured using IUCN ranges for amphibians (IUCN, 2016) and reptile ranges from Roll *et al.* (2017). I used logistic regression to test for relationships between species' characteristics and whether a species was detected in a plantation in any of my transects (i.e. plantation tolerant, coded as 1) or only found in forest (plantation intolerant, coded as 0). I fit models with each species' characteristic independently and a model including all variables. Due to relatively low sample size I did not consider interaction terms.

## 2.3 Results

I recorded a total of 195 observations of 41 species (25 reptile and 16 amphibian). Numbers located varied from 43 (*Calotes emma*) to single individuals of many species. I located more species of reptile in secondary forest (17) than in either rubber (7) or oil palm (7) plantations (Figs 2.2, 2.3). Forest and oil palm both produced nine species of amphibian each, rubber contained six. Occurrences were not spread evenly across transects with some being consistently productive (max 17 individuals across 9 species) while I failed to locate any animals on some others throughout the study period (Table 2.2). Rubber shared more species of reptiles (3) and amphibian (4) with forest than oil palm did (one and two, respectively) although it also shared almost the same number of species with oil palm (three and three). Forest had the highest number of unique species with 18 (four amphibians, 14 reptiles), followed by oil palm with nine (five amphibians, four reptiles) and rubber contained the fewest with three (one amphibian, two reptiles) (Figs 2.2, 2.3).



**Figure 2.2:** Reptile species richness, unique species and shared diversity across focal habitat types.



**Figure 2.3** Amphibian species richness, unique species and shared diversity across focal habitat types.

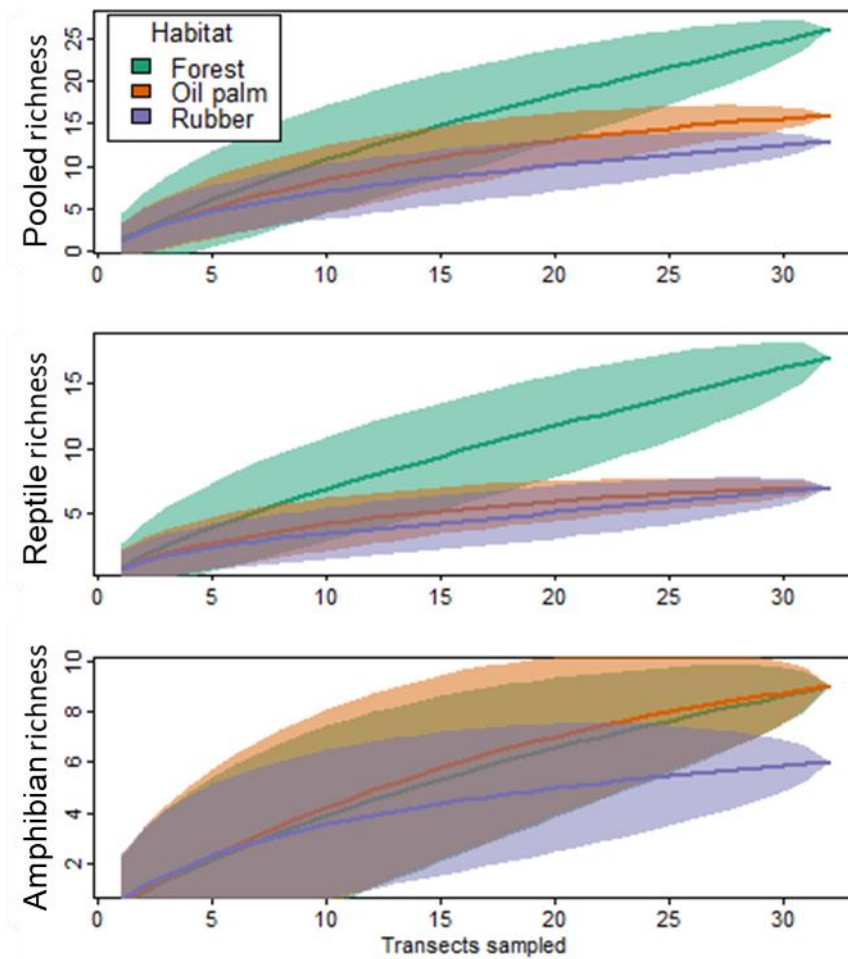


**Table 2.2:** Species presence, absence and counts for the transect data, partitioned by site, habitat and transect. Data are entered as follows: (number seen during day surveys),(Number seen during night surveys).

Site	Oil palm 1				Oil palm 2				Rubber 1				Rubber 2				Forest 1				Forest 2				Totals												
Transect number	1	2	3	4	1	2	3	4	1	2	3	4	1	2	3	4	1	2	3	4	1	2	3	4													
<i>Aphaniotis fusca</i>																							0,1		1												
<i>Boiga cynodon</i>																							0,1		1												
<i>Calotes emma</i>	0,3	1,0	1,0	0,2	0,6	6,1	2,2		0,2	1,0	1,0	1,0	0,6	0,2	1,1	1,3									43												
<i>Chalcorana labialis</i>																			0,2	0,1	0,2	0,3			8												
<i>Dendrelaphis caudolineatus</i>							0,1							0,1											2												
<i>Dogania subplana</i>																			0,1						1												
<i>Draco fimbriatus</i>												1,0													1												
<i>Draco formosus</i>																				0,1					1												
<i>Draco melanopogon</i>											1,0					1,0									2												
<i>Draco sumatranus</i>												1,0								1,0					2												
<i>Dryocalamus subannulatus</i>																	0,1								1												
<i>Eutropis multifasciata</i>	1,0				1,0	2,0			1,0	2,0	2,0	1,0	2,0								4,0	4,0	1,0	3,0	24												
<i>Fejervarya limnocharis</i>	0,1	0,1				0,1			1,1	1,0	1,0	1,0	0,1				0,1								10												
<i>Gehyra mutilata</i>																				0,1					1												
<i>Gekko monarchus</i>																				0,3					3												
<i>Gekko smithii</i>								0,1																	1												
<i>Gonocephalus bellii</i>																		0,2							2												
<i>Gonocephalus grandis</i>																						0,1	0,5	0,3	9												
<i>Gonyosoma oxycephalum</i>							1,0																		1												
<i>Hemidactylus frenatus</i>	0,2	0,1			0,1																				4												
<i>Hemiphyllodactylus typus</i>	0,2	0,1																							3												
<i>Humerana miopus</i>		0,1			0,1	0,3							0,1	1,0	4										20												
<i>Ingerophrynus parvus</i>									0,2										0,4						6												
<i>Kaloula pulchra</i>					0,3	0,2																			5												
<i>Leptobrachium hendricksonii</i>																				0,1					1												
<i>Limnonectes blythii</i>		0,1																		0,1					2												
<i>Lipinia vittigera</i>																				1,0					1												
<i>Microhyla berdmorei</i>					0,1																				1												
<i>Microhyla butleri</i>					0,1																				1												
<i>Microhyla heymonsi</i>														0,3											3												
<i>Occidozyga lima</i>					0,1	0,1																			2												
<i>Odorrana hosii</i>																				0,4					4												
<i>Phrynoidis asper</i>																				0,2	0,1	0,1			4												
<i>Polypedates leucomystax</i>									0,1	0,3			0,1	0,5	0,3							0,1			14												
<i>Polypedates macrotis</i>						0,1									0,1										2												
<i>Pulchrana glandulosa</i>						0,2																			2												
<i>Sphenomorphus scotophilus</i>																							1,0		1												
<i>Tropidolaemus wagleri</i>																				1,0					1												
<i>Varanus nebulosus</i>			2,0																						2												
<i>Varanus salvator</i>																							1,0		1												
<i>Xenopeltis unicolor</i>																							1,0		1												
Transect total individuals	9	3	4	4	9	8	11	12	5	6	9	4	9	11	2	22	6	3	0	7	9	17	12	13	195												
Site total individuals	20				40				24				44				16				51																
Habitat total individuals	60												68												67												
Transect species	5	3	4	2	7	2	4	6	3	5	5	4	4	5	1	5	3	2	0	3	4	9	8	7													
Site species totals	8				13				7				10				8				19																
Habitat species totals	16												13												26												

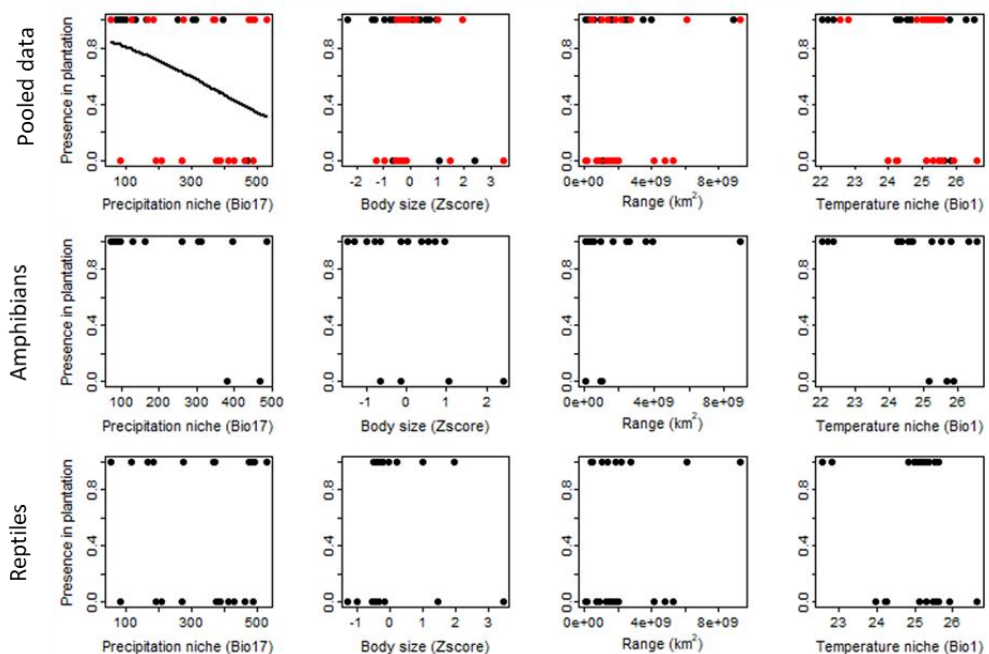
The shape of species accumulation curves suggested that, overall, finding more species in either plantation type would take considerable additional effort, i.e., I succeeded in locating a good representation of the true number of species present (Fig. 2.3). In contrast, the curve for forest did not begin to plateau by the end of my sampling efforts, suggesting that given extra time I would observe considerable further diversity (Fig. 2.3) in this habitat. Curves indicate that both plantation types contained similar reptile species richness with the curve having plateaued by the end of my sampling effort. Forest, however, contained more species than either plantations, and the curve is steeper, indicating further probable species not sampled during my transects (Fig. 2.3). Amphibians showed a different pattern with oil palm and forest containing the same number of species during my transects (the curve indicates forest may

have contained slightly more undiscovered species however, Fig. 2.4), while rubber contained fewer species and the curve for this habitat plateaus before reaching the end of my sampling effort.



**Figure 2.4:** Species accumulation curves (with shaded 95% confidence intervals) for overall richness, reptiles, amphibians in descending order. Curves are generally steeper in forest, indicating higher accumulating species richness and continue to increase to the end of my study period, indicating likely unrecorded species being found with more survey time. The curves for both plantation type have largely plateaued by the end of my study period, indicating few additional species would be accumulated with additional survey time.

When reptiles and amphibian species were pooled, I found a significant relationship between plantation tolerance and precipitation niche (Fig. 2.5;  $z=-2.126_{38}$ ,  $P=0.03$ , explained deviance=0.095), indicating that species found in drier areas are more likely to be found in plantations than species found in wetter regions, though there is considerable scatter in the relationship. Contrary to results for the precipitation niche, and to my prediction, I found no relationship between temperature niche and plantation tolerance (Fig. 2.5;  $z=-1.823_{38}$ ,  $P=0.07$ , explained deviance =0.021). Body size and range size were not significantly related to plantation tolerance (Body size:  $z=-0.209_{37}$ ,  $P=0.521$ , Range size:  $z=0.227_{38}$ ,  $P=0.209$ ) and no variables were significant in a multiple regression (Table 2.3). I also found no significant relationship between plantation tolerance and any species' characteristics when reptiles and amphibians were analysed separately (Table 2.3). This could be due to the relatively small number of species in each Class ( $n=15$  for amphibians and  $n=25$  for reptiles) and thus lower statistical power. Despite the lack of a significant relationship with precipitation niche in reptiles and amphibians, examination of Fig. 2.5 suggests that the significant relationship with precipitation niche in the pooled data is not due to an overall difference between reptiles and amphibians as there are plantation tolerant and intolerant species in both.



**Figure 2.5:** Presence in plantations plotted against species characteristics. z-score was derived by first subsetting the data (lizard/amphibian/snake) to account for differences in body size metrics across these groups. Precipitation niche in the pooled data (reptiles and amphibians) was the only significant relationship ( $z=-2.126_{38}$ ,  $p=0.034$ , explained deviance=0.095), although even this relationship was not significant after a Bonferroni correction. In the pooled analysis, amphibians are shown in black and reptiles in red.

**Table 2.3:** Logistic regression results on plantation presence on the dataset as a whole and divided into amphibians and reptiles. The only parameter that significantly predicted a species' presence in plantations was the mean precipitation of the driest quarter across its entire distribution (denoted by an asterisk).

<b>Pooled data</b>	Estimate	Standard error	Z value	P
Body Size	-2.95E-01	3.28E-01	-0.898	0.369
Range Size	-3.13E-11	2.33E-10	-0.135	0.893
Temperature niche	-4.30E-01	5.43E-01	-0.792	0.428
Precipitation niche	-3.57E-03	3.16E-03	-1.129	0.259
<u>Single-predictor regressions</u>				
Body Size	-2.09E-01	3.26E-01	-0.641	0.521
Range Size	2.27E-10	1.81E-10	1.258	0.209
Temperature niche	-7.12E-01	3.90E-01	-1.823	0.068
Precipitation niche	-5.25E-03	2.47E-03	-2.126	0.034*
<b>Reptiles</b>	Estimate	Standard error	Z value	P
Body Size	5.58E-02	4.48E-01	0.124	0.901
Range Size	1.24E-10	2.47E-10	0.5	0.617
Temperature niche	-6.42E-01	6.50E-01	-0.988	0.323
Precipitation niche	1.60E-03	4.16E-03	0.384	0.701
<u>Single-predictor regressions</u>				
Body Size	1.11E-01	4.10E-01	0.271	0.786
Range Size	2.15E-10	2.05E-10	1.047	0.295
Temperature niche	-7.20E-01	5.41E-01	-1.333	0.183
Precipitation niche	-1.95E-03	2.92E-03	-0.668	0.504
<b>Amphibians</b>	Estimate	Standard error	Z value	P
Body Size	-8.93E+01	3.47E+04	-0.003	0.998
Range Size	2.28E-07	8.89E-05	0.003	0.998
Temperature niche	1.22E+02	5.68E+04	0.002	0.998
Precipitation niche	-9.64E-01	3.94E+02	-0.002	0.998
<u>Single-predictor regressions</u>				
Body Size	-1.01E+00	6.78E-01	-1.492	0.135
Range Size	9.48E-10	8.37E-10	1.132	0.258
Temperature niche	-8.06E-01	7.57E-01	-1.064	0.287
Precipitation niche	-1.47E-02	9.32E-03	-1.579	0.114

## 2.4 Discussion

Given ongoing expansion of plantations in biodiverse tropical regions (Koh and Wilcove 2008), the ability to predict species' tolerances to these environments could make a valuable contribution to conservation planning. I found that forests contained more species of reptile than either rubber or oil palm plantations. These differences are likely conservative with considerable cryptic diversity unsampled in forests. In contrast, amphibians showed more similar richness across all habitats with similar richness in forests and mature oil palm but lower richness within rubber plantations. My analysis of species'

characteristics suggest that the diversity within plantations is not a random subset of species, but rather tends to be composed of species that are found in drier regions, suggesting that water retention within drier plantation environments presents a key challenge for species attempting to utilise these habitats.

#### 2.4.1 Niche characteristics as predictors of plantation tolerance

A drier precipitation niche appears to offer species an advantage in plantation environments. My results could be attributed to either amphibians or reptiles being reliant on relatively drier or wetter precipitation niches and biasing the result, however examination of the figure reveals plantation tolerant and intolerant species in both. Species with the highest precipitation niches (i.e., heavier rainfall in the driest quarter of the year across their range) showed a cluster that were intolerant of plantations in both groups. Plantation tolerant species in both groups largely occupied the breadth of range of values for precipitation niche, with a cluster of drought adapted amphibian species being present in plantations. These findings are consistent with expectations from previous findings of microclimate conditions within oil-palm plantations, which tend to have lower humidity than the forests they replace (Luskin and Potts 2011, Hardwick *et al.* 2015). Thus, species whose ranges encompass drier regions may be better able to withstand arid conditions, through reduced water loss through the skin, or by behavioural modifications such as adjustment of activity time or selection of moister microhabitats (Moore *et al.* 2018). An association between use of human-modified environments and drier precipitation niches has also been found in a broad survey of 300 bird species (Frishkoff *et al.* 2014), suggesting that this may be a general pattern across taxa and biogeographical regions. However, my results need to be interpreted with caution as the relationship between plantation tolerance and precipitation niche occurred only when reptile and amphibian data were pooled and did not remain significant after a Bonferroni correction. This relationship is not, however, due to difference in habitat use by amphibians and reptiles as both groups are found in both habitats, but rather the lack of significance for reptile and amphibians individually may simply reflect the reduced statistical power from lower sample sizes when analysing groups separately.

In contrast to the precipitation niche, I found no evidence that species with warmer temperature niches are more likely to occur in modified environments, in this case plantations. These results contrast with those of Frishkoff *et al.* (2015) and Nowakowski *et al.* (2017), who found evidence of heat tolerance acting as a predictor of amphibians' deforestation tolerance in the Neotropics. I measured temperature niches on a macroecological scale, from range and climate maps, rather than organismal traits, like the critical thermal maximum, which directly relate to heat tolerance.  $CT_{max}$  tends to be strongly evolutionarily conserved among taxa (Araujo *et al.* 2013) and along elevation gradients in reptiles (Muñoz *et al.* 2014) and thus may not covary highly with measures of the temperature niche (Araujo *et al.* 2013). This cannot be the complete explanation, for the differences between my results and those of Frishkoff *et al.* (2015 & 2016) as they also considered temperature niches from macroecological data, rather than just physiological traits, and still found relationships with increased occurrence in disturbed environments by heat-tolerant species. There are several other potential explanations for the lack of relationship between temperature niche and plantation use in Malaysian plantations. Firstly, all of my sites were lowland tropical environments, so it may be that there is little variance in temperature niche across species in these environments; had I included sites at cooler, high elevations, I may have been more likely to find a relationship with temperature niche. Secondly, while oil palm plantations are hotter than forests during the day, they are not hotter at night (Luskin and Potts 2011). As all of the amphibian and gecko species I found were predominantly nocturnal, they are unlikely to have faced thermal challenges during their activity period in plantations. Provided there are enough cooler thermal refuges during the day, such as under coarse woody debris (e.g. palm fronds), nocturnal species may be able to behaviourally avoid plantation heat (Lenoir *et al.* 2017). Secondly, temperature within oil palm plantations varies greatly across the oil palm life cycle, with temperatures declining as plantations mature (Luskin and Potts 2011) as canopy cover and density increases (Hardwick *et al.*, 2015). As all my sites were mature plantations, thermal differences may not be as extreme as between forest and younger plantations (Luskin and Potts 2011).

I also found no clear relationship between range size and plantation tolerance across amphibians and/or reptiles. Species' assemblages in disturbed habitats, including plantations, are generally thought to be composed predominantly of widespread, cosmopolitan species (Foster *et al.* 2011, Faruk *et al.* 2013). My

results are partially consistent with this hypothesis as the largest-ranged species were predominantly or exclusively found in plantations and not in forest (Table 2.2). These species include *Hemidactylus frenatus* (house gecko), and the frogs *Kaloula pulchra* and *Occidozyga lima*, all of which are human-associated species. However, both forests and plantations also included narrower-ranged species, like the near-threatened *Limnonectes blythii* (Van Dijk and Iskandar 2004) which was found in both forest and oil palm. Thus, while widespread, cosmopolitan species tend to dominate plantation assemblages, these habitats are able to support at least some more localised, range-restricted species.

#### 2.4.2 Reptile diversity

My results present a rare analysis of the effects of oil palm and rubber plantations on reptile diversity in Southeast Asia. The reduced richness of reptiles in oil palm and rubber is consistent with findings from the neotropics in oil palm (Gallmetzer and Schulze, 2015) and agricultural landscapes (Glor *et al.* 2001). I found that forests contained more reptile species overall and more unique species than either rubber or oil palm plantations, both of which contained similar assemblages of species (Fig. 2.2, Table 2.2). These differences are likely to be conservative as species accumulation curves suggest there remains more unsampled diversity in forests than plantations, which could partially reflect more open sightlines in plantations than forests. In seeming contrast to my results, Wanger *et al.* (2010) found reptile diversity was slightly higher in agroforest habitats than forests on Sulawesi (Indonesia), the only other comparable study on effects of land use change on reptile diversity in Southeast Asia. A key difference between my work and Wanger *et al.* (2010) is in the type of land uses examined. While I focused on oil palm and rubber, they focused on shaded cacao plantations, suggesting that the latter may more closely mimic forest environments than either oil palm or rubber. Together, these two sets of results highlight that land use change affects reptile diversity, leading to losses when habitat modification is extensive, but also that diversity responses are not necessarily uniform across land use types.

Wanger *et al.*'s (2010) results suggest that milder forms of disturbance can increase reptile richness, consistent with the intermediate disturbance hypothesis (Connell 1978). My findings from my two forest sites are qualitatively similar with this observation. I found substantially higher richness in my Forest 2 site, which accounted for 17 of the total species seen in forest

habitat (vs seven at Forest 1 and a single shared species) and 76% of the individual animals observed in forest overall. Forest 1 was a more heavily vegetated site, with lower overall disturbance, while Forest 2 was located around a recreational park and thus had higher disturbance levels and also potentially greater edge effects, though it is also possible that some of the difference arose because of increased detectability of species in the less densely vegetated forest site. Nonetheless, while further surveys in a range of forest types is needed, my two forest sites appear to suggest that limited disturbance can increase reptile species richness, as suggested by Wanger *et al.* (2010, but see Glor *et al.* (2001) and Gallmetzer and Schulze (2015)).

### 2.4.3 Amphibian diversity

Consistent with Faruk *et al.* (2013), my results indicate amphibian species richness is only slightly affected by land use conversion, with equal numbers of species detected in oil palm and forest, although the species accumulation curve predicts slightly more undetected species richness in the latter (Fig. 2.4). Despite this, oil palm contained more unique amphibian species than forest (Fig. 2.3). However, I stress that these results reflect only the portion of the amphibian communities that were visually detectable, and particularly, does not include canopy species. Further reflecting the results of Faruk *et al.* (2013), I also find that species composition is nevertheless very different between oil palm and forest (Table 2.2). Rubber's amphibian species richness was lower than the other habitat types, although they resembled the assemblage in forests more than oil palm, and also had the lowest number of unique species (Fig. 2.3). These results differ from Wanger *et al.*'s (2010), who found a steady decline in amphibian richness as human land use intensity increased. Thus, even more than for reptiles, responses of Southeast Asian amphibians to human habitat modification may be especially sensitive to the type of land use change and caution should be used when extrapolating responses among land use types.

### 2.4.4 Conservation implications

Previous findings have highlighted the conservation value of disturbed, logged and secondary growth forests to reptiles and amphibians (Herrera-Montes and Brokaw 2010) and my results suggest logged forest, even when disturbed and managed for recreational purposes can support substantial species richness in Southeast Asia relative to plantations. However, as I lack comparison with



primary forest, I cannot evaluate the conservation value of disturbed versus pristine forests, though there is little of the latter remaining in Malaysia and Southeast Asia more broadly (Morales-Hidalgo *et al.* 2015, Hughes 2017).

In addition to the conservation value of disturbed forests, my findings also suggest areas of further investigation for improving the biodiversity value of plantations in the region although they must be interpreted with some caution in this regard as they likely represent “best case scenarios” for plantations. The age and maturity of the vegetation at each of my chosen localities was not quantified precisely however all of my chosen plantation sites were mature. This may have increased species richness of the plantations in my study, in particular, as older plantations have had more time to accumulate more diversity from colonisation events from neighbouring habitat types than younger plantations and their more heterogenous understorey vegetation and structures also offer more niches for colonising reptiles than the homogenous vegetation of young plantations (Mariau, 2001, Snaddon *et al.*, 2013). As my sites all represented mature plantations further work could be conducted to examine the initial diversity differences between very young plantations, mature plantations and forests.

Patchwork systems of stands of trees within and around plantations have been suggested as a means of mitigating the impact of oil palm (Koh 2008), however with sympathetic habitat management to replicate some of the microhabitats used by amphibians in forests, plantations could potentially support further diversity within the active cropping matrix. Maintaining shallow streams as irrigation for the crop and allowing undergrowth to accumulate along the edges of these watercourses provides several additional habitats that amphibian species could occupy. Riparian portions of oil palms are already maintained in some areas for hydrological reasons and have been shown to simultaneously support levels of diversity equal to logged forests in some taxa (Gray *et al.* 2015). Pesticides have profound implications on amphibian growth and survival (Baker *et al.* 2013) and are known to pollute major Malaysian rivers (Leong *et al.* 2007) although whether differing levels of pesticide applications in plantations could also affect the countries’ amphibian species’ use of these habitats remains unstudied.

Allowing the discarded fronds, a by-product of growing oil palm, to accumulate is also a vital strategy in increasing the value of this habitat to biodiversity with

many of my recorded animals utilising this microhabitat in some way. I refrained from disturbing these piles excessively but expect many more species could have potentially been found sheltering beneath this microhabitat, especially nocturnal species as it serves as a potential thermal and humid buffer against the more extreme conditions in plantations during the day (Luskin and Potts 2011). While moving between transects I also observed Malayan krait (*Bungarus candidus*) utilising these piles. While a common species, *C. emma* seems to rely on these frond piles in oil palm plantations (50% of *C. emma* observed in oil palm were using these microhabitats). Undergrowth that hadn't been cut back or had herbicide applied in rubber plantation harboured some of the less common species found in this land use type including *D. caudolineatus* and *G. smithii*. Species closely tied to forest specific microhabitats e.g., smooth tree trunks in the case of *Draco*, are unlikely to benefit from anything less than drastic changes in the way oil palm plantations are configured and buffer zones within and around plantations may be the only way to improve the overall suitability of plantation landscapes for such species.

My methodology did not incorporate pitfall traps and drift fencing which would have allowed better sampling of fossorial and leaf litter species (e.g., skinks and some snakes) and actively foraging terrestrial species (e.g., many snakes). As this was not used in any of the habitats it will not have biased against any habitat in particular, the frond piles in oil palm could potentially support fossorial species that would otherwise occupy leaf litter in forest and rubber plantations, but rather, may have revealed further differences in leaf litter species richness composition. Similarly, I could not sample the canopy layers at any of my sites, a microhabitat that is especially important to amphibian diversity (Roll *et al.* 2015) and only observed canopy species opportunistically when they moved into the 5m zone from the transects. It's likely that further diversity of both amphibians and reptiles went unobserved in the canopies of all three of my habitat types.

My study, provides a rare record of reptile diversity in plantations in Southeast Asia and adds support to previous results for amphibians in this anthropogenic habitat. It shows that while plantations fail to match the species diversity some forests can support, they can include some rarer species of amphibian and reptile rather than solely the cosmopolitan species often reported for these habitats in other taxonomic groups (Foster *et al.* 2011). Whether these habitats represent population sinks or sources (Dias 1996) remains to be examined as

the rarer species found in plantations in this work were often represented by single individuals and thus may not constitute viable populations of conservation value. Future studies would ideally include transects in riparian primary forest as a further contrast to the (in both cases) somewhat disturbed forest sites I could access during my study period. The plantations included in this study were mostly smallholdings (the prevalent source of rubber in Malaysia (Lea, 2005)) or small-scale oil palm monocultures which are not representative of the vast agro-industrial landscapes in the Southern states of Malaysia. These much larger and more active plantations may harbour different species compositions to the ones I recorded in Perak, especially in the absence of water sources and future work should focus on identifying levels of reptile and amphibian diversity in these more homogenous and expansive plantations.

## **3 Ecomorphological change in *Calotes emma* in plantations**

### **3.1 Introduction**

Behavioural shifts have been shown to prelude evolutionary adaptation and behaviour is often the first trait to change in response to the occupation of anthropogenic environments (Wong and Candolin 2015, Keith and Bull 2016). In particular, behavioural flexibility (or plasticity) may be a key predictor of invasion success in human created habitats (Sol *et al.* 2002), whereas behavioural rigidity may reduce exposure to novel selection pressures in these same environments, limiting evolutionary change and increasing maladaptation to conditions during and after rapid environmental change (Muñoz *et al.*, 2014, 2016; Buckley, Ehrenberger & Angilletta, 2015). Species' vulnerability to environmental change depends on their exposure to novel environments, their sensitivity and resilience to changes, and their ability to adjust or adapt to novel conditions (Williams *et al.* 2008, Huey *et al.* 2012).

Much of the Earth's surface has been greatly modified by humans, resulting in habitat loss, increased threats of extinction, and homogenization of species assemblages (McKinney and Lockwood 1999). As accelerated land cover change continues throughout much of the world (Hansen *et al.* 2013), increasing numbers of species will be exposed to alien environmental conditions. Species that are pre-adapted to similar conditions will be likely to prosper, while others will increasingly be forced to adjust or adapt to human-created environments, or face extinction. Land cover changes also present opportunities for behavioural and morphological adaptations to be observed on relatively short timescales (Winchell *et al.* 2016)

Tropical plantations are considered a threat to biodiversity (Foster *et al.* 2011). Large-scale conversion of forest to more economically profitable monocultures, primarily oil-palm (Koh and Wilcove 2008), is ongoing in Southeast Asia, usually via intermediate land uses such as logging and/or rubber plantations (Margono *et al.* 2014). Rubber plantations are also expanding (Warren-Thomas *et al.* 2015). The most favourable conditions for both types of plantation are found in lowland areas that were historically forested (Fitzherbert *et al.*, 2008). Diversity loss and population declines have been reported in plantations (reviewed by Foster *et al.*, 2011; Warren-Thomas, Dolman & Edwards, 2015),

but little research has attempted to identify the ecological processes behind why certain species can occupy these plantations and others are displaced (a few conservation flagship species, like the orangutan, are the exception (Ancrenaz *et al.* 2004). The cyclical nature of palm oil production also induces additional pressures on organisms occupying this habitat: once productivity of the current crop dwindles, the entire plantation may be removed, potentially eliminating a great deal of the biodiversity that had managed to accumulate in the plantation over its lifecycle (Snaddon *et al.* 2013). Rubber's effects on biodiversity have received less attention than oil palm and although rubber plantations superficially resemble forests more than oil palm does, they still support fewer species than even logged forests (Fitzherbert *et al.*, 2008). While diversity is lower in these habitats, the abundance of species that are present is usually greater than in 'natural' situations (Fitzherbert *et al.* 2008, Foster *et al.* 2011).

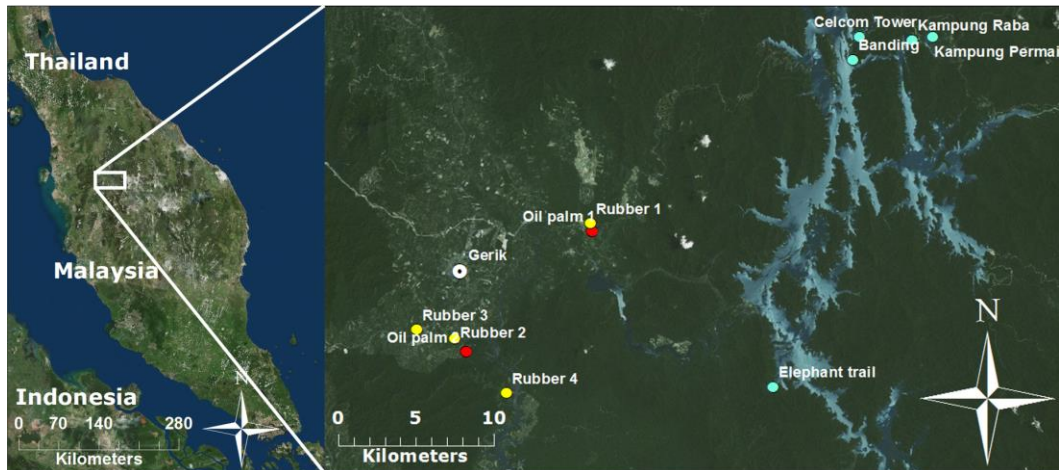
Plantations harbour physical microhabitats that differ from native habitats along multiple axes, including thermal, light, and structural complexity (Foster *et al.*, 2011) which may prevent many species from exploiting plantations and will exert novel selection pressures on those species that do. Structural changes may be particularly important for arboreal lizards, which display close links between microhabitat, form and function, with morphologies that optimise performance in the structural niches they have evolved to occupy (Losos *et al.* 1994, Irschick 2002, Losos 2009, Mahler *et al.* 2010). Specifically, wider perches favour longer legs for higher sprint speed, whereas narrow-perches favour short legs for improved stability (Losos *et al.* 1994, Irschick and Losos 1999, Irschick 2002, Losos 2009, Hsieh 2016, Winchell *et al.* 2016). While not universal, these relationships also extend beyond anoles to a range of lizard taxa and environments (Bauwens *et al.*, 1995, Olberding *et al.*, 2016, Melville & Swain 2000, Grizante *et al.*, 2010). Behaviour can, however, modulate the relationship between microhabitat availability and ecomorphology (Irschick 2002, Zhuang and Higham 2016). For example, lizards may avoid perches where their performance is sub-optimal (Irschick 2002), which could buffer their exposure to novel perches in modified environments. Thus, behavioural flexibility that allows for the use of novel microhabitats in plantations may play a key role in determining whether species can utilise these heavily modified environments.

Moving in from the general results of species richness in Chapter 2, here I test whether land use change in peninsular Malaysia has stimulated a shift in microhabitat use by one of the species able to invade plantation environments (i.e., behavioural flexibility) and whether these shifts are accompanied by ecomorphological differences between native and modified habitats, as predicted by morphology–performance relationships. Alternatively, species may exhibit microhabitat fidelity and fail to exploit the range of novel microhabitats available in plantations. I test these hypotheses for *Calotes emma* Gray 1845, an agamid lizard which is native to forest edges and gaps but is found in a range of human-modified habitats in northern Malaysia (Grismer, 2011).

## **3.2 Materials and methods**

### **3.2.1 Study area**

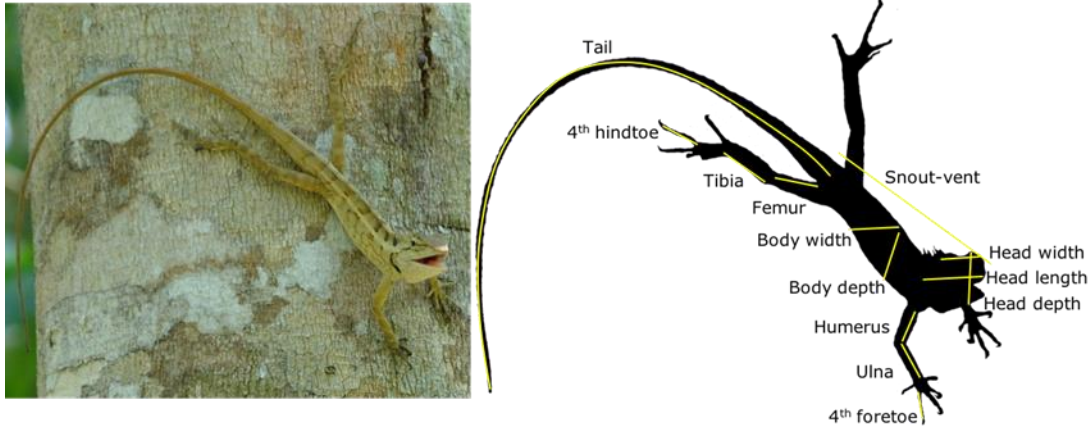
I focussed on a patchwork of forest and plantation habitats near and within the Belum-Temenggor forest complex in northern peninsular Malaysia near the town of Gerik, Perak state. The Royal Belum State Park is well known for its primary rainforest and associated biodiversity and includes almost all of the country's megafauna species (Norsham *et al.*, 2000). The area also harbours a high diversity of reptile species (Grismer *et al.*, 2004; Hurzaid *et al.*, 2013; Grismer 2011). The Temenggor forest reserve is a large tract of forest subjected to ongoing logging which surrounds the human-made Tasik (lake) Temenggor. Surrounding the forest reserve is a mosaic of land use types including rubber and oil palm plantations, small kampungs (villages) and small and medium-sized towns. My study sites included secondary forest edge and gap situations in and around Temenggor forest reserve and oil palm and rubber plantations on the outskirts of Gerik itself (Fig. 3.1).



**Figure 3.1:** Study sites encompassing two oil palm plantations (Red), four rubber plantations (Yellow) and five sections of secondary forest edge habitat (Blue) around Lake Temenggor and Gerik in northern Peninsular Malaysia. Imagery source: Esri, DigitalGlobe, GeoEye, Earthstar Geographics, CNES/Airbus DS, USDA, USGS, AEX, Getmapping, Aerogrid, IGN, IGP, swisstopo and the GIS user community.

### 3.2.2 Study species

*Calotes emma* (Agamidae) is a medium-sized scansorial agamid found in forest gaps, edges and plantations (Grismer 2011). It is native to India through Myanmar, Laos, Cambodia, China, Thailand and Peninsular Malaysia (Grismer 2011). *C. emma* is tan dorsally, with dark longitudinal stripes and dark patterns radiating from the eye and both sexes have nape crests of enlarged scales and three pairs of spines above and behind the eyes (Fig 3.2). *C. emma* is sympatric with *C. versicolor*, the oriental garden lizard, in parts of its range in northern Malaysia, but across both field seasons I only observed a single *C. versicolor* 50km to the southwest of Gerik and none in my study sites.



**Figure 3.2:** (Left) Adult male *Calotes emma* showing typical adult colouration, (Right) The 13 morphological parameters I measured and associated reference points on a silhouette of *C. emma*.

### 3.2.3 Habitat structure characterisation

I carried out 2x50m random transects in each of the three focal habitats: forest edge, rubber, and oil palm. Beginning at a representative location in the interior of a patch, subject to accessibility and safety, I chose a transect direction at random by dropping a spinning pen. I recorded habitat measures at 10m intervals along the transects. Percentage cover of ground flora, coarse woody debris (CWD) and canopy cover were estimated visually, while distance to nearest tree, and diameter at breast height (DBH) of nearest tree were recorded using a standard 30m measuring tape. It is usual to randomly measure the heights of potential perches to characterise perch availability to lizards in a habitat e.g., (Irschick et al. 2005) however I did not, as unlike the typical *Anolis* sp. based lizard ecomorphology study system, *C. emma* rarely uses branches of varying heights, instead using the entire height of tree trunks and is therefore not limited by branch height.

### 3.2.4 Lizard sampling

Lizards were sampled between 10:00 and 15:00 for four weeks in April-May 2015 and again in March-April 2016. I surveyed the interior of plantation habitat. Edge habitats were selected in forested areas as *C. emma* is rare in forest interiors in this part of Malaysia (personal observation, Grismer, 2011). I used an active search method to locate lizards rather than random transects because the low density of animals would not have allowed sufficient sample sizes to be collected within time constraints. Searchers actively scanned ground, trunk and branches for lizards to minimize searching bias. Adult male *C. emma* were caught by noose or by hand. I focused on male lizards because



females are less conspicuous and I could not capture sufficient numbers for analysis. Following capture, I measured 11 morphological traits to the nearest 0.01mm using digital calipers (Fig 3.2). I used a transparent plastic ruler to measure snout-vent length (SVL) and tail length, to the nearest mm. I also recorded perch use and perch characteristics to quantify microhabitat use. Perch types were classified as 'trunk' ( $\geq 10$ cm diameter), 'branch' (including shrubs and live fronds  $< 10$ cm diameter), 'coarse woody debris' (CWD; including dead frond piles), 'ground' or 'other' (e.g. rocks, stumps). A total of 59 adult male *C. emma* were measured for ecomorphological analyses.

### 3.2.5 Sprint speed

Please refer to Chapter 4, section 4.2.5 for details regarding the sprint speed experiment.

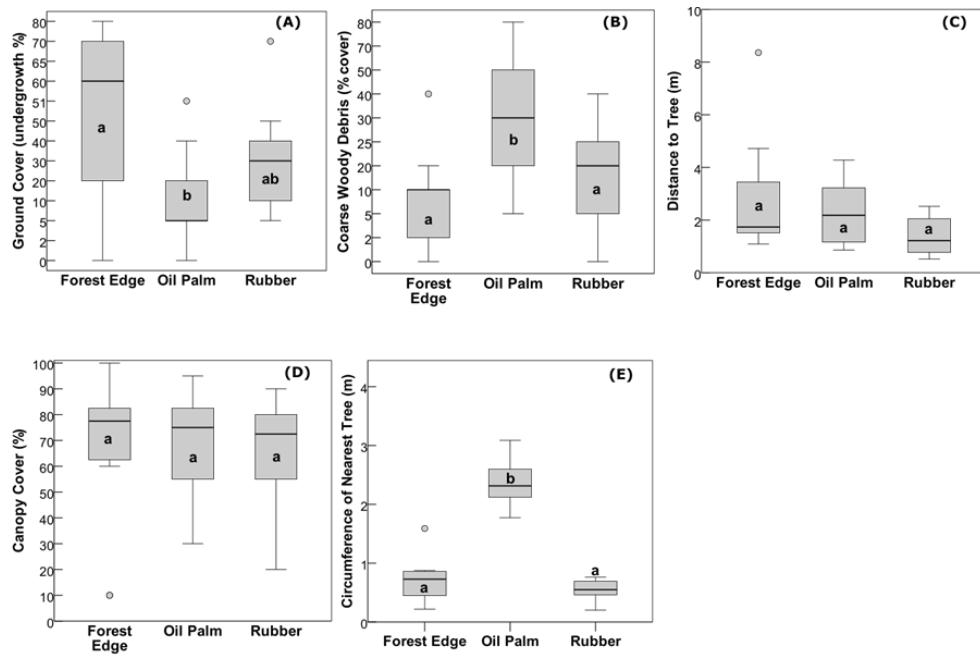
### 3.2.6 Hypothesis testing

I first compared habitat structure among land covers. Percentage data (canopy cover, CWD) were arcsine transformed to meet assumptions for MANOVA. Wilk's lambda was selected as the test statistic over Roy's great root due to greater power in cases where the dependant variables are not highly correlated (Warne 2014). I then tested for differences in all habitat variables between rubber, palm and secondary forest habitat, excluding canopy cover because it remained non-normal even after transformation. I tested for differences in canopy cover between habitats separately. To test ecomorphological traits of lizards between habitats, morphological data were  $\log_{10}$  transformed to meet assumptions of normality. I corrected for body size differences by regressing each trait against  $\log_{10}$  snout-vent length (SVL), a proxy for body size in lizards and used the residuals of this regression in further analyses. I used discriminant function analysis (DFA) to test for differences in overall morphology among lizards from different habitats and whether an individual lizard's habitat could be predicted based on morphological characteristics. For the latter, I used a jackknifing approach to calculate the percentage of individuals whose habitat type could be correctly predicted by the DFA. Next, I tested for differences in individual morphological traits between habitats, including body condition, which I calculated using the residuals of a regression of body mass against SV. I also tested for a difference in the frequency of perch-type between habitats. Lastly, I tested for relationships between perch width, leg length and sprint speed.

### 3.3 Results

#### 3.3.1 Habitat structural differences

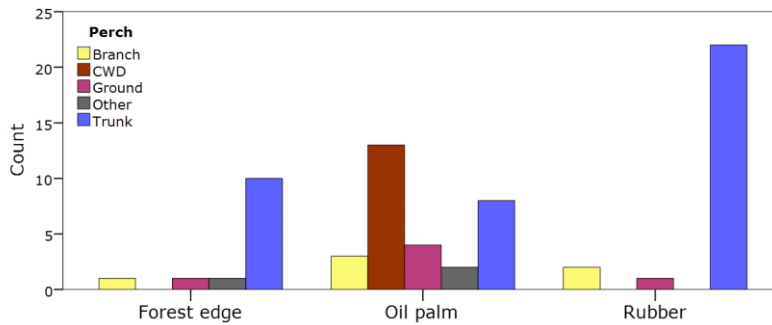
I found overall differences in multivariate structure between all habitat types (Wilk's Lambda:  $F_{18, 50}=13.060$ ,  $P<0.001$ ). Ground cover percentages differed ( $F_{2,35}=6.244$ ,  $P=0.005$ ) among habitat types, as did the percentage of cover of coarse woody debris ( $F_{2,35}=7.978$ ,  $P=0.001$ ) and the circumference of the nearest tree to each sampling point ( $F_{2,35}=123.710$ ,  $P<0.001$ ) (Fig. 3.3). Post-hoc Tukey's HSD tests revealed significantly higher ground cover percentages in forest edges than oil palm ( $HSD_{2,35}=32.917\pm 9.007$ ,  $P=0.002$ ) but no significant differences between forest edge and rubber ( $HSD_{2,35}=17.917\pm 9.007$ ,  $P=0.131$ ) or rubber and oil palm ( $HSD_{2,35}=15\pm 9.007$ ,  $P=0.233$ ). Oil palm had a considerably higher percentage of CWD ground cover than both rubber ( $HSD_{2,35}=18.333\pm 6.826$ ,  $P=0.029$ ) and forest edges ( $HSD_{2,35}=25.667\pm 6.826$ ,  $P=0.001$ ), but these latter two habitats did not differ from one another ( $HSD_{2,35}=7.333\pm 6.826$ ,  $P=0.319$ ). This pattern was the same for the circumference of the nearest tree (oil palm vs rubber:  $HSD_{2,35}=181.5\pm 12.806$ ,  $P<0.001$ , oil palm vs forest edge:  $HSD_{2,35}=166.417\pm 12.806$ ,  $P<0.001$ , rubber vs forest edge:  $HSD_{2,35}=-15.083\pm 12.806$ ,  $P=0.474$ ). Percent canopy cover and the distance from sampling points to the nearest tree did not differ significantly between habitats ( $H_2=0.390$ ,  $P=0.823$ ;  $F_{2,35}=0.015$ ,  $P=0.985$ , respectively).



**Figure 3.3:** Differences in habitat structure between forest edge, rubber, and oil palm plantations in northern Malaysia. Significant differences in various measures of structure are denoted by different letters (a or b), while non-significant differences share a letter.

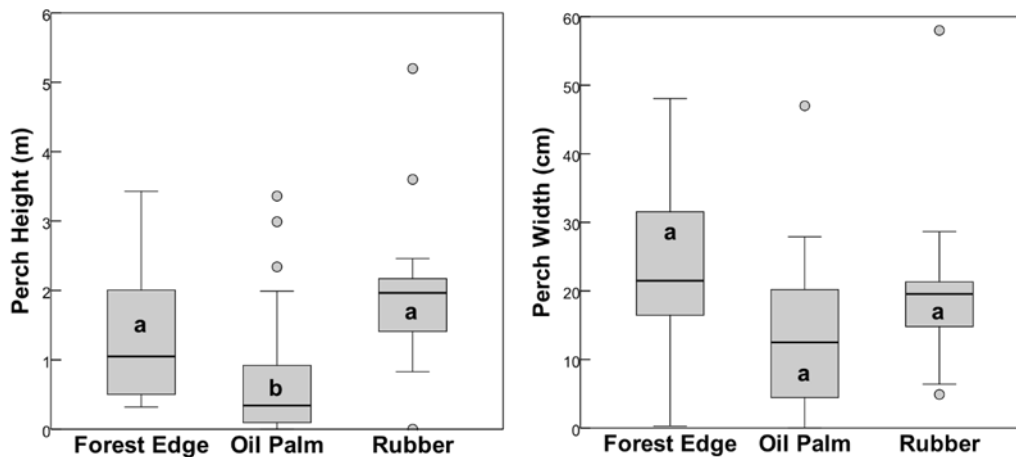
### 3.3.2 Differences in perches and behaviour

I found differences in perch selection ( $\chi^2=19.742$ ,  $P<0.001$ ) and perch height ( $F_{2,60}=0.956$ ,  $P<0.001$ ) by *C. emma* among the three habitat types. In its 'natural' habitat of forest gaps and edges, *C. emma* was primarily arboreal, perching on trunks and shrubs, although also, on one occasion, using a rock pile at ground level (Fig. 3.4). In rubber plantations, lizards were almost exclusively arboreal (perches  $\geq 83$ cm high apart from a single individual found on the ground, Fig. 3.4) with correspondingly high median perch heights (median  $\pm$  interquartile range =  $204.5\text{cm} \pm 96.5$ , Fig. 3.5). Rubber plantations also contained the highest perch height recorded for *C. emma* during my study (5.2 m). Mean values for perch height in rubber plantations were significantly higher than those in oil palm ( $\text{HSD}_{2,62}=119.989 \pm 28.357$ ,  $P<0.001$ , Fig. 3.5). Lizards in oil palm were primarily terrestrial, i.e. not on trunks, tending to perch on or under CWD, predominantly horizontal dead palm fronds (40% of lizards found in oil palm, Fig. 3.4). Median perch height ( $\pm$  interquartile range) in oil palm was  $44.6\text{cm} \pm 131.2$  (Fig. 3.5). Perch heights in forest edge were highly variable and did not significantly differ from either of the other habitats.



**Figure 3.4:** Frequency of perch-type use by *Calotes emma* in different habitat types. Perch selection differed across habitat types ( $X^2=19.742$ ,  $P<0.001$ ), with arboreality being less common in oil palm than forest and rubber plantations.

Perch widths were not significantly different between habitats (Fig. 3.5) ( $F_{2,62}=0.586$ ,  $P=0.560$ ). This lack of difference was due to two individuals from a uniquely managed section of oil palm plantation where the frond bases had been removed, leaving trunks smooth. This small section of plantation was unique amongst my sites. Removing these individuals resulted in significant differences in perch width ( $F_{2,60}=4.096$ ,  $P=0.021$ ), with narrower perches being used in oil palm than in forest ( $HSD_{2,60}= 6.152\pm 5.739$ ,  $P=0.02$ ), but no differences between oil palm and rubber ( $HSD_{2,60}=-1.153\pm 4.614$ ,  $P=0.172$ ).



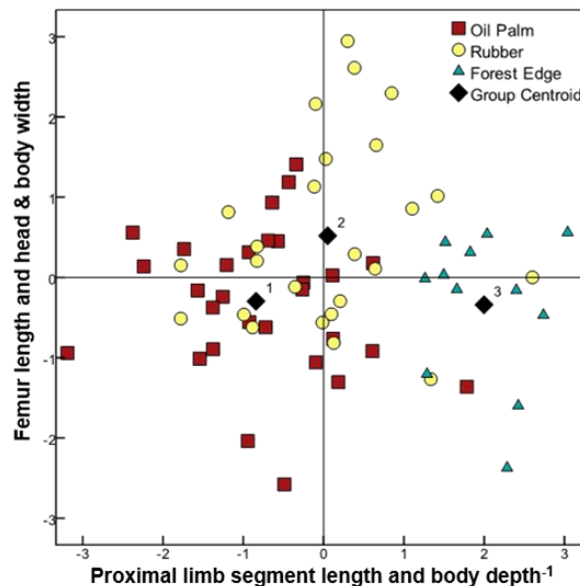
**Figure 3.5:** Perch heights (left) and widths (right) of *Calotes emma* in forest edge, oil palm and rubber habitats. Significant ( $P<0.05$ ) differences between habitat types (within panels) are indicated by different letters. Lizards tended to perch lower in oil palm than rubber, with forest variable. Perch widths did not differ between habitat types (see Results for more explanation of this result).

### 3.3.3 Differences in morphology

I found weak evidence for distinct morphotypes between habitats. Discriminant function analysis (DFA) revealed separation between oil palm and forest edge individuals along Function 1, which relates to body depth and limb length (Table 3.1, Fig. 3.6). Animals from rubber plantations had intermediate morphologies, overlapping with both (Fig. 3.6). Jackknifing found that the DFA could correctly classify 36 of 67 animals into the right habitat type, which is significantly better than random (binomial test, proportion correctly classified =0.537, null proportion=0.333, P=0.007).

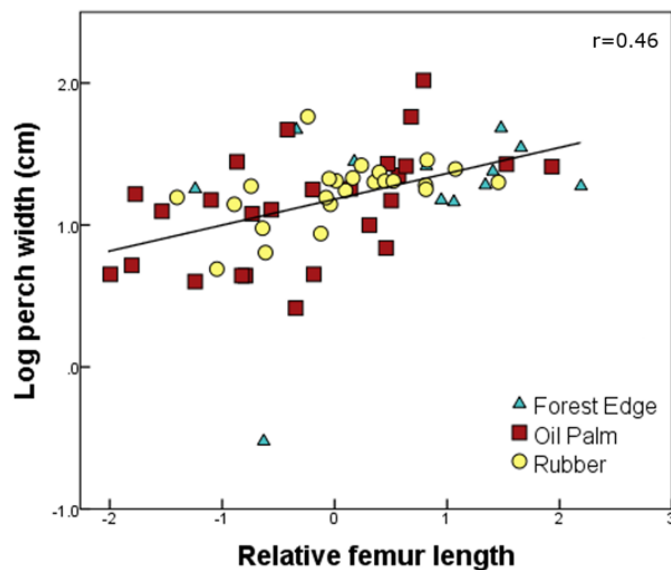
**Table 3.1:** Loadings of morphological traits for the first two functions of the discriminant function analysis.

Morphology trait	Function 1	Function 2
femur	.808	.588
tibia	-.692	-.955
humerus	.756	-.020
ulna	.303	-.607
4 <sup>th</sup> hindtoe	.267	-.079
4 <sup>th</sup> foretoe	.033	.144
head length	-.530	.138
head depth	-.580	-.033
head width	.173	.412
body depth	-.746	.115
body width	.276	.437



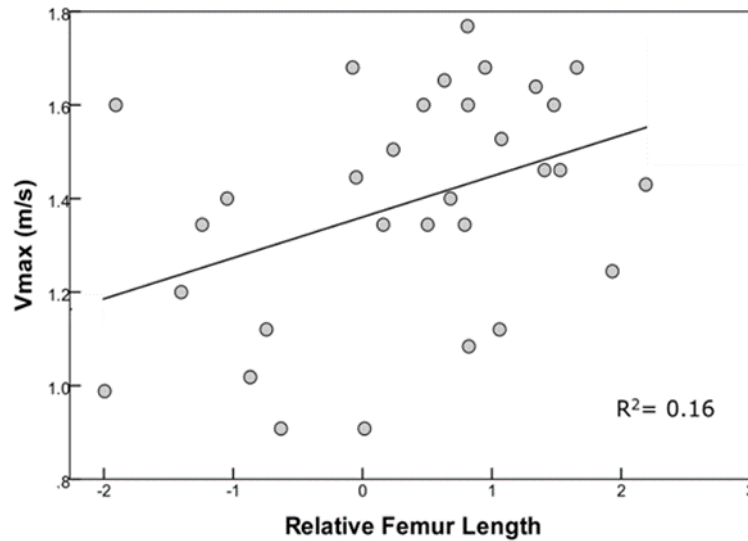
**Figure 3.6:** Discriminant functions analysis of *C. emma* morphology in different habitat types. Group centroids are shown as black diamonds (1=oil palm, 2=rubber, 3=forest edge). Jackknifing showed that 36 of 67 animals were correctly classified into their habitat of origin (binomial test, P=0.007) Individuals from oil palm and forest separate along function 1, which is related to limb length and body depth; individuals from rubber plantations have intermediate morphology.

Comparison of individual traits among habitats found that femur length, head and body depth, and body width differed among habitats ( $P < 0.05$ , Table S1). None of the other traits were significant ( $P > 0.08$  in all cases). Lizards in oil palm had shorter femora than lizards found in forest edge ( $P = 0.004$ ), but there was no difference in this trait between rubber and forest edge ( $P = 0.104$ ), or between oil palm and rubber ( $P = 0.303$ ). Perch width was positively correlated with femur length across habitat types ( $r = 0.46$ ,  $df = 61$ ,  $P < 0.001$ ; Fig. 3.7).



**Figure 3.7:** Correlation between relative femur length and perch width of *Calotes emma* ( $r = 0.46$ ,  $df = 61$ ,  $P < 0.001$ ). Relative femur length is the residuals from a regression of log femur length on log SVL. The extreme low value for perch width is due to a lizard found perching on a stem of grass in forest edge habitat. Relative femur length is examined to discount the fact that some lizards were larger than others in my dataset and these larger lizards may be mechanically capable of using wider perches than smaller lizards.

Maximum sprint speed was correlated with femur length ( $r = 0.40$ ,  $df = 28$ ,  $P = 0.028$ , Fig. 3.8) although not with tibia length ( $r = 0.20$ ,  $df = 28$ ,  $P = 0.282$ ) or the length of the fourth hindtoe ( $r = -0.072$ ,  $df = 28$ ,  $P = 0.7$ ). Overall hindlimb length, standardised against lizard body length maintained a correlation with max sprint speed ( $r = 0.40$ ,  $df = 28$ ,  $P = 0.03$ ).



**Figure 3.8:** Correlation between relative femur length and maximum sprint speed ( $V_{\max}$ ) of male *Calotes emma*. Lizards with relatively longer legs reached higher maximum velocities ( $F_{1,29}=5.501$ ,  $P=0.026$ ) along a 2m racetrack. Relative femur length is the residuals of a regression of log-transformed femur length on log SVL.

### 3.4 Discussion

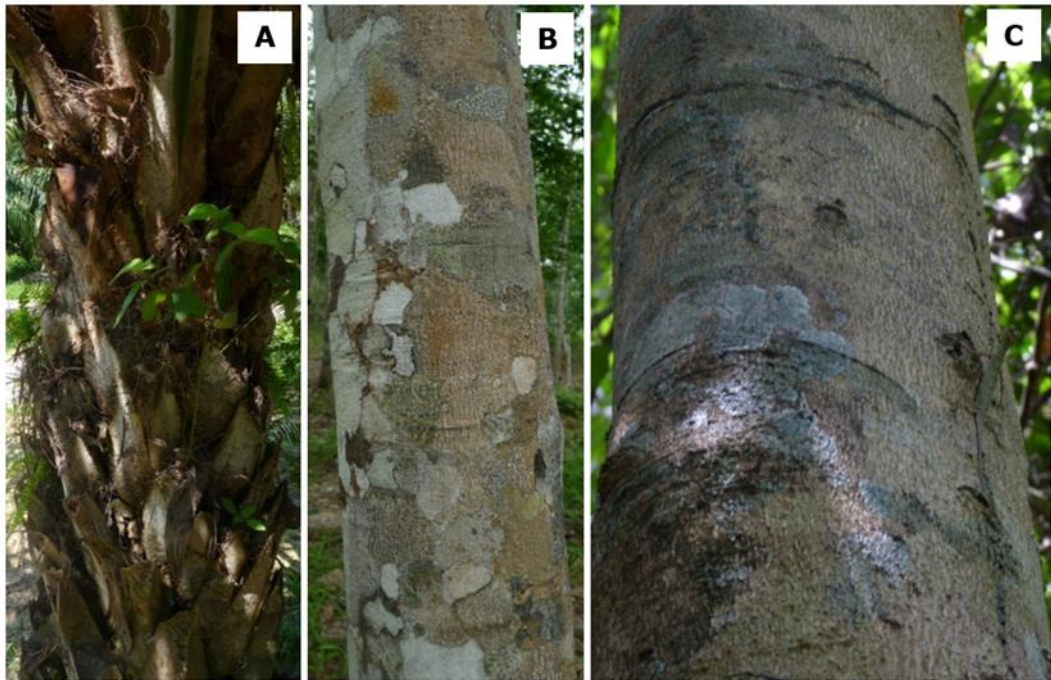
Land cover change is globally pervasive and is especially intense in Southeast Asia, where a century of logging and planting of rubber and oil palm has greatly reduced natural forest cover (McKinney & Lockwood, 1999, Hansen *et al.*, 2013). While the loss of natural forest has received substantial attention, what replaces it will have important implications for the future of tropical biodiversity as anthropogenic land covers vary in the intensity and range of ecological challenges they present to native fauna. Species that rapidly take advantage of novel, anthropogenic habitats, like plantations, must either be pre-adapted for these novel conditions, or be highly 'adaptable' (Williams *et al.*, 2008); the latter could include evolutionary adaption or plasticity (which itself may be adaptive, Ghalambor *et al.*, 2007). I found that *C. emma*, a primarily arboreal lizard in its native forest edge habitat (Grismer, 2011), has shifted its ecological niche to become predominantly terrestrial to successfully exploit oil palm plantations. My finding also show that modified habitats, like plantations, can be a source of intraspecific, ecomorphological variation related to ecological performance on modified substrates, in this case, relative femur length.

The shift in microhabitat use I observed between native and modified habitats suggests that behavioural flexibility has played a key role in facilitating the exploitation of oil palm plantations by *C. emma*. While pre-adaptation may play

an important role in allowing species to persist under land cover change, especially when departures from native habitat structure are small, behavioural flexibility will become increasingly important as the difference between original and replacement land covers increases. This is consistent with Foster *et al.*'s (2011) suggestion that species that persist in oil palm tend to be generalists. However, my findings imply that such species may not be generalists within any single habitat, i.e. use a large range of microhabitats, but rather have the behavioural flexibility to exploit novel niche space when confronted with new opportunities.

The niche shift to a terrestrial lifestyle I observed only occurred in oil palm, while arboreality was maintained or enhanced in rubber plantations. One potential reason for these differing responses is differences in trunk morphology between the habitats. Dipterocarp trunks in native habitats tend to have few low branches, with relatively smooth trunks. These characteristics are enhanced in *Hevea brasiliensis* in rubber plantations, with smooth, almost branch-free trunks below the canopy (Fig. 3.9). Such wide, smooth surfaces are conducive to sprinting in lizards (Mattingly and Jayne 2005), which is important for ecological functions like predator escape and prey capture (Irschick and Losos 1998) and possibly territory defence. In contrast, palm trunks (*Elaeis guineensis*) are composed of many individual frond bases in an upturned scale-like arrangement (Fig. 3.9), which do not provide broad pathways for sprinting. I hypothesize that this distinct structure of oil palm trunks inhibits effective locomotion, forcing *C. emma* to adjust its behaviour and become predominantly terrestrial. This shift may also be facilitated by the large amounts of coarse woody debris typical of these oil palm plantations, which provide cover that is lacking in rubber where ground cover is sparse.





**Figure 3.9:** Differences in trunk structure between oil palm, rubber and native dipterocarps. The trunks of oil palm are composed of diagonal whorls of broken frond bases, forming a blocky structure (A). Rubber trees (B) have relatively smooth bark that resembles many forest tree species and a straight trunk that typically branches off above 4m. Trees in forest tend to be smooth and straight (C), but are variable in terms of bark rugosity and branching. Photographs by Leslie Bode, used with permission.

Other differences between habitat types may also contribute or drive this behavioural shift. For example, higher densities of ground predators can push lizards to seek higher perches (Losos *et al.* 2004, Lopez-darias *et al.* 2012). If oil palm plantations have lower numbers of ground predators than forest-edge and rubber plantations, which is possible given they tend to have the lowest diversity of the three (Glor *et al.* 2001, Koh and Wilcove 2008, Foster *et al.* 2011), this could relax selection for an arboreal lifestyle in *C. emma*, leading to increased terrestriality. However, the relative density of ground predators in different habitat types is unknown. If ground predators are not reduced in oil palm, then the extensive use of CWD by *C. emma* when on the ground could also be a strategy to avoid predation while simultaneously avoiding the complex locomotory environment of oil palm trunks. Another speculative explanation for perch bias towards these frond piles could be due to increased prey availability around the dead frond piles which may have drawn *Calotes* from the trees to concentrate activity around these structures, although further data collection would be required to test this hypothesis. Finally, microclimatic variation between the habitats could theoretically drive *C. emma* lower in oil palm plantations as the simplified canopy (Foster *et al.* 2011) and widely

spaced trees could equate to higher operative temperatures than the other habitat types I considered.

Shifts in microhabitat use can select for ecomorphological adaptation. For example, the convergent evolution of *Anolis* ecomorphs on Greater Antillean islands demonstrates links between perch width, locomotory performance, and limb length, with longer legs allowing for faster sprint speeds on wide surfaces (Losos 1990; Losos & Sinervo 1989; Irschick & Losos 1999 and reviewed by Losos 2009). Similar ecomorphological relationships between limb length and perch/substrate use have been found in a range of lizard taxa (e.g. tropidurids, Grizante *et al.*, 2010; Kohlsdorf *et al.*, 2001; Vitt *et al.*, 1997, and chameleons, Bickel & Losos 2002). Consistent with these relationships, I found that *C. emma* males with relatively longer femurs attained higher sprint speeds; longer femora have been linked to faster sprinting on wide surfaces (Kohlsdorf *et al.* 2001, Grizante *et al.* 2010). Based on this ecomorphological link, I would expect *C. emma* to have longer femora in oil palm where they are more terrestrial, following patterns in the partially ground dwelling trunk-ground anole ecomorph (Losos 2009). I instead found the opposite to be true: femora were shorter in oil palm plantations than other habitats. This apparent anomaly can be explained by examining the specific terrestrial microhabitat used by *C. emma* in oil palm. Lizards were rarely found on open ground, but rather amongst piles of dead fronds, which are composed of many narrow perches and do not allow unimpeded sprinting, suggesting that longer legs may not be favoured. Even when using arboreal microhabitats in oil palm, the macrostructure of oil palm trunks (Fig. 9) likely constrains sprinting, unlike the broad, relatively smooth trunks of native and rubber trees which may favour long legs and high sprint speeds. Thus, when microhabitat use and structure is considered, shorter femora in more terrestrial populations of *C. emma* match predictions of the effects of perch width on lizard ecomorphology.

Differences in leg length between oil palm and forest edges/rubber plantations could reflect either evolutionary adaptation or phenotypic plasticity. The major industrial increase in oil palm plantations in peninsular Malaysia occurred over 30 years ago (Snaddon *et al.*, 2013) although its origins as a crop lie in the early 20<sup>th</sup> century (Corley and Tinker 2015). Given a generation time of one year for *C. emma* (based on estimates for Chinese populations of the *C. versicolor* species complex by Huang *et al.*, 2013 and captive observations in other *Calotes* species, pers. obs.), this could equate to over 30 generations.

Rates of similarly rapid evolution in relation to perch use have been observed in *Anolis* toe pads (Stuart *et al.*, 2014), suggesting that rapid ecomorphological evolution in *C. emma* in response to oil palm plantations is not inconceivable. However, such a scenario would also depend on selection in oil palm not being diluted by gene flow from neighbouring habitats (Sultan and Spencer 2002). Observed differences in femur length between habitats could also be due to phenotypic plasticity, which has been described in *Anolis* lizards (Losos *et al.*, 2000), where juveniles raised on wider perches grew longer legs during development. A common garden experiment is needed to disentangle the evolutionary basis of the ecomorphological changes I observed in *C. emma*.

These patterns have ramifications for the wider understanding of the mechanisms linking habitat modification, behaviour, ecological niche dynamics and displacement of native species in tropical plantations. My data indicate that when the structural suitability of a habitat is poor for *C. emma*, behavioural flexibility allows it to shift its ecological niche use to regions of niche space that it only occasionally occupies in its native habitat. Other species occupying the interiors of forests which have evolved in highly stable environments (Tscharntke *et al.* 2007) to occupy narrower niche spaces (Williams *et al.* 2009) than those living in more disturbance prone forest edges and gaps and may lack the behavioural flexibility to function in the novel niche space made available by plantation expansion. This behavioural flexibility may be an important precursor to evolutionary adaptation to plantations or other anthropogenic environments like cities, since without it, species will not be exposed to the novel selection pressures imposed by these rapidly expanding anthropogenic habitats, as is proposed by the Bogert effect for selection on thermal traits (Bogert 1949, Muñoz *et al.* 2014, Buckley *et al.* 2015). A lack of flexibility in niche use by forest interior species may be further exacerbated by competition with behaviourally flexible species like *C. emma* which can rapidly colonize human modified habitats, limiting the niche space available for subsequent invasions by less flexible species.

Land use change will continue to affect species over the coming decades, compounded by the fact that most of the world's land use change occurs in its most biodiverse regions with the highest levels of species endemism (Sodhi *et al.*, 2010). Exposure to these new habitats is unavoidable as plantations and other anthropogenic land covers expand. To successfully exploit these habitats, species must either be pre-adapted to their conditions (Williams *et al.*, 2008),

or possess ample behaviour flexibility (which itself may be a form of pre-adaptation). This flexibility may also be necessary to encourage exposure to the selection pressures these novel environments present, promoting adaptation to optimise performance over time. These modified environments may also act as sources of ecomorphological variation, creating intraspecific diversity within the relatively narrow cross section of species that can occupy these plantations. Lastly, the rapid conversion of natural land covers provides a setting to study the rapid behavioural and ecomorphological shifts in colonising species which may be key to their persistence in environments that are quickly becoming the new tropical normal.

## 4 The Thermal Ecology of a Tropical Lizard During Land Use and Climatic Change

### 4.1 Introduction

Temperature is a key parameter for an organisms' survival. It governs physiological and ecological rates, which in turn have ramifications for suitable niches and, moreover, distribution of the species in question (Angilletta 2009). Changes in environmental temperatures can render areas uninhabitable for certain species, while increasing suitability for others, resulting in range shifts (Walther *et al.* 2002, Parmesan and Yohe 2003, Parmesan 2006). Climate change has already been implicated in the range shifts observed in many species, with the extent and direction of change dependent on the habitat use. Species' distributions are predicted to shift towards the poles (Walther *et al.* 2002) and to higher altitudes (Sekercioglu *et al.* 2008) as the climatic suitability of their habitats changes with mean temperature, while species that use habitats that already exist at high altitude or latitude are expected to contract as they are already at their limit (Foster 2001). Although this prediction does not hold in every case (Chen *et al.* 2011), many examples of this altitudinal/latitudinal shift have already been detected (Parmesan and Yohe 2003).

Despite the documented effects of climate change, land use change however remains as the most prominent, immediate threat to biodiversity (Sala *et al.* 2000). It also, in turn, feeds back into climate change through direct CO<sub>2</sub> emissions from burning, for example, and indirectly through loss of carbon sequestration when mature forests are cleared (Searchinger *et al.* 2008). The highest levels of land use change coincide with the world's most biodiverse regions and it is an immediate, ongoing and increasing process (Hansen *et al.* 2013). Land use change can also cause substantial changes in the local thermal environments available to organisms (Luskin and Potts 2011), although this aspect of their impact on organisms, past the initial habitat conversion process, is largely unknown.

At the organismal scale, ectotherms have often been shown to be particularly sensitive to subtle thermal changes in their environment. These animals rely on environmental temperatures for their metabolism and ecological performance (Huey and Stevenson 1979). Many reptiles have narrow thermal

tolerances and are already existing near their tolerance limits (Sunday *et al.* 2014). Research has mapped organisms' reactions to temperatures in the context of thermal performance curves (TPCs). These curves are anchored at either extreme by critical values that represent the lowest and highest temperatures an organisms' body can still function at ( $CT_{min}$  and  $CT_{max}$ , respectively). The curve typically rises gradually to reach an optimum ( $T_{opt}$ ) where physiological and ecological processes, digestion and locomotion take place at their maximum velocity. Further warming sees performance decrease rapidly to the  $CT_{max}$  where the organism cannot function, usually measured in terms of a loss of righting response in reptiles (Angilletta 2009). These limits are tested in short term exposures; the true 'lethal' temperatures lie above and below the  $CT_{min}$  and  $CT_{max}$ . However, prolonged exposure to these limits in the wild would, in all likelihood, result in mortality. The preferred body temperature of an organism ( $T_{pref}$ ) and body temperatures selected in controlled laboratory temperature gradients ( $T_{sel}$ ) also supply useful information on organisms' responses to temperature. Additionally, the range of temperatures that an organisms' performance is within or above an arbitrary threshold value (usually 80%),  $T_{breadth}$  (Angilletta *et al.* 2002b) is a useful proxy of the breadth of an organisms' thermal niche.

Thermal tolerance in reptiles has been shown to evolve if sufficient selection pressures are introduced into a system. Extreme inclement weather has been shown to result in widespread mortality of all but the most thermally tolerant individuals of a species, exerting strong selection pressure and inducing rapid adaptation (Campbell-Staton *et al.* 2017) and gradual cold tolerance is also thought to evolve fairly readily, at least in diurnal species (Muñoz *et al.* 2014). However, heat tolerance is not as variable as cold tolerance, with many species displaying similar  $CT_{max}$  values (Huey and Bennett 1987). An apparently physiologically constrained ability to evolve greater heat tolerance is further complicated by the 'Bogert effect' (Huey *et al.* 2003a) whereby diurnal lizards behaviourally buffer against adverse conditions, thereby reducing the pressure on their physiology to evolve.

Much research has focussed on critical thermal maxima, but the driving force behind reptile range shifts may be more likely to be long term incremental decreases in the time a given habitat spends at suitable operative temperatures ( $T_e$ ), far before these habitats ever reach the absolute thermal tolerance limits of these animals. Reductions in time spent in optimal thermal zones will increase time spent thermoregulating, reducing available time for foraging,

territory defense, predator avoidance and reproduction, resulting in slow, subtle losses of fitness (Sinervo *et al.* 2010). The relatively gradual increases in temperature resulting from climate change may lead to behavioural buffering to compensate for reductions in fitness, especially of altering microhabitat use (Scheffers *et al.* 2013, 2014), but are unlikely to mitigate the increase indefinitely and could actually increase future maladaptation (Buckley *et al.* 2015).

Research into the effects of global climate change on reptiles has largely focused on model-driven simulations of range suitability under varying future climatic scenarios and in identifying last glacial maximum refugia, mostly with regards to molecular ecology (Barlow *et al.* 2013). In terms of future climatic suitability, Araújo *et al.* (2006) modelled range changes for 66 European reptiles and found that, given unlimited dispersal ability, most species would expand their range. Eliminating dispersal ability resulted in widespread predicted losses with the most severe losses centred around the warmest regions in Southern Europe, indicating many reptile species in the temperate latitudes may have some buffering areas to potentially expand into as climate change progresses. Broader scale studies (Sinervo *et al.*, 2010) report local reptile extinctions already linked to climatic change and generally present a bleak outlook for montane species in particular. Despite these findings, and at least in structurally complex habitats, there is some potential for microhabitats to buffer in the short term against extreme climatic conditions (Scheffers *et al.*, 2014) and for more long-term climatic warming (Scheffers *et al.*, 2013). However, via the 'Bogert effect', this buffering may again shield these taxa from selection on their physiological thermal traits in the same way as diurnal lizards show capability to evolve low thermal tolerances but are buffered against high tolerances by thermoregulatory behaviour (Munoz *et al.*, 2014).

Land cover is changing at an unprecedented rate with plantations in Southeast (SE) Asia continuing to expand faster than elsewhere (Sodhi *et al.* 2010). Much effort has been made to quantify the change in biodiversity that accompanies this process, but little relates to how these anthropogenic habitats also offer novel microclimatic conditions to species that do occupy them. Microclimatic conditions in SE Asian oil palm monocultures at ground level more closely resemble those in the forest canopy (Hardwick *et al.* 2015) than any other zone of the native habitat, being between 2.8°C-6.5°C warmer on average during the day (Luskin and Potts 2011, Hardwick *et al.* 2015), but similar at night. They resemble logged forests more than primary forest in terms of humidity

and temperature although are far more variable throughout the day in both these measures than either forest type (Hardwick *et al.* 2015). As these plantations mature however, their structure changes, accumulating more structural complexity, heterogeneity and consequently, microhabitats that could feasibly act as buffers against further warming (Luskin and Potts 2011, Scheffers *et al.* 2013) for species that succeed in colonising them. Rubber plantations are also warmer than the forests they replaced (Song *et al.* 2017, Meijide *et al.* 2018), to a broadly similar degree as oil palm although the latter has been shown to be the warmer of the two plantation types (Meijide *et al.* 2018).

Tropical regions have been predicted to experience the effects of climatic warming rapidly (Deutsch *et al.* 2008) and tropical forest lizards have been shown to be at particular risk (Tewksbury *et al.* 2008, Huey *et al.* 2009, 2012), although see results from Logan *et al.* (2015, 2013). These regions are predicted to experience relatively low levels of climatic warming compared to higher latitudes, however the species here are thought to be existing closer to their thermal maxima (Gunderson and Leal 2012). Some species in tropical regions are thought to be experiencing stressful temperatures in warm seasons already (Huey *et al.* 2009). Many species of tropical lizard exhibit thermoconforming behaviour, i.e., they allow their body temperature ( $T_b$ ) to track  $T_{air}$  which is thought to allow relatively high overall performance in situations where thermoregulating accurately is either too costly or impossible (Rummary *et al.* 1995). This mode of thermal ecology is not inherently thought to increase a species' risk of extinction (Sinervo *et al.* 2010) and may even buffer or result in small performance gains in those thermoconforming species currently operating at relatively low  $T_e$ , when considering thermal performance in isolation from other ecological niche axes. The abrupt thermal changes introduced with land use change could, potentially, contribute a much more significant thermal change for species in the tropics than the more gradual process of climate change.

After identifying the two main candidate niche axes that could be affected by land use change in Chapter 1 and dealing with the structural changes in Chapter 3, I will now evaluate the thermal implications of land use change on ectotherms, again using *C. emma* as a study organism. I measure thermal characteristics of three common land uses in the region: forest edge, oil palm plantation and rubber plantation and consequently lizards' thermal traits (tolerance, performance) from each habitat. I then draw from both to predict



the thermal suitability of the various land uses under current and future climates. I predict plantations will display higher mean and maximum operative temperatures ( $T_e$ ), greater diel fluctuations than native forest habitats, in equivalent microhabitats. Furthermore I predict lizards from warmer habitats (e.g. plantation versus forest) will display higher thermal tolerance and performance to coincide with their warmer environments. Finally, I measure climate change's predicted effects on the region and I predict it will decrease thermal suitability of plantations for *C. emma*.

## **4.2 Materials and methods**

### **4.2.1 Study system**

I conducted this research in Northern Peninsular Malaysia around the town of Gerik in Perak state. Study sites consisted of oil palm plantations, rubber plantations and secondary forest edges. The study species was *Calotes emma* (Agamidae), a medium-sized scansorial agamid lizard commonly found in forest gaps, edges and plantations (Grismer 2011).

### **4.2.2 Habitat thermal characterisation**

I measured operative temperature using copper models (Shine and Kearney 2001). 1mm thick copper sheets were shaped into cylinders with one flattened end and another left open with a lid also made to cover the end during sampling. Cylinders measured approximately 8cm in length and 3cm in diameter to reflect the approximate body size of an adult *C. emma*. An iButton thermocron datalogger ([www.maximintegrated.com](http://www.maximintegrated.com)) was suspended inside, free of the outer walls. I applied pale tan coloured paint to mimic the typical, relaxed state colouration of *C. emma*.

Models were placed in microhabitats at each site (bare ground, low undergrowth, low trunk and high trunk) to mimic lizard perch use and capture small-scale nuances in temperature. One model was used for each microhabitat except for low trunk and high trunk (two models each, on opposite sides of the trunk). Microhabitats were sampled every 15 minutes at two locations per site (total of 13 iButtons per habitat, 39 models deployed per sampling effort) between 08/04/17-15/04/17 and 17/04/17-23/04/17, hitherto labelled as sets 1 and 2 and analysed separately. My sample size was limited to 39 models due to logistical and financial constraints. I calculated mean daytime temperature using the measurements between 06:00 and 18:00, inclusive, for each microhabitat and site combination. I compared environmental temperatures

between habitats and microhabitats using linear mixed effect models, with day and time as random effects (Luskin and Potts 2011), and compared microhabitats within macrohabitats using ANOVAs.

#### 4.2.3 Lizard sampling

I sampled lizards between 09:00 and 15:00 (March – May) in 2015 and 2016 simultaneously with the ecomorphological data collection for Chapter 3. I surveyed the interior of plantations and edges in forests as *C. emma* is rare in forest interiors in this area (personal observation). I actively searched perches to locate lizards rather than employ a randomised approach due to time constraints and an inadequate density of lizards. Adult male *C. emma* were caught by noose. Females are cryptic during the day and I could not locate sufficient numbers for analysis.

I measured  $T_b$  and the air and surface temperatures ( $T_{air}$ ,  $T_{surf}$ ) at the lizard's perch to establish field active body temperatures and the difference in temperature between lizards and the environment. For  $T_b$  I used a datalogger (Omega HH806WE) and type-T thermocouple (Omega) inserted approximately 5mm into the cloaca. I used the same datalogger and thermocouple to measure  $T_{surf}$  and  $T_{air}$  where the probes' tip was held against the surface or approximately 10cm above the surface. Differences in means of thermal characteristics between habitat groups (i.e.,  $T_b$ ,  $T_{air}$ ,  $T_{surf}$ ) were compared using ANOVA with post-hoc Tukey's HSD test. Lizards were transported to the field station in cool boxes. While in captivity lizards were kept in plastic faunaria at ambient temperature (approx. 28-32°C) with access to natural light and drinking water. Each was released at its precise site of capture from GPS coordinates.

#### 4.2.4 Thermal tolerance

To measure  $CT_{max}$  I followed Muñoz *et al.* (2014). A thermocouple was inserted into the cloaca and fixed with tape at the base of the tail. Each lizard (32 in total) was warmed at a rate of approximately 1°C/minute using a 100W tungsten bulb. At onset of gaping (a behaviour used by lizards to increase evaporative cooling (Tattersall *et al.* 2006)) lizards were turned onto their dorsum and prompted to right themselves. If lizards failed to right themselves within 10 seconds this was recorded as their  $CT_{max}$  and I placed them in a mesh vivarium in a cooler room. If the lizards righted themselves within 10 seconds they were warmed further and the procedure repeated every 0.2°C until a result was obtained.  $CT_{min}$  is less meaningful to my research than  $CT_{max}$  as under

natural conditions at my study sites, my species would never reach temperatures this low and so a smaller sample size was used to provide an estimate of  $CT_{\min}$  of *C. emma* in this area. The same procedure was used for  $CT_{\min}$  as for  $CT_{\max}$ , by putting nine lizards in a plastic container lined with paper to avoid direct contact with ice, inside a domestic refrigerator to overcome the high ambient temperatures (28-35°C).

#### 4.2.5 Sprint speed

Thermal performance was estimated using footage recorded at 120 frames per second using a Fujifilm HS50EXR digital camera. Lizards were recorded dorsally running along a track constructed using general specifications described by Huey (1981). I ran ten lizards from each focal habitat type at four temperatures within this species' expected thermal performance curve (22°C, 28°C, 35°C, 38°C), twice consecutively at each temperature. The order lizards ran at these temperatures was randomised initially to give a sequence of 28°C, 38°C, 35°C, 22°C. Lizards were heated/cooled using the same heating/cooling procedures described for thermal tolerance experiments. The track's length was divided into six equal segments (28cm) marked with white tape for subsequent video analysis and was maintained at an incline of approximately 20° to avoid hopping (Losos, 2009). I ran lizards every 12 hours at 08:00 and 20:00 after an initial 24 rest/acclimation period following capture. 12 hours rest between runs gave all lizards a substantial rest time while also minimising overall time spent in captivity. Each lizard was run twice at each temperature and given 12 hours rest between each temperature. For each run, I measured the fastest time to travel a 28cm track segment using the free software, Windows moviemaker (Microsoft, 2015). I extracted maximum sprint speed ( $V_{\max}$ ) in m/s attained across these eight runs for each individual. Sprint speed and the corresponding temperature values were used to generate thermal performance curves using R (see below). Footage sequences where lizards failed to cover this 28cm distance while running were discarded.

#### 4.2.6 Fitting thermal performance curves

Thermal performance curves (TPCs) have a characteristic, asymmetric, shape (Angilletta 2006, 2009). I fitted five potential function shapes to the  $T_b$ -sprint data, using the R function `tpc`, written by A.C. Algar. I compared the fit of five asymmetric functions previously used for fitting TPCs: Brière2 (Shi and Ge 2010), Logan1 (Shi and Ge 2010), exponentially modified Gaussian (Shi and Ge 2010) and Gompertz\*Gaussian (Frazier *et al.* 2006, Frishkoff *et al.* 2015).

Before fitting curves, I standardized sprint speed values to the proportion of maximum velocity for each individual, following Frishkoff *et al.* (2016). Of the six functions tested, the Gompertz\*Gaussian function fit the best, based on AICc (see Results), so I used this function to test for differences in TPC among habitat types. The Gompertz\*Gaussian function has the form (Frazier *et al.* 2006, Frishkoff *et al.* 2015):

$$v = v_{max} \exp\left(-\exp(\rho(T_b - T_{opt}) - 6) - \sigma(T_b - T_{opt})^2\right)$$

where  $v$  is standardised sprint velocity,  $v_{max}$  is the maximum sprint velocity inferred from the curve,  $T_{opt}$  is the temperature at which  $v_{max}$  occurs,  $T_b$  is body temperature and  $\sigma$  and  $\rho$  determine the rate at which the curve rises and falls and thus relate to performance breadth. I fit a model that allowed all parameters ( $v_{max}$ ,  $\sigma$ ,  $\rho$ , and  $T_{opt}$ ) to vary among habitat types. I then tested models that constrained  $v_{max}$ ,  $\sigma$ , and  $\rho$  and allowed  $T_{opt}$  to vary and that constrained  $v_{max}$  and  $T_{opt}$  and allowed  $\sigma$ , and  $\rho$  to vary.

#### 4.2.7 Thermal suitability of habitats

I quantified the thermal suitability of habitats using the following measures: time (between 06:00 and 18:00) spent above  $CT_{max}$ , time spent within 2°C of  $CT_{max}$  (as a proxy of warming tolerance, in light of the fact that species will probably retreat from habitats before they reach their  $CT_{max}$ ) and time spent within  $T_{breadth}$  (as a proxy of thermal suitability) and compared these under current and future predicted warming of +3°C, following Buckley (2008).

#### 4.2.8 Habitat characterisation

I examined temperature differences between microhabitats within and between habitat types using linear mixed effects models under current and predicted future conditions for the region of 3°C warming.

### 4.3 Results

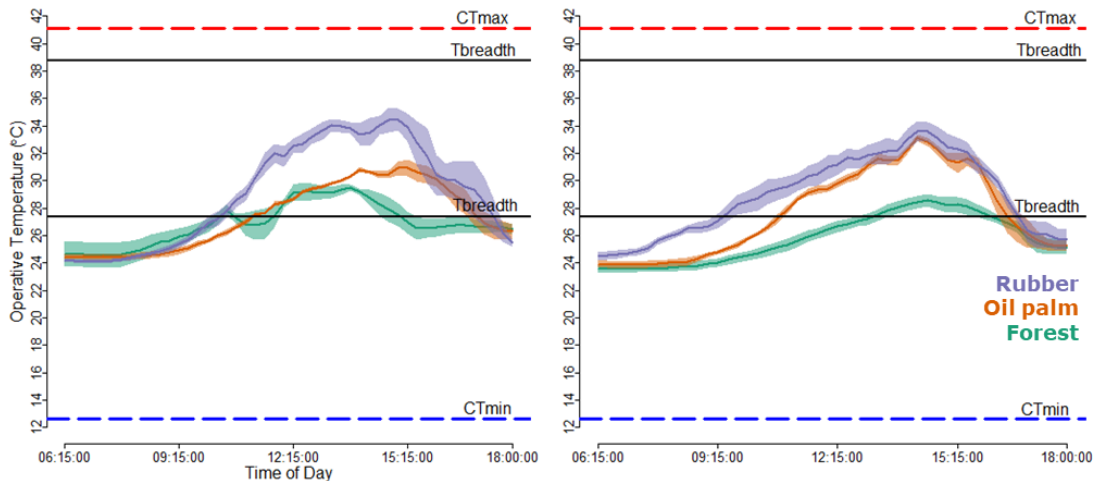
#### 4.3.1 Habitat characterisation

The copper temperature models recorded overall hotter temperatures in plantations than in forest. The linear mixed effects model recovered a significant habitat effect. Forest had an average temperature of 26.5°C in set 1 and 25.6°C in set 2. On average, oil palm was 0.75°C hotter in set 1 and 1.9°C hotter in set 2 (both with  $P < 0.01$ ) with oil palm's intercept higher (+0.748°C/1.894°C, set 1 and 2 respectively) than forest's (26.513°C/25.620°C) on average. Rubber was warmer still; 2.3°C and 2.9°C

( $P < 0.01$  in both) above forest in sets 1 and 2 respectively (Table 4.1 and Fig. 4.1). Oil palm in set 2 recorded conspicuous spikes in temperature under vegetation. This is likely due to shafts of sunlight penetrating the dead palm fronds as the angle of incidence changed throughout the day, heating the model directly, despite my best efforts to prevent this during model placement.

**Table 4.1:** Results of a linear mixed effects model on temperature in each habitat, allowing time of day and day to vary.  $t$  and  $P$  values represent differences from  $T_e$  in Forest.

Habitat	Intercept (°C)	$\Delta T_e$ (from forest, °C)	Standard Error	df	t value	P value
Forest	26.51	0.00	0.30			
Oil Palm	27.26	0.75	0.07	3105.00	10.65	<0.01
Rubber	28.83	2.32	0.07	3105.00	32.35	<0.01
Forest (set 2)	25.62	0.00	0.36			
Oil Palm (set 2)	27.51	1.89	0.09	2078.00	20.07	<0.01
Rubber (set 2)	28.50	2.88	0.09	2078.00	31.29	<0.01



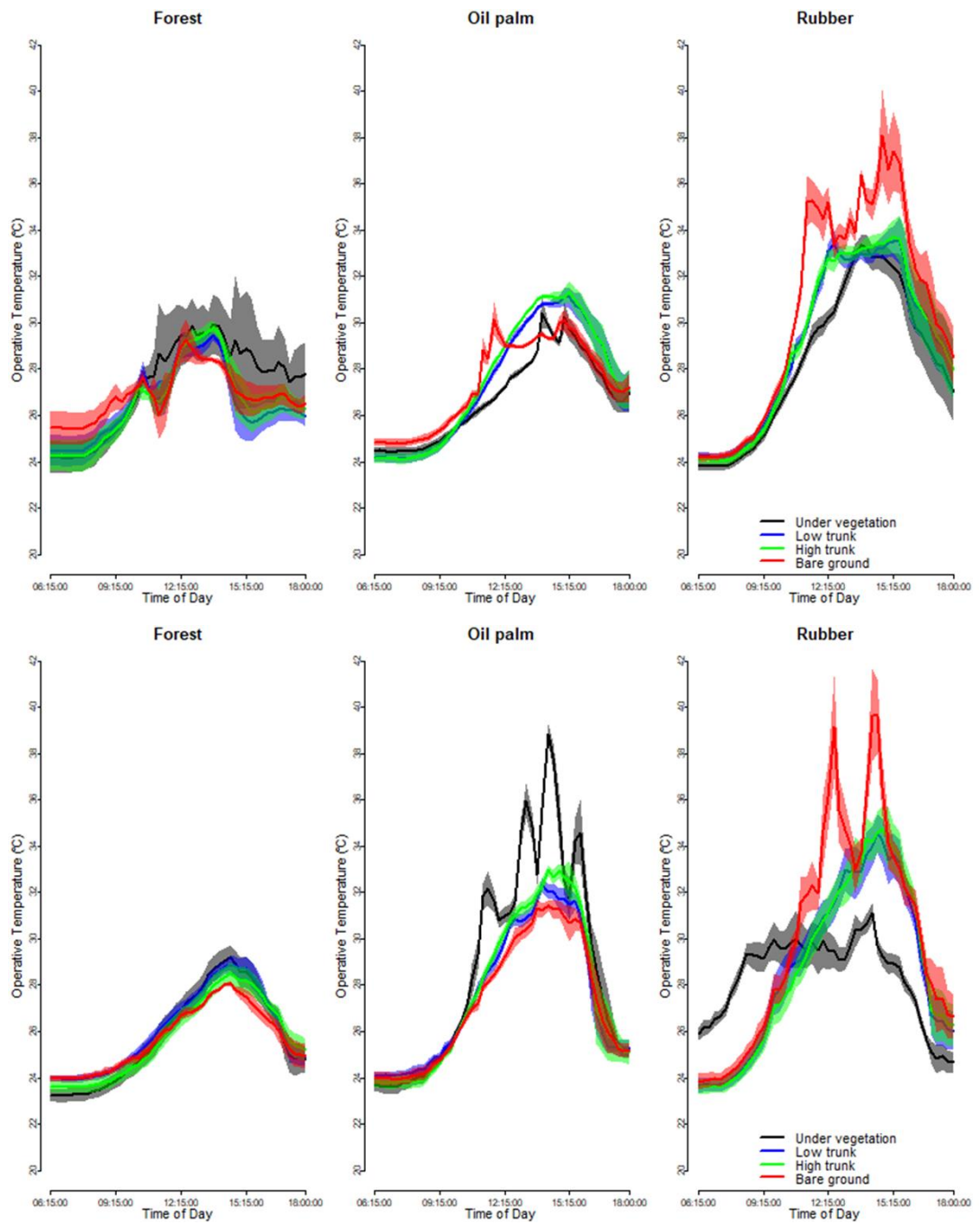
**Figure 4.1:** Mean temperature within each habitat across a single representative day for set 1 (left) and set 2 (right). Standard error is included in the shaded polygons and  $CT_{max}$ ,  $CT_{min}$  and both edges of the range of  $T_{breadth}$  are annotated.

Linear mixed effects models within each habitat type revealed that bare ground was predominantly the warmest microhabitat (See Table 4.2). It was significantly warmer than the other microhabitats in rubber in set 1 ( $t_{920} = -7.23, -7.36, -11.09$ , for high trunk, low trunk and under vegetation, respectively.  $P < 0.01$  in all cases) and rubber and oil palm plantations in set 2 (Rubber:  $t_{647} = -5.09, -5.30, -5.79$ , for high trunk, low trunk, under vegetation respectively.  $P < 0.01$  in all cases. Oil palm:  $t_{582} = -4.71, -6.21, -3.73$  for high trunk, low trunk, under vegetation, respectively.  $P < 0.01$  in all cases, Table 4.2). It was also warmest in forest set 1 although not significantly so versus either high trunk ( $t_{1011} = -2.1, P = 0.04$ ) or low trunk ( $t_{1011} = -0.41, P = 0.69$ ). High and low trunks were warmer in forest set 2 ( $t_{712} = 3.66, 5.62$ , respectively,  $P < 0.01$  in both cases) and oil palm set 1 ( $t_{1011} = 1.59, 0.32$ , respectively,

P=0.11, 0.75, respectively) although not significantly so in the latter case. Similarly, under vegetation tended to be coolest; significantly so in all habitats in set 1 (Forest:  $t_{1011}=3.48$ ,  $P<0.01$ , Oil Palm:  $t_{1011}=-4.86$ ,  $P<0.01$ , Rubber:  $t_{920}=-11.09$ ,  $P<0.01$ ) and rubber in set 2 ( $t_{647}=-5.79$ ,  $P<0.01$ ). Low trunk was coolest in oil palm set 2 ( $t_{582}=-6.21$ ,  $P<0.01$ ) and bare ground was coolest in forest set 2 ( $\Delta$ bare ground= High trunk=0.13, Low trunk= 0.2, Under vegetation= 0.13 ). Forest was thermally more homogenous than either plantation type with smaller overall differences between microhabitat temperatures (Table 4.2, Fig 4.2).

**Table 4.2:** Results of a linear mixed effects model on temperature in each microhabitat, allowing time of day and day to vary. Microhabitat temperatures' deviance from the previous microhabitat is represented by a t value. The first t value in each set per habitat is large as it is compared to zero.

Habitat	Microhabitat	Estimate	Standard Error	df	t value	P value
Forest	Bare ground	26.61	0.39	5.20	68.27	<0.01
Forest	High trunk	-0.14	0.07	1011.00	-2.10	0.04
Forest	Low trunk	-0.03	0.07	1011.00	-0.41	0.69
Forest	Under vegetation	-0.27	0.08	1011.00	-3.48	<0.01
Oil Palm	Bare ground	27.27	0.30	84.10	91.12	<0.01
Oil Palm	High trunk	0.13	0.08	1011.00	1.59	0.11
Oil Palm	Low trunk	0.03	0.08	1011.00	0.32	0.75
Oil Palm	Under vegetation	-0.47	0.10	1011.00	-4.86	<0.01
Rubber	Bare ground	30.02	0.47	90.70	64.51	<0.01
Rubber	High trunk	-1.11	0.15	920.00	-7.23	<0.01
Rubber	Low trunk	-1.13	0.15	920.00	-7.36	<0.01
Rubber	Under vegetation	-1.86	0.17	920.00	-11.09	<0.01
Forest (set 2)	Bare ground	25.49	0.24	65.70	108.66	<0.01
Forest (set 2)	High trunk	0.13	0.04	712.00	3.66	<0.01
Forest (set 2)	Low trunk	0.20	0.04	712.00	5.62	<0.01
Forest (set 2)	Under vegetation	0.13	0.04	712.00	3.08	<0.01
Oil Palm (set 2)	Bare ground	28.06	0.43	69.90	65.89	<0.01
Oil Palm (set 2)	High trunk	-0.60	0.13	582.00	-4.71	<0.01
Oil Palm (set 2)	Low trunk	-0.75	0.13	582.00	-6.21	<0.01
Oil Palm (set 2)	Under vegetation	-0.64	0.17	582.00	-3.73	<0.01
Rubber (set 2)	Bare ground	30.02	0.53	112.00	56.77	<0.01
Rubber (set 2)	High trunk	-1.57	0.31	647.00	-5.09	<0.01
Rubber (set 2)	Low trunk	-1.64	0.31	647.00	-5.30	<0.01
Rubber (set 2)	Under vegetation	-1.96	0.34	647.00	-5.79	<0.01



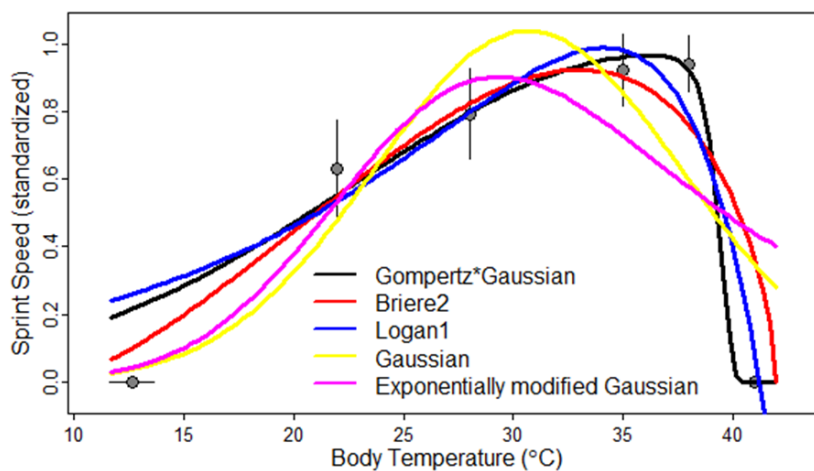
**Figure 4.2:** Mean daily temperatures plotted for each microhabitat and macrohabitat combination from set 1(upper panel) and set 2 (lower panel). Shaded polygons show 95% confidence intervals.

### 4.3.2 Lizard thermal traits

Neither  $CT_{max}$  ( $F_{2,29} = 1.505$ ,  $P=0.239$ ) or  $CT_{min}$  ( $F_{2,6}=0.199$ ,  $P=0.825$ ) differed between habitats. The best fitting thermal performance function was the Gompertz\*Gaussian (Table 4.3, Fig. 4.3), which identified  $T_{opt}$  at 36.65°C. The shape of the thermal performance curve did not differ significantly as a function of lizard's habitat of origin, in either breadth ( $\sigma$  and  $\rho$ ),  $T_{opt}$  or  $v_{max}$  ( $P$  values  $>0.3$  relative to the forest curve; Table 4.4 and Fig. 4.4) and so data were pooled for further analyses (Fig. 4.5).

**Table 4.3:** Fit parameters for the five functions tested to fit *Calotes emma* thermal performance data, ranked in terms of best fit. Function references are given in the main text.

Function	AICc	$\Delta AICc$	Explained Deviance
Gompertz*Gaussian	-198.49	0	0.91
Logan1	-88.15	-110.34	0.81
Brière2	-22.35	-176.14	0.70
Gaussian	28.07	-226.55	0.57
Exponentially modified Gaussian	63.77	-262.26	0.45

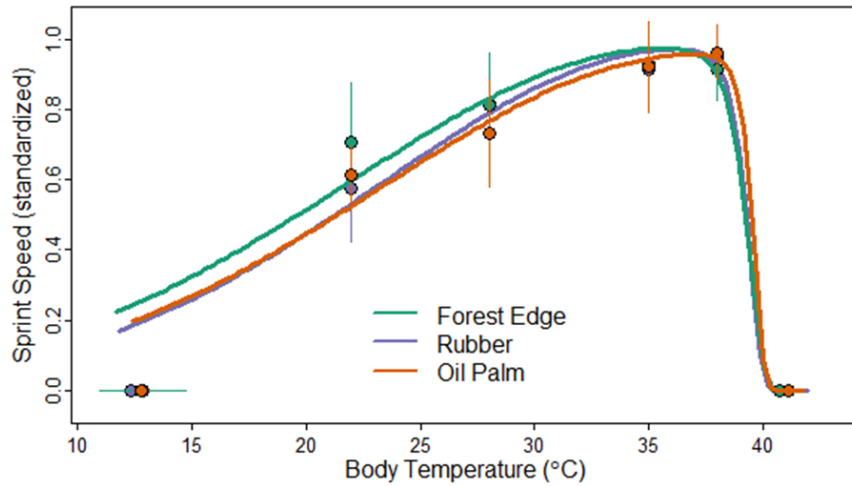


**Figure 4.3:** Alternative thermal performance curve functions for sprint speed of *Calotes emma*. Sprint speed was standardized to the proportion of maximum for each individual. The Mean and standard deviation of sprint speed across individuals is shown at each temperature. The Gompertz\*Gaussian function (black) best fit the data (Table 4.3).

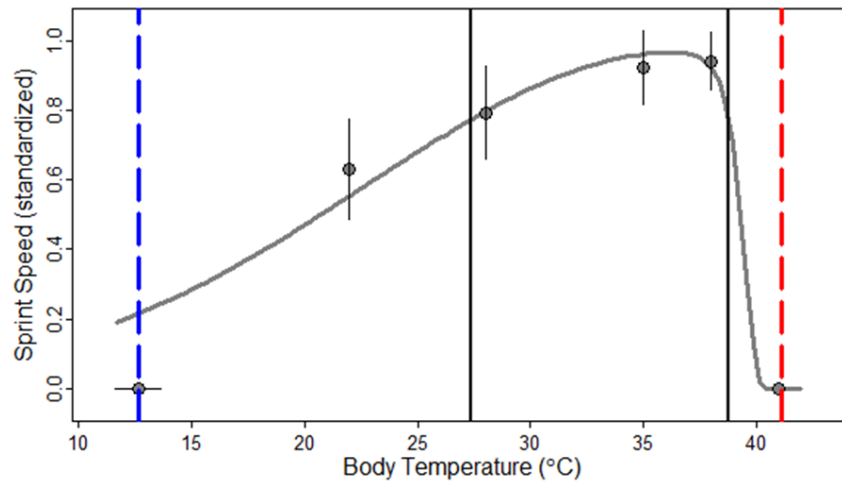


**Table 4.4:** The significance of the variation in various parameters of the thermal performance curves of lizards from each habitat type.

Habitat	Rho	$\Delta$ Rho P	Sigma	$\Delta$ Sigma P	Pmax	$\Delta$ Pmax P	T <sub>opt</sub>	$\Delta$ T <sub>opt</sub> P
Forest	2.30	0.00	0.00	0.00	0.98	0.00	36.50	0.00
Rubber	-0.18	0.85	0.00	0.16	-0.02	0.54	0.42	0.37
Oil palm	-0.30	0.75	0.00	0.13	-0.03	0.41	0.66	0.19

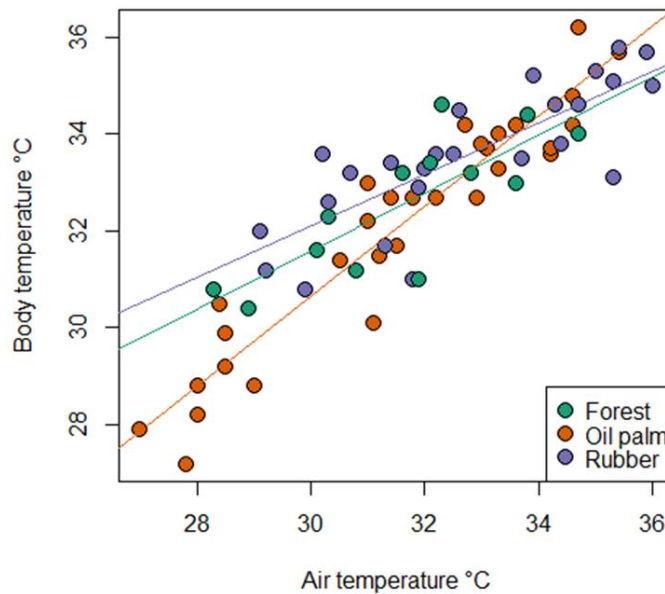


**Figure 4.4:** Thermal performance curves generated from lizards from the different habitat types fitted using the Gompertz\*Gaussian function.



**Figure 4.5:** The finalised thermal performance curve for *Calotes emma* based on the pooled data of individuals from all three habitat types with CT<sub>min</sub> (blue), CT<sub>max</sub> (red) and T<sub>breadth</sub> (black) annotated.

Field active  $T_b$  was strongly related to both  $T_{air}$  ( $t=15.28$ ,  $df=66$ ,  $P < 0.001$ ,  $R^2=0.88$ ) and  $T_{surf}$  ( $t=12.372$ ,  $df=65$ ,  $P < 0.001$ ,  $R^2= 0.84$ ). Correcting for air temperature (i.e., regressing  $T_b$  against air temperature and using the residuals in further analyses), the  $T_b$  of lizards captured from each habitat differed significantly ( $F=65.315$ ,  $df=62$ ,  $P < 0.001$ , adjusted  $R^2=0.83$ ) as did the relationship between  $T_{air}$  and  $T_b$  (Fig. 4.6).



**Figure 4.6:** Field active  $T_b$  plotted against  $T_{air}$  recorded from lizards in each land use type with regression lines to illustrate differences in the relationship between these variables in each habitat. The strong ( $t=15.28$ ,  $df=66$ ,  $P < 0.001$ ,  $R^2=0.88$ ) correlations are suggestive of thermoconforming behaviour although see Hertz *et al.* (1993) on why this cannot be confirmed.

### 4.3.3 Thermal suitability of habitats

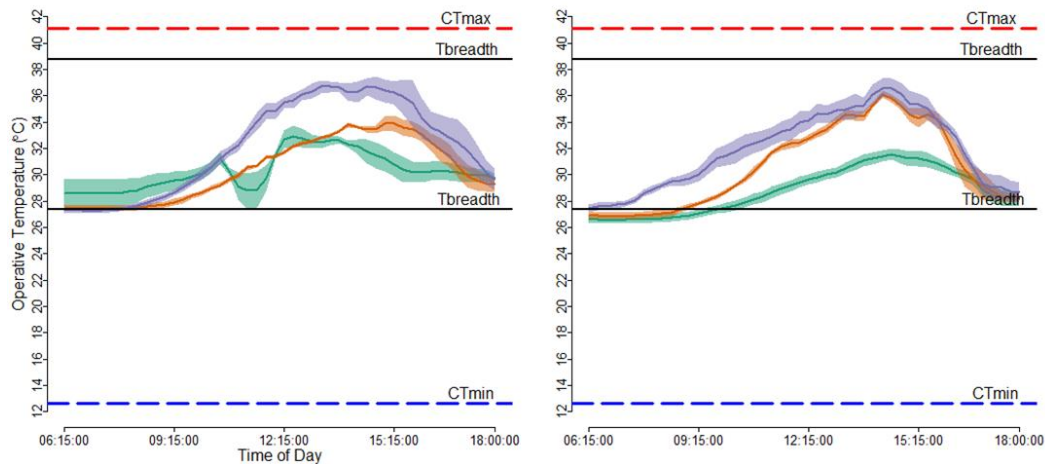
Temperatures did exceed  $CT_{max}$  of *C. emma*, in both plantation types, but only very rarely and never in forest. In rubber, temperatures exceeded  $CT_{max}$  for an average of 0.015 hours per model day (pmd), where a model day is defined as one model, recording between 6:00 and 18:00, exceeded  $CT_{max}$  for only 0.015 hours on average pmd in rubber set 1 and 0.018 hours pmd in rubber set 2. Under a 3°C warming scenario, this would rise to 0.121hrs and 0.236hrs (sets 1 and 2, respectively; (Table 4.5). Temperatures in oil palm did not exceed  $CT_{max}$  in set 1, and for just a daily average of 0.02hrs in set 2. A 3°C increase in temperature would increase the time exceeding  $CT_{max}$  daily in oil palm, based on set 2 to 0.14hrs, but set 1 remained below  $CT_{max}$ . Temperatures in forest never exceeded  $CT_{max}$  under current or future conditions (Table 4.5).

**Table 4.5:** Habitat suitability for *Calotes emma* in my three focal habitat types measured in terms of hours spent within the relevant measure/model day (between 6am-6pm). Future conditions used were the predicted 3°C rise for the region (Buckley, 2008).

Habitat	Current conditions			Future conditions		
	$>CT_{max}$	$T_{breadth}$	$CT_{max}-T_e < 2$	$>CT_{max}$	$T_{breadth}$	$CT_{max}-T_e < 2$
Rubber	0.015	8.076	0.0756	0.121	11.955	0.439
Oil palm	0	6.736	0	0	12.708	0.014
Forest	0	5.736	0	0	11.681	0
Rubber (set 2)	0.018	6.836	0.182	0.236	7.636	0.618
Oil palm (set 2)	0.02	5.72	0.08	0.14	7.883	0.16
Forest (set 2)	0	2.483	0	0	6.986	0

*C. emma* had a considerable thermal safety margin in all habitats. While, temperatures in rubber spent the most time within 2°C of  $CT_{max}$  under current conditions, this was only for a daily average of 0.76hrs in set 1 and 0.182hrs in set 2 (Table 4.5). Warming of 3°C would increase these values to 0.439 and 0.618 hours (set 1 and set 2 respectively). Temperature in oil palm spent a daily average of 0.08hrs within 2°C of  $CT_{max}$  in set 2 but did not enter this range in set 1. Under future warming, these values are predicted to increase to 0.16hrs/13hrs in set 2 and 0.014 hours in set 1. Forest temperatures did not come within 2°C of  $CT_{max}$  under current or future climatic conditions.

$T_{breadth}$  was defined as the range of temperatures within 80% of peak performance (Angilletta 2009). Based on the thermal performance curve, *C. emma*'s  $T_{breadth}$  ranged from 27.41°C to 38.79°C. Time within  $T_{breadth}$  was greatest within rubber, an average of 8.08 hours between 06:00 and 18:00 in set 1 and 6.84 hours in set 2 (Table 4.5, Fig. 4.7). Oil palm temperatures spent 6.74 and 5.72 hours within  $T_{breadth}$  in sets 1 and 2, respectively, and forest spent the least time per day in  $T_{breadth}$ : 5.74 and 2.48 hours. All habitats spent more time of the day on average within *C. emma*'s  $T_{breadth}$  under future conditions (Table 4.5, Fig. 4.7), however oil palm is forecast to spend the most time: 12.71 and 7.88 hours (out of 13 hours between 6:00 and 18:00) for sets 1 and 2 respectively; rubber was second (11.95 and 7.64) and forest spent the least time in this range (11.68, 6.99). The percentage increase of time within  $T_{breadth}$  under future conditions however showed forest to benefit the most in terms of thermal suitability relative to current conditions with increases of 103% and 181.3%, compared to 88.7% and 37.8% in oil palm and 48% and 11.7% in rubber.



**Figure 4.7:** Temperature traces for each habitat, condensed into a single 'mean day' generated from the predicted 3°C rise in air temperature. With  $T_{breadth}$ ,  $CT_{max}$  and  $CT_{min}$  labelled and polygons representing standard error. When compared with Fig. 4.1 it shows a relative increase in time, per model day, spent within  $T_{breadth}$ .

#### 4.4 Discussion

Climate change is predicted to affect the earth's biota profoundly over the coming decades by changing thermal environments, resulting in gains and losses of suitable thermal conditions for most of the species studied (Walther *et al.* 2002, Parmesan and Yohe 2003, Parmesan 2006). However, land use change is a much more rapid process that has already affected biodiversity worldwide (Sala *et al.* 2000) and may have radical effects on the thermal environments available to organisms (Tuff *et al.* 2016, Frishkoff *et al.* 2016). Here I analysed how land use change in the tropics changes the thermal suitability of relevant microhabitats available to a diurnal lizard in terms of thermal performance.

I found forests to be the most thermally homogenous land use type, with less difference between microhabitats than either plantation type (Fig. 4.2). This is important in the context of thermoconforming lizards as it may limit the need for thermoregulating and is likely the reason this physiological state arose, where high canopy cover leads to limited ability to raise body temperature to a narrow range of temperatures and so physiological evolution to operate relatively well at a wider range of lower temperatures becomes the less costly pathway (Rummary *et al.* 1995). Similarly, forests were cooler than both plantation types, consistent with previous results (Luskin and Potts 2011, Hardwick *et al.* 2015, Meijide *et al.* 2018). However, unlike previous studies (Meijide *et al.* 2018), I found rubber plantations to be warmer than oil palm. One possible explanation for this difference may be the maturity of my study

plantations. The oil palm plantations in this area of northern Malaysia are largely old, small scale operations with relatively complete canopies (see Chapter 3), leading to well-shaded microhabitats below this canopy, a key factor reported by Hardwick *et al.* (2015) and Meijide *et al.* (2018) in lowering microhabitat temperature in plantations. Immature oil palm plantations are much hotter (Luskin and Potts, 2011) and thus may not offer the same quality of cooler microclimates to lizards or other ectotherms as the mature plantations I studied.

My data are the first concerning the thermal ecology of a Southeast Asian agamid lizard. I found that *Calotes emma* has thermal limits of around 41°C and 12°C ( $CT_{max}$  and  $CT_{min}$ , respectively), similar to convergent lineages of new world lizards (Losos 2009) and its broad thermal performance curve and field collected body/air temperatures (Fig. 4.6) suggest it is a thermoconformer (although see Hertz *et al.* (1993) on why caution should be applied to this assumption) found in warm habitats with field active body temperatures between around 28°C and 36°C, during my survey time periods.

The habitat temperature data, when compared against *C. emma*'s thermal traits show varying levels of suitability across the day for this species in my focal habitat types. Surprisingly, since it is a known forest gap/edge species, forest edge was overall thermally poorly suited to *C. emma*, spending the least amount of time within 80% of its  $P_{max}$ . This poor suitability arises because forests are too cool, rather than too hot, as they had the largest thermal safety margin (Deutsch *et al.*, 2008) and never exceeded  $CT_{max}$  in any microhabitat. Rubber was thermally most suitable spending much of the day within *C. emma*'s 80%  $T_{breadth}$ , but rarely exceeding  $CT_{max}$ . Oil palm showed slightly less thermal suitability than rubber but was still within  $T_{breadth}$  for several hours more per day than forest was under current conditions. Thus, the increase in temperature due to land use change has created a more favourable thermal landscape for *C. emma*. It may be the case that *C. emma* evolved in warmer, open grasslands, in light of the poor thermal suitability of forests however this theory would need additional data collection to verify. I found no evidence of thermal niche shifts in plantations, suggesting that *C. emma*'s high  $T_{opt}$  and broad thermal niche were a pre-adaptation to the expansion of hotter habitats that accompanied the establishment of oil palm and rubber plantations in the early 20<sup>th</sup> century (Corley and Tinker 2015), and even more so by their rapid expansion in recent decades (Koh and Wilcove 2007, Fitzherbert *et al.* 2008). This could have induced a large range and population expansion of this, and

other forest gap specialists, though new data on the population genomics of this species would be needed to test this hypothesis. My findings, however, also raise the question of why *C. emma* was pre-adapted to hotter conditions than I found in its native habitat. One possibility is that *C. emma* was found, historically, in only the hottest gap microhabitats, while my thermal surveys sampled a wider range of conditions. The relative lack of thermal suitability in forest shows *C. emma* is capable of occupying habitats with seemingly poor thermal suitability. Being a thermoconformer is likely an evolutionary advantage in such habitats by still allowing relatively high performance at cooler temperatures that may fall outside the 80%  $T_{\text{breadth}}$  whereas a more strict thermoregulator would be forced to spend time seeking basking opportunities that could otherwise be spent foraging, defending territories or seeking mates. South American *Anolis* lizards with similar ecology to *Calotes* have been shown capable of switching between a thermoregulatory mechanism in open habitat and thermoconforming in closed habitat (Huey and Stevenson 1979) in order to maximise the thermal resources available. If this is also true for *C. emma* it may be the case that *C. emma* historically inhabited relatively hot and open grasslands and that the forest populations are the result of a secondary invasion. I already showed in Chapter 3 that this species is capable of pronounced shifts in behaviour to cope with niche shifts. A behavioural shift to thermoconforming behaviour to maximise performance in habitats with lowered thermal suitability may well have buffered against any physiological selection pressure upon a lower  $T_{\text{opt}}$ .

Although my use of a 3°C predicted rise in air temperature, following Buckley (2008), is crude, it provides a general indication of how future climate change will affect thermal suitability for *C. emma*. *C. emma* is predicted to gain in thermal suitability in all habitats, with oil palm, rather than rubber, becoming the most thermally suitable habitat with 12 out of 13 hrs of the day on average falling within *C. emma*'s  $T_{\text{breadth}}$  in my set 1 data. Forest, while still the least thermally suitable will gain the most in thermal suitability for *C. emma*. These data are consistent with previous hypotheses (Huey *et al.* 2009) where open habitat lizards are predicted to gain thermal suitability in historically cooler environments and potentially expand their range at the detriment of more range-restricted species (although see Logan *et al.* (2013). However, this increased thermal suitability also comes at a cost of increased thermal stress in plantations, but not forests, at the hottest times of day

Future climate change is predicted to begin pushing these habitats nearer *C. emma*'s thermal limits, but is also likely to result in further net increases in the thermal suitability of these habitats. This is a rare case of an optimistic outlook for an element of tropical biodiversity under climate and land use change, however it comes with a large caveat. Forest is predicted to experience proportionally larger increases in thermal suitability for this species than either plantation type. While this will likely allow *C. emma* to further expand into these previously relatively unsuitable environments it may also lead to detrimental effects on interior forest species already occupying them such as *Aphaniotis fusca*, *Bronchocela cristatella* and *Gonocephalus bellii*. Direct competition with *C. emma* over food and perch sites, increased predation risk from *C. emma* on hatchling forest lizards and a loss of thermal suitability may cause the range of these species to contract, leading to eventual biotic homogenization (McKinney and Lockwood 1999). Forests are predicted by my data to buffer against future climate change (remaining cooler than rubber and oil palm plantations under future conditions, despite gaining proportionally higher thermal suitability for *C. emma*) and have already been shown currently to act as better buffers than plantations during short term climatic events, such as 2015's extreme El-Nino event (Meijide *et al.* 2018). In addition to being common in plantations, *Calotes emma* is already more abundant in urban environments than any other agamid lizard in my study area (pers. obs.) and so could feasibly be classified as being of less conservation value than the forest specialists it could eventually replace in their native habitats.

Negative effects on interior forest specialists will likely be compounded in the future by the fact that forest loss continues to accelerate in this region (Hansen *et al.* 2013), shrinking the available habitat of the forest specialists even further. However, we lack even basic information on the thermal requirements of all of Malaysia's forest agamids, severely limiting my understanding of how they will respond to increasing temperatures and increasing competition from plantation species re-expanding into forest environments. I suggest that future research is needed to document thermal niches of more of Malaysia's diverse reptile fauna, coupled with improved understanding of the magnitude of thermal changes in microclimates across the productive lifetime of plantations in the area, from the initial forest clearance to mature closed-canopy situations similar to my plots. This could then be related back to organismal suitability over time and fed back into policy to try to improve the biodiversity value of this controversial land use across its lifespan.

## 5 Natural history of Malaysian Agamid lizards

The ecology of reptiles in Malaysia is generally poorly understood (although see Grismer (2011) and references therein). The vast diversity of species present and inaccessible terrain has led to gaps in the knowledge of little further than initial species descriptions in some cases and in others, new species are regularly described from previously known sampling sites (Grismer *et al.* 2015). This chapter does not aim to test hypotheses or present new results but instead will serve as a repository for observations I made on the reptile species encountered during this research. My personal philosophy is that making meaningful observations on the ecology or behaviour of species is a disappearing skill and without such observations, what do we really know about a species? Large scale datasets can show patterns but what happens within individuals at ground level is often completely obscured by the very scale that makes these studies important. Collected here are short notes and photographs I took, where possible, on each agamid species I located during my research, limited to Peninsular Malaysia but I include species seen across the peninsula outside my study region.

Detailed localities for each species are available for research purposes on an individual basis but are withheld here on ethical grounds due to poaching concerns.

### **5.1 *Aphaniotis fusca***

This small agamid species (<7cm SVL) was observed at two sites in my study area: during night transects at Lata Kekabu, approximately 60km southwest of Gerik and at Kampung Air Ganda's water source around 7km from Gerik itself. At Lata Kekabu a single adult male was found sleeping in the typical position for this species; aligned along the central vein of a large leaf. This site comprises heavily disturbed, mature secondary forest either side of a wide, fast flowing river used for swimming and by visitors. A single adult male in display colouration was also found at the water source but during the day. It was perched approximately 1m high on a very thin (<2cm diameter) sapling and upon discovery, very rapidly rotated around the sapling before jumping to the ground and running bipedally across the leaf litter to escape. Both these sites are heavily disturbed with numerous human structures and shelters but both are situated within very mature, fairly open secondary forest near permanent



water. This is fairly typical habitat for *Aphaniotis fusca* and this species is probably more common across the area than my limited observations would suggest, probably a result of its cryptic colouration (Fig. 5.1).



**Figure 5.1:** An adult male *Aphaniotis fusca* at Lata Kekabu after having been disturbed from its usual resting position in the centre of a large leaf.

## **5.2 *Bronchocela cristatella***

This species seems to be widespread throughout my study region although not often observed. There are reports of this species being outcompeted by *C. versicolor* in Singapore, although I found this species at R2, perched on a trunk in mature rubber plantation (Fig. 5.2), amongst a dense population of *C. emma*. I also found this species near Gua Badak perched on a trunk in a disused rubber plantation where it also occurred alongside *C. emma*. This species was also found in the interior of Temenggor forest reserve sleeping in vegetation overhanging a logging road and was found in multiple visits to Ulu Yam, Selangor state an area of riparian and mature but open secondary forest. I also found a single individual in Penang National Park in a heavily vegetated forest clearing near the Western beaches. The extent of the ecological interactions between this species and *Calotes spp.* remain unstudied although both species are of similar size and habits. It's possible *Bronchocela cristatella* favours more heavily vegetated microhabitats than *Calotes*, where its vivid green colouration makes it more cryptic although it also shows a tendency towards open areas

and gaps within forests. It is an example of a potential canopy dwelling species going under-recorded due to my limitations.



**Figure 5.2:** An adult male *Bronchocela cristatella* found during surveys for *Calotes emma* in the rubber plantation R2. I also saw this species in a much older, disused rubber plantation near Lenggong but otherwise it was predominantly observed in forests.

### **5.3 *Bronchocela shenlong***

This recently described taxon was found at Parit Falls, near Tanah Rata in the montane cloud forest of the Cameron Highlands, Pahang State. It was distinguished from *B.cristatella* by the presence of a white labial stripe (Fig.5.3). The individual I found was a young juvenile sleeping on a fern at the edge of trail 4.



**Figure 5.3:** Juvenile *Bronchocela shenlong* found sleeping on a fern in the Cameron Highlands with labial stripe visible; the distinguishing feature between *B. cristatella* and this species.



#### 5.4 *Calotes emma*

*Calotes emma* is the most readily observed agamid in my study area, occupying all land use types surveyed (including at least one stand of trees in the middle of Gerik town itself) and was even present in closed canopy forest situations in Temenggor forest reserve although at lower observable densities than in plantations. Several individuals were also seen on the Gerik-Jeli highway and a gravid roadkilled specimen containing seven eggs was found on the A171 at the boundary between an old rubber plantation and secondary forest. Lizards were most often perched on tree trunks, especially in rubber plantations and forested habitats, but can also shift to a more terrestrial niche space as is seen in the oil palm plantations of the region (see Chapter 3). Here, males perch and display conspicuously on the main filaments of dead fronds that the plantation workers collect into elongated piles. Females are infrequently observed during the day but at night approximately equal numbers of both sexes sleep on the same frond piles or, more commonly, on epiphytic ferns growing on the 'trunks' of the oil palms. Several gravid females were seen each year and juveniles were also present although not observed as often as adults. Male *C. emma* in this region turn black and red on the head (Fig. 5.4) and gravid females also display some red colouration.



**Figure 5.4:** Sexual dimorphism in *Calotes emma*: (Left) Male *Calotes emma* from oil palm plantation displaying typical display colouration of a red head and black dorsum. (Right) Gravid female *C. emma* in typical oil palm microhabitat, showing the discarded frond filaments this species relies on in this land use.

I observed bipedal running in several specimens during thermal performance experiments (Fig. 5.5) and also in a single animal that escaped in a car park during data collection. This specimen leapt from a handler's grasp and proceeded to run extremely rapidly on its hindlimbs, with forelimbs held forwards, tail dragging behind and head held elevated at approximately 50-60° towards the tuft of nearby rushes it was originally captured in. This bipedal running behaviour has been described previously in *C. versicolor* (Annandale 1902) but not to my knowledge in *C. emma*. I hypothesise that the limbs being held forwards is useful in arboreal agamids for quickly switching interface between terrestrial running (to the nearest tree) and then quickly escaping up it by grasping with the already extended forelimbs (pers. obs.).



**Figure 5.5:** An example of the bipedal running posture of *Calotes emma*, cropped from footage of thermal performance experiments, taken from above the apparatus.

*Calotes* are one of the only agamid genera capable of making vocalisations (Manthey and Schuster 1996) and I observed this in *C. emma* several times during the thermal performance experiments. Vocalisations consisted of a brief, high pitched squeak, usually in one burst when the animal was restrained or captured quickly while it was active and always accompanied gaping and attempts to bite. One individual in particular repeatedly squeaked while held while some individuals never displayed the behaviour. I have observed this behaviour in captive *C. bachae* and *C. mystaceus* (although not in the ubiquitous *C. versicolor*) and several members of *Calotes* are referred to as "whistling lizards" in their various vernacular names and so it is likely a widespread but under-reported behaviour in this genus.

### **5.5 *Calotes versicolor***

It would appear that this 'cosmopolitan' species in Peninsular Malaysia is nearly absent from my immediate study area. A single male was found in 2016 on a

fencepost bordering an abandoned house near Gua Badak, Lenggong but no other individuals were seen here despite several return visits. *B. cristatella* and *C. emma* are present the other side of the nearby, small karst formation in an abandoned rubber plantation and it would be interesting to see if and how these species interact, and whether competitive interactions are inhibiting range overlap. Outside my study area *C. versicolor* is abundant throughout University of Nottingham's Malaysia Campus (Fig. 5.6), with several being observed engaging in male-male combat in the trees outside the School of Geography building and several more observed on the lawn and in the small trees in front of the Trent building and in nearby rubber and oil palm plantations. This species is also abundant on the University of Malaya's campus in Kuala Lumpur, where once frequent sightings of *B. cristatella* have become increasingly rare (Daicus Belabut, pers. comm.). It would appear that *C. versicolor* is even more well-adapted to living in proximity of humans than *C. emma* is. Both species occur sympatrically near Ipoh in Perak state and it would be interesting to conduct further research to study how they interact and partition resources at this boundary and whether it follows similar patterns to interactions in *Anolis* lizards e.g., Stuart *et al.* (2014).



**Figure 5.6:** Disturbance tolerance in *Calotes versicolor*: (Left) Adult male *Calotes versicolor* in an ornamental tree on the lawn near the Trent building, UoNM campus (Right) gravid female *C. versicolor* from an oil palm plantation at Bukit Broga, near UoNM campus.

## **5.6 *Draco***

This is a genus of slender, highly arboreal agamids with 41 species (Reptile Database, 2018) ranging throughout South-Southeast Asia. *Draco* are most notable for the patagial membranes, suspended by elongated ribs that they use to locomote between the tall, vertical trees they tend to perch on. Both sexes also possess gular flags (larger and brighter in males), analogous to the dewlaps of the *Anolis* lizards and smaller neck 'lappets' that are also used during gliding and display. During the course of this study I detected six species in the region and initially hoped to analyse the thermal tolerance of *Draco melanopogon* as a more forest-affiliated comparison species to *C. emma*. Not only did this genus prove wary and difficult to catch using our noosing methodology, the experimental protocols being used for *C. emma* were far too stressful for *Draco* and so all individuals were released unharmed. It would be extremely interesting to learn more about the thermal tolerances of *Draco* in light of land and climatic change however and low impact protocols should be developed in future research to examine this (for more detail and my suggestions on this, see Chapter 7).

## **5.7 *Draco abbreviatus***

I only observed this species along a fresh logging road leading into the mature hill forest near Kampung Air Ganda. Exclusively males were seen which tended to perch >3m up on very tall dipterocarps, especially dead trees. This is a very heavy-bodied species of gliding lizard with a grey dorsum, and black banded tail. The patagia are dark grey and gular flag is pale red/orange and large, with a rounded tip. I observed a male land on a tree with a second male. The two then circled each other performing press-ups with gular flags extended until one glided to another tree (Fig. 5.7). *D. abbreviatus* was only seen at this site and only after it was opened to vehicles in 2017, prior to this only *D. melanopogon* were seen here.





**Figure 5.7:** Intraspecific territorial interaction between male *Draco abbreviatus*, consisting of gular flag extensions until one of the lizards glided to a different tree.

### **5.8 *Draco fimbriatus***

This species of *Draco* seems to be fairly common in rubber plantations around the Gerik area, despite it being recording from relatively few sites in Peninsular Malaysia (Grismer, 2011). I observed males on two occasions at R2 in 2015 and again here in 2017 and also at R3. This is a fairly large, conspicuous species with very dark grey patagia which appear black in flight, a pale grey, speckled dorsum, spiny tail and bicolored yellow and white gular flag (Fig. 5.8). Individuals of this species perched relatively high on rubber tree trunks in R2 and R3 and also used smaller branches to some degree and were active at the same time as the more commonly observed *D. sumatranus*.



**Figure 5.8:** An adult male *Draco fimbriatus* found in R2 in 2015. Note the bicoloured yellow and white gular flag and lappets and the spiny tail. Not shown here are the extremely dark patagial membranes, a characteristic feature of this species while gliding.

### **5.9 *Draco formosus***

This species is fairly common in the forests around Gerik and was recorded at Lata Kekabu (Fig. 5.9), Temenggor Forest Reserve and Air Ganda and additionally a single male was seen in R2. Adults are slender and pale grey/greenish with few dark speckles on the dorsum and head. The patagia are diffuse red/grey and the gular flag widens from the red base to a rounded grey coloured section with enlarged scales. *Draco formosus* was most often seen in open areas of the forest during the day on both wide and narrow trees from approx 1m-5m high. Specimens were sometimes found in male-female pairs on a tree and in some parts of Lata Kekabu, in particular, the population of this species appears quite dense. A single individual was found in R2 in 2017 which suggests a capability of numerous *Draco* species to invade rubber plantations, in addition to the abundant *D. sumatranus* and occasional *D. fimbriatus* and *D. melanopogon* observed in this plantation type. Whether rubber plantations support these species or serve as population sinks from nearby forest remains to be seen.

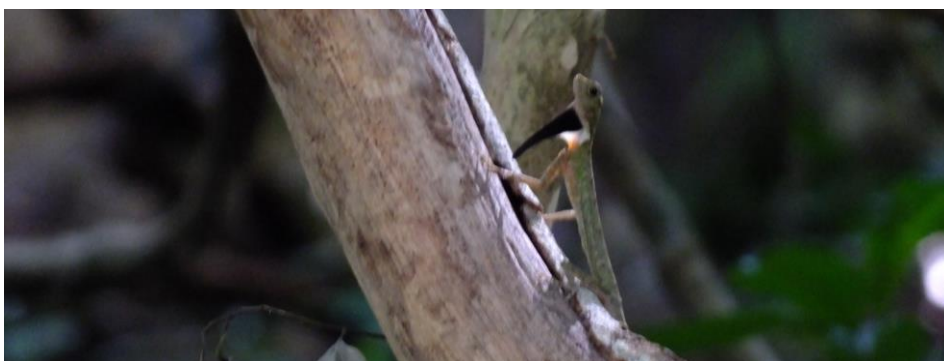




**Figure 5.9:** *Draco formosus* seen at Lata Kekabu in 2017. This species is abundant here, where it occupies tall riverside trees higher up the river, away from the buildings and car park.

### **5.10 *Draco melanopogon***

This is a very common *Draco* species in disturbed forest areas, often in patches of forest with more undergrowth than the habitat seemingly preferred by the larger *Draco spp.* I found numerous individuals of this species at all of my forest sites and additionally at R2 in 2015 and 2017. It is a small, slender *Draco sp.* with males possessing a long, narrow black gular flag (Fig. 5.10) and distinctive large eyes. Patagia are black with yellow speckling. My group noosed two male *D. melanopogon* at Air Ganda in 2016 before it was opened to logging.



**Figure 5.10:** Male *Draco melanopogon* seen in Temenggor Forest Reserve, note the black gular flag, one of the distinguishing features of this species.

### 5.11 *Draco quinquefasciatus*

This is a very large species of the genus, seemingly restricted to mature forest in my study area. I found this species at two sites on one occasion each; a mammal mineral lick in Temenggor Forest Reserve in 2015 and Lata Kekabu in 2016. At Temenggor a male-female pair was seen high on a fairly thin dipterocarp and an additional male was seen nearby in a low lying part of the forest, in close proximity to the lake. A juvenile was found in 2016 at Lata Kekabu in the open, concreted area before reaching the main rest areas or the closed canopy forest, on a tree with several *Draco sumatranus*. Adults are green with darker crossbands, a large, rounded head and a relatively small yellow-orange dewlap. Their patagia are vivid red and orange with contrasting black bands (Fig. 5.11). This species is fairly easily noosed however it was not found in high enough abundance to function as a study organism and was restricted to undisturbed areas of forest, offering no comparison to anthropogenic habitat.



**Figure 5.11:** An adult male *Draco quinquefasciatus* showing the brightly coloured patagial membranes of this species.

### **5.12 *Draco sumatranus***

This *Draco* species seems to be the most tolerant of human modified habitats of any of its congeners in my study area and was exclusively found in rubber plantations and highly degraded forest during this study, sometimes in considerable numbers. I found numerous individuals in both R2 and R3. *D. sumatranus* here used every part of the rubber trees apart from the canopy, where it existed in sympatry with *D. fimbriatus*, *D. formosus* and *D. melanopogon* although was observed in higher numbers than all other congeners combined. This species was also present at Lata Kekabu with several male-female pairs and juveniles seen on the trees between the car park and the main concreted entrance area. A male-female pair were observed displaying to each other in 2017 (Fig. 5.12): the male displayed the gular flag while circling the female performing 'press ups'. The female then arched her spine displayed her gular flag before running around to the other side of the trunk with limb extended below the body and then gliding to a nearby trunk. The male pursued her and glided to the same trunk. Both sexes are grey with a speckled dorsum and orange-brown patagia. Males have a bluish head and a pale yellow, pointed gular flag. *Draco sumatranus* seemed to be most active during the hottest periods of the day in April 2016 and I did not observe any thermoregulatory behaviour during my study period. I posit it does not actively bask but limits activity to the warmest parts of the day when basking becomes unnecessary to maintain an optimal  $T_b$ , similar to the conclusions reached on this species from Borneo by Mori and Hikida (1993).



**Figure 5.12:** Courting display by male *Draco sumatranus* (Lower trunk) involved extensions of the gular flag and rapid press-ups. The female (upper trunk) arched her back and displayed the patagial membranes before gliding to a different tree.

### **5.13 *Gonocephalus***

These are large, robust agamids endemic to Asian forests I had hoped to examine the thermal niches of as a contrast to *C. emma*. They are poorly studied, although from captive observations, seem to be shade-favouring thermoconformers with specific requirements as regards to high humidity and show an intolerance of rapid temperature changes. Unfortunately, this genus proved difficult to both observe and capture during this study and was only found in relatively undisturbed areas of forest near water. During the relatively dry year of 2016 only a single specimen was seen in four weeks of fieldwork. It is preferable to survey for the presence of these species at night when they are readily observed sleeping on thin exposed branches as a predator avoidance strategy and drop to the ground if these branches are even lightly shaken, however this removes any ability to record active body temperatures which would have been valuable data.



#### **5.14 *Gonocephalus abbotti***

A rare species of large forest agamid. I found a single female of this species in a single place near the Sungai Selaur, deep into Temenggor Forest Reserve as described by Grismer (2004). The lizard was near a small stream that leads into the Sg. Selaur itself, found sleeping at night on a small branch extending from the trunk of a dipterocarp approximately 1.5m high (Fig. 5.13). This species is likely restricted to relatively undisturbed hilly forest situations, at moderate altitudes near water and has a sparse distribution in Peninsular Malaysia (Grismer 2011) although this may be the result of under-recording in these inaccessible habitats.



**Figure 5.13:** A young *Gonocephalus abbotti* found sleeping in Temenggor Forest Reserve.

#### **5.15 *Gonocephalus bellii***

I found this species on one of the forest transects in Air Ganda forest and also at the water source for Kampung Air Ganda. Both sites are mature secondary hill forest however lizards were absent from seemingly similar habitat in many of my other survey sites. A male and female were found in close proximity at Air Ganda (Fig. 5.14), where the male was initially disturbed from a sleeping position by a team member brushing against the branch and after further searching the female was found on the same tree, sleeping horizontally amongst the foliage of an approximately 1.8m high, thin branch. The male was then located upon the return through the transect later in the night. Unusually for a *Gonocephalus sp.* the male-female pair at the Air Ganda transect were a

considerable distance from any permanent water sources. The male I found here had a distinctive bright blue eye which is not always present in *G. bellii* from other locations (pers. obs.). It remains to be understood whether this is a locality specific trait or a sign of maturity in *G. bellii* as some congeners uniformly display blue colouration of the eye (*G. liogaster*, Grismer 2011).



**Figure 5.14:** A pair of *Gonocephalus bellii* found within close proximity at Air Ganda, male displaying the blue iris present in some mature male *G. bellii*.

### **5.16 *Gonocephalus grandis***

This species was only found at Lata Kekabu during transects in 2017 but was found on every transect there. In addition, a single specimen was found in Royal Belum Reserve by Adam Algar during pilot work for this project in 2014 and I found numerous specimens at Ulu Yam near Kuala Lumpur in 2017 (Fig. 5.15). It is a riparian specialist and was always found within ~5m of the main river at each site, most often at night sleeping on thin stemmed vegetation overhanging the river although I also occasionally saw individuals of all age groups sleeping amongst the foliage on low branches of trees.

I observed all life stages including numerous adults of both sexes of a breeding size and many juveniles. I observed an adult male perched <2m in a bush on a steep slope that led into the river and a large female perched <1m on a thick tree less than 2m from the river's edge. The upper section of river before the reservoir at Lata Kekabu proved to be highly productive for this species. A prominent behaviour displayed in the sleeping position of these lizards is the draping down of the long and heavily banded tail from the, usually horizontal, sleeping perch and this was often the means by which lizards were located. The banded tail, which is widely seen in agamids (e.g., *C. emma*, *C. versicolor*,

*B. cristatella*, *G. bellii* all display similar patterning on the tail) could constitute batesian mimicry of the banded and primarily ophiophagous *Bungarus candidus* to deter nocturnal snake predators.



**Figure 5.15:** (Left) Male *Gonocephalus grandis* displaying dark tail banding (Right) Female found sleeping on a very thin sapling.

### **5.17 *Malayodracon robinsonii***

This species is endemic to montane forest in Peninsular Malaysia where it appears to occupy a similar niche to *Gonocephalus spp.* but is not closely related and was recently reclassified from that genus and placed within its own monotypic taxon (Denzer *et al.* 2015). This species was seen at Parit Falls, a recreation park near the town of Tanah Rata in the Cameron Highlands once in each of my 3 sessions of fieldwork. Each time it was seen perched between approximately 3-10m on moderately wide trees within 50m of a river (Fig. 5.16). It would make an interesting study organism for future research as its habitat already exists at the altitudinal limit of Peninsular Malaysia which represents a similar system to high elevation forests of Mexico which have already lost ectotherm diversity as a direct result of climate change (Sinervo *et al.* 2010).



**Figure 5.16:** Adult male *Malayodracon robinsonii* found in the Cameron Highlands in 2015.

### **5.18 *Pseudocalotes flavigula***

This cryptic species was seen on a single occasion at the same site as *M. robinsonii* and *B. shenlong* in 2016. A single adult individual was seen deep within the foliage of the undergrowth near the upper path at Parit Falls (Fig. 5.17). Like *M. robinsonii* it is also a high altitude endemic and would feasibly be at high risk from future climate change.





**Figure 5.17:** The single *Pseudocalotes flavigula* seen during my fieldwork. It was seen through the foliage, deep in vegetation in montane forest. When disturbed it rotated quickly around the horizontal stem it was perched on. The overall colouration is highly cryptic and it is likely under-recorded as a result of this.

### **5.19 *Leiolepis belliana***

*Leiolepis* are the only truly terrestrial agamid species in Peninsular Malaysia and are a basal outgroup on the acrodont phylogeny, not closely related to the Draconinae subfamily which constitute the previous species accounts. *Leiolepis* construct burrow systems which they retreat to at high speed when disturbed and maintain large flight initiation distances. They are examples of convergence with the North American iguanid genus *Dipsosaurus*, being omnivores that are active at high environmental temperatures, construct burrows and rely on speed to escape predators. I observed several individuals of both sexes near Beruas in Perak state during the 2017 field season. The animals were seen primarily in a grassy field near a large oil palm estate but several large males were also observed outside burrow systems in sand banks (Fig. 5.18) that had been constructed along the border of the oil palm system to separate it from the irrigation ditch. The animals were seen fairly late in the afternoon (circa 16:00) before a storm, UV index had dropped to 8.4,  $T_{\text{air}}$  was 35°C and  $T_{\text{surf}}$  exceeded 45°C. *L. belliana* has a limited distribution in Peninsular Malaysia as much of the ancestral coastal and riverine floodplain habitat has been developed on but this shows the ability of specific microhabitats within oil palm plantations to support a species that would otherwise not occupy this land use type and is something that should be encouraged in future plantations.



**Figure 5.18:** Adult male *Leiolepis belliana* observed outside its burrow by the roadside, East of Beruas, Perak state.

### **5.20 *Leiolepis triplida***

This parthenogenetic member of the genus was seen briefly on a single occasion near the rice paddies at the side of the BKE highway near Kulim in Southern Kedah state in 2016 but no photographs were taken. It is another example of a lizard that is tolerant of anthropogenic land uses and would be a good future candidate for comparative study across land use types with *L. belliana* which it perhaps outcompetes in disturbed habitats (Grismer 2011).

## 6 General conclusions

In Chapter 1 I present pessimistic results for reptiles under land use change. Transects in each of my focal habitats revealed forests to contain greater species richness of ectotherms overall, however results were not consistent across all sites or taxonomic groups. Amphibians were equally diverse in oil palm as they were in my forest sites, a result echoing that of Faruk *et al.* (2013). Similarly however most of the species found in oil palm were shared, cosmopolitan species that are also found in cities and gardens but some rarer, usually forest affiliated amphibian species were also found in oil palm e.g., *Limnonectes blythii*. This shows there is some hope for oil palm to support rarer species if it is managed specifically for biodiversity, at least in terms of amphibian diversity. Reptile diversity was lacking in both plantation types, with both sharing many of the same species although rubber shared more species with forests than oil palm did. Rubber was notable for containing more species of *Draco spp.* than the other habitat types although it was unclear whether it was functioning as a source or a population sink from nearby forests. Forests contained by far the most unique species of reptile, as expected from previous studies (Foster *et al.* 2011).

I went on to analyse various traits of both the climate of a species' range and traits of a species itself in an attempt to distinguish which of these variables, if any, predicted a species to be tolerant of oil palm plantation (i.e., those species recorded in it during my study). I found that only the precipitation of the driest quarter of the year (a proxy for drought tolerance) predicted presence in oil palm and only when reptiles and amphibian samples were pooled together (likely a result of my relatively small sample size for this type of analysis). However this result is consistent with previous findings, that species tolerant of drier climates can tolerate the drier environments and microhabitats that are created when oil palm replaces forests (Luskin and Potts 2011). This is important in terms of predicting which species will be displaced by further oil palm expansion and could be used to focus conservation efforts and perhaps to tailor mitigation efforts within oil palm matrices in terms of planting buffer zones and creating riparian areas.

In chapter 2 I focussed in on a single species of lizard to serve as a model species in order analyse differences between plantations and forests and how these compare in terms of the thermal suitability of microhabitats relevant to

this lizard. I showed that prior thermal differences recorded from plantations by other authors persist at the microhabitat scale. Plantations are almost always hotter than forests whatever microhabitat is being examined, although rubber was the hotter of the two plantations in my study, whereas oil palm is often the warmest of the three habitats reported in other research (Wanger *et al.* 2010, Meijide *et al.* 2018). This is likely due to the relative maturity of my study sites, all of which possessed nearly complete canopy cover, an important mediator of microhabitat temperature (Meijide *et al.* 2018).

I revealed *Calotes emma* to be a thermally tolerant lizard with critical thermal minima and maxima of similar values to New World anoline lizards: around 12°C and 41°C, respectively. The  $CT_{max}$  is fairly typical of lizards of this size however the thermal minimum is far lower than would ever be experienced in Peninsular Malaysia, even in the highlands where *C. emma* seems to be absent from (Pers. obs., Grismer 2011). This likely represents a shared ancestral trait from more northern populations of this species and the *Calotes* genus as a whole. Its optimum temperature fell just above 38°C on average, which is again similar to *Anolis* equivalents but was fairly high when compared to my environmental temperature traces, especially those for what is assumed to be its 'ancestral' habitat type i.e., forest edges and gaps.

Thermal suitability when measured in terms of time in  $T_{breadth}$  reflected this, showing fairly low suitability for *C. emma* in forest environments but much higher suitability in both plantation types, especially rubber. Under current climatic conditions no habitat was indicated to pose serious thermal stress on *C. emma*, with all spending less than a minute of each sampling day (6am-6pm) on average, above  $CT_{max}$ , likely only represented by a single model catching the sun for a few of the 15 minute sampling intervals and forest never exceeded  $CT_{max}$  or even came within 2°C of this threshold.

Future climatic conditions show differing predictions for *C. emma*'s future in my study region. Oil palm became slightly more suitable than rubber after a 3°C rise in air temperature, although the latter remained suitable for large periods of the day. These two habitats however began showing increasing evidence of thermal stress with more of the average sampling day falling within 2°C of  $CT_{max}$  or above it. Here *C. emma* would likely shift to a more bimodal activity pattern, to avoid the midday heat although our data suggest even the coolest microhabitats may become excessively warm at these times in

plantations. However forest gained relatively more thermal suitability for *C. emma* than either plantation type and still remained outside the thermal stress zone of  $CT_{max}-2^{\circ}C$ . This result would indicate the potential for *C. emma* to expand its current range further into forests, supporting Huey *et al.*'s (2009) viewpoint of the invasion hypothesis in tropical lizards. The result of this hypothesis is that under future climatic change forests will gain thermal suitability allowing open habitat species to invade forest interiors and displacing the more thermally restricted endemics, pushing them further into the interiors or to higher elevations to track their own thermal niches as they retreat. This is of great concern in SE Asia as land use change continues to replace the habitat of these latter, arguably more 'valuable' species at ever increasing rates with those land covers that favour the species that will soon replace them in their own habitats under climatic change.

I found in chapter 3 that oil palm plantations present lizards with novel structural habitats from the forests they replace. The historic rubber plantations in the region more closely resembled forests than oil palm did, offering similar arboreal perching opportunities to forest, albeit with limited options for perching terrestrially. Oil palm represents a much more derived and unique habitat with matrices of discarded frond piles offering ample terrestrial cover and perching opportunity, while the rows of palm trees themselves are quite different in terms of size and structure to the trunks of trees in rubber or forests. Forests tended to be diverse and structurally complex habitats with plenty of terrestrial and arboreal perches suitable for lizards.

*Calotes emma* seemed to utilise the wealth of both terrestrial and arboreal perching opportunities in forest edge habitat, although they did show a noted tendency towards arboreality, consistent with descriptions of this species' overall ecology by Grismer (2011) and were rather more difficult both to locate or catch from this habitat type than either plantation type, a potential difference in abundance or detectability by human surveyors. In rubber plantations *C. emma* acted as the populations in forest edge did albeit with even more pronounced arboreal tendencies. I recorded a single individual on the ground in this habitat which was moving at the time and so potentially foraging, chasing a competitor or moving between trunks. *C. emma* in oil palm showed a distinctive shift towards terrestriality, perching primarily on the discarded frond piles, a landscape feature unique to this plantation type, reflected by lower perch heights and narrower perch widths. From my

observations I strongly suspect the trunks in oil palm are not analogous perches to the trunks in forest or rubber, their blocky structure hindering lizard locomotion. I suspect *C. emma* is forced to shift from an arboreal ecology in forest edges to use these terrestrial perches in oil palm in lieu of suitable tree trunks to perch on. Thermal results in chapter 2 don't suggest any thermal benefits to perching on the frond piles over the palm trunks (if anything they are less thermally suitable for such a heat tolerant species) and the large number of primarily terrestrial *Eutropis multifasciata* (a similarly sized skink that is also diurnal and insectivorous Grismer 2011) observed in oil palm during the transects in chapter 3 would feasibly represent competition to *C. emma* in this novel, terrestrial portion of its niche space. Perhaps in the absence of the various other medium-sized terrestrial and arboreal insectivorous agamids and skinks these two species can seemingly co-occur in sympatry in the otherwise relatively uninhabited oil palm understory.

## 7 Concluding remarks and future directions

Overall, I found that reptile diversity was lower in plantations than in forest habitats, while plantations managed to support fairly high amphibian diversity although of altered species composition to forests. After focusing on a single reptile species that occupies forests and plantations I found it to have been thermally pre-adapted to the warmer conditions in plantations by occupying the warmest parts of forests. It was also capable of adjusting its behaviour to fit the novel structural niches introduced in plantations and displays some of the ecomorphological differences expected from these shifts.

I postulate that *Calotes emma* occupied only the warmest parts of the ancestral forests that would have at one time covered the north of Peninsular Malaysia and at this time, was likely a fairly rare species. When humans fragmented this forest cover and planted open, unsheltered plantations in their place this much warmer, novel landscape was likely well-suited to *C. emma*'s thermal ecology needs. It would be interesting to conduct further research to reconstruct historic land cover types in the region using sedimentary analyses. The population genetics of *C. emma*, *C. versicolor* and other reptiles and amphibians tolerant of occupying anthropogenic habitats in the region could then be analysed for expected patterns in gene flow and structure in an attempt to discover whether these species have historically followed human activities in Malaysia. Another, more fine-scale project, would be to examine the extent that elephants in the region act as habitat engineers for *C. emma* and other forest edge species. *C. emma* was difficult to find in the interior of forests during my research and the only individuals I caught were along the trails and mineral licks created in the forest by megafauna. This would involve extensive surveying in the forests in the wake of megafauna and would need to include some temporal and longer term monitoring data on the ages of paths and clearings but would prove an interesting example of a seldom studied inter-species interaction.

What is concerning from my study is that I failed to obtain data on the deep forest species e.g., *Gonocephalus spp.* that appear to be entirely absent from plantations and the highly morphologically specialised *Draco spp.* These species are already poorly understood in their native environments and their cryptic nature, inaccessible remaining habitat and apparently low population densities in the former case hinder further study. This is a subject I would particularly

like to focus on in future. Limited interactions with these deep forest species in captivity would suggest they are thermally sensitive and are especially sensitive to desiccation. Perhaps in a similar vein to the desiccation prone vipers of the same areas (Daltry *et al.* 1998) these species appear to hygroregulate as much as thermoregulate and so future studies should also measure water vapour pressure deficits and relative humidity and control for these parameters in laboratory experiments. They are poorly suited to the current thermal performance protocols commonly used on lizards as a result of this. They occupy isothermal habitats where less variation is experienced on a yearly basis than the temperature difference imposed by simply capturing them and bringing them into a non-airconditioned room in Northern Malaysia, before the thermal experiments even begin. While the risks are higher than with more robust species like the *C. emma* I worked with, the data that could be generated would be a valuable tool in understanding how and why these species fail to utilise plantations and contribute more to our scant knowledge of the general ecology of these unusual animals. Bringing these species into temperature and humidity controlled rooms, with spraying systems installed in their enclosures and direct human contact minimised would likely allow some limited experimentation and thermal tolerance estimations to be made. A similar protocol could be used for *Draco*, which react poorly to being handled but are similarly important targets for future research. Replacing the flat, horizontal track used for the majority of lizards in thermal performance research with a structure that more closely resembles the environment an arboreal agamid interacts with i.e., some form of artificial 'tree trunk' would allow much more meaningful comparisons of thermal performance. Thin wooden dowels are already used to test grip strength and running stability in *Anolis* and chameleons (Herrel *et al.* 2013, Donihue *et al.* 2018). Furthermore, adaptations could be made in coatings to mimic differing bark structures and rugosity and test whether the blocky structure of oil palm trunks do limit lizard locomotory performance as I suggested in Chapter 3.

The lizards of SE Asia are very poorly studied but their biology offers many interesting research opportunities. Their ecology, while similar to patterns seen in the well-studied reptile systems, e.g., *Anolis*, differs due to the increased age of the forests in SE Asia, offering increasingly more complex and subtle niche differences and the deeper divergences between the genera of the draconine subfamily. I often found several species of a genus within a few metres of each other and with no prior data on perch use, prey availability or



thermal preferences they would appear to be utilising exactly the same niche space. The main unknown factor is the canopy and what these lizards are doing once they ascend above the understorey and out of a human observer's view. Forests are truly three dimensional environments and are as diverse in their microhabitats and niches vertically as they are horizontally. Techniques need to be developed and refined to quantify reptile diversity above the forest floor, where potentially much of the biomass lies, unrecorded by simple line transects along the ground. Further efforts should also take into account aquatic and fossorial species as differences would appear to exist in these environments between the habitat types I examined. Improving and developing these two survey techniques could be incorporated into future species richness transect based methodologies, alongside already established techniques such as pitfall and live trapping and the recording of amphibian calls for later identification in the laboratory to gain much more comprehensive representations of the true diversity of reptile and amphibian species present in each of these habitats.

I would urge researchers to further solidify our understanding of the pathways species utilise to colonise plantations in SE Asia, which may allow us to predict and conserve those most at risk of future expansions. I would also implore continuing research and effort into improving the sustainability of oil palm and increasing the productivity of alternatives to this 'megacrop' that would appear to be here to stay for the foreseeable future. I do however recognise oil palm as a valuable source of employment and livelihoods for the people living nearby and would implore the media and NGOs to stress this aspect of the debate more heavily: conservation does have costs as well as benefits and it's up to researchers to identify where both of these may balance.

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