

Shifting correlates of lizard thermal biology through space -
The effect of climate and habitat on lizard body temperatures

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ABSTRACT

With climate warming, many lizard species are at risk of extinction. This is largely due to low dispersal abilities, which may prevent range shifts to more thermally suitable environments, and due to low capacities of species to physiologically adapt to warmer temperatures. Therefore, understanding relationships between body temperatures and environmental variables, and how they vary with habitat, is key to understanding the relative vulnerability of species to climate change.

Here I use regression to examine relationships between lizard body temperatures and environmental variables, including environmental temperature, temperature seasonality, precipitation, precipitation seasonality, potential evapotranspiration, leaf area index (LAI) and land surface temperature, at a global scale. These variables have been linked in local scale studies to lizard thermal biology. However, little research has been done to examine broadscale trends, or how environmental variables interact to influence body temperature. I then evaluate whether relationships vary with land cover (closed, semi-open and open vegetation, urban, and barren), preferred substrate (arboreal, saxicolous, psammophilous, ground, fossorial and semi-aquatic), activity time (nocturnal, diurnal) and insularity (island, mainland). Again, habitat effects on body temperature are yet to be considered beyond local scales.

Results show that accounting for habitat in global models significantly improves model fit. The global model explained 33.7% of the variation in body temperature, rising to 70.0% for closed vegetation and barren environments, and 82.1% for urban environments. The relationships between environmental variables and body temperature, and the relative contribution of variables to explaining body temperature, vary with land cover, substrate and insularity, suggesting that species within different habitats will face different threats as climate changes. For example, reduced canopy covers expected with climate change may increase the rate of warming for tropical forest species, indicative through negative correlations between LAI and body temperature amongst closed vegetation. In barren environments, increasing drought frequency and intensity may be the greatest threats, suggested through the strong influence of temperature seasonality and precipitation in the barren model. For diurnal species, LAI was the strongest contributor to body temperature, however LAI was absent from the nocturnal species model. This suggests that the effect of LAI on body temperature is related to shade availability, and suggests that LAI data can be used to capture the effects of shade availability on operative temperatures. Although previous studies have noted the importance of shade for thermoregulation, no attempts have

been made to incorporate remotely sensed data such as LAI as a measure of shade availability.

Incorporating climate and habitat data into models, including LAI, will allow for improved predictions of lizard body temperatures at global scales. Extending models to include future climates and shade levels under different land cover and climate change scenarios may therefore provide more accurate predictions about which species and habitats are most vulnerable to climate change.

Contents

Abstract		1
1	Introduction	5
1.1	The threat of global warming	5
1.1.2	Global scale patterns	6
1.1.3	Climate change and habitat	8
1.2	Body temperature and climate	10
1.3	Body temperature and habitat	12
1.4	Body temperature and vegetation	12
1.5	Body temperature and substrate	13
1.6	Body temperature and insularity	16
1.7	Study aims	17
2	Methodology	19
2.1	Data collection	19
2.1.1	Lizard data	19
2.1.2	Environmental data	21
2.2	Data processing and analysis	23
2.3	Methodological limitations	25
3	Results	27
3.1	Global	27
3.2	Differences with land cover	33
3.3	Differences with activity time	37
3.4	Differences with substrate	37
3.5	Differences with insularity	39
4	Discussion	41
4.1	Evaluation of the global model	41
4.2	Global scale environmental correlations with T_b , and the effects of habitat	42
4.3	Variability in T_b with activity time	47
4.4	The effect of substrate on T_b and model predictions	47
4.5	Model predictions with insularity	59
5	Conclusion	51
6	Acknowledgements	51
7	References	52
Appendices		
Appendix A	Global 1 km consensus land cover dataset – Satellite imagery details	64

Appendix B	Global 1 km consensus land cover dataset – Land cover classes	65
Appendix C	Collinearity of main effect variables	66
Appendix D	Sources, acquisition dates and spatial resolution of data	68
Appendix E	Temperature and precipitation PCA plots	70
Appendix F	Table F1: Pearson’s correlations BioClim and body temperature	71
	Table F2: Collinearity of BioClim variables	72
Appendix G	Table G1: Summary of lizard body temperatures	75
	Table G2: Kruskal-Wallis – comparisons of mean body temperatures with land cover and substrate.	76
	Figure G1: Scatterplots - body temperature ~ environmental temperature relationships with land cover, activity time, substrate and insularity	77
	Table G3: ANCOVA - comparison of body temperature ~ environmental temperature slopes; land cover, activity time, substrate, insularity	78
Appendix H	Table H1: Linear regressions - body temperature and environmental variable relationships, Global	79
	Table H2 Linear regressions - body temperature and environmental variable relationships with land cover	80
	Table H3 Linear regressions - body temperature and environmental variable relationships with activity time	82
	Table H4: Linear regressions - body temperature and environmental variable relationships, with substrate	83
	Table H5: Linear regressions - body temperature and environmental variable relationships with insularity	86
Appendix I	OLS, GLS and PGLS multiple regression models for global (Table I1), land cover (Table I2-I6), activity time (Table I7-I8), substrate (Table I9-I12) and insularity (Table I13-I14).	87
Appendix J	Table J1: Spatial autocorrelations, OLS models – Moran’s I correlations	97
	Table J2: Phylogenetic signal, OLS models – Blomberg’s K and Pagel’s Lambda	98
Appendix K	OLS models with land cover, climate data only	99
Appendix L	OLS global model, reduced data.	103

Figures

Figure 1	Global map of lizard locality points	20
Figure 2	Box plots – Summary of body temperature data	28
Figure 3	Scatterplots – global scale correlations between body temperature and environmental variables	31
Figure 4	Scatterplots – correlations between T_b and LAI with land cover	35
Figure 5	Scatterplots – correlations between T_b and T_{env} with land cover	36

Tables

Table 1	Lizard localities globally and with land cover	20
Table 2	OLS multiple regression model summaries	29
Table 3	OLS multiple regression model summaries with land cover – all environmental data and climate data only	32

1. INTRODUCTION

1.1 The threat of global warming

Ectotherms, such as lizards, are dependent on the external environment for heat (Hare and Cree, 2010). Environmental temperatures affect all aspects of life history, from embryonic development and incubation periods, phenology, to growth and survivorship (Shine et al. 2002; Hare and Cree, 2010). Most aspects of ectotherm ecology and physiology, such as metabolism, foraging and locomotion are also strongly temperature dependent (Seebacher and Grigg, 1997; Kearney et al. 2009; Meiri et al. 2013), with performance peaking at an optimum body temperature (T_{opt}). Below and above optimum body temperature, lizard performance drops until temperatures reach critical thermal limits, beyond which lizards lose the ability to function, e.g. lose righting ability. Although the decline in performance is gradual as body temperature drops to a thermal minimum (CT_{min}), performance declines rapidly as body temperature rises to a thermal maximum (CT_{max}). Body temperatures approaching CT_{max} as a result of rising environmental temperatures are a potential key threat to lizard survival.

As lizard performance is strongly temperature dependent, changing environmental temperatures—global warming—are putting many species at the risk of extinction (Sinervo et al. 2010). It is plausible that, given time, species may adjust to their new environmental conditions. This may occur through genetic evolution, phenotypic plasticity involving behavioural, morphological and physiological adaptations (Chevin et al. 2010), or through shifting of geographical ranges to track more suitable thermal environments. (Chevin et al. 2010; Sinervo et al. 2010; Muñoz et al. 2014). However, many terrestrial ectotherms have low dispersal abilities, and are therefore unlikely to shift their geographical ranges (Hare and Cree, 2010). The rapid rate of environmental warming may have also exceeded the capacity of species to adapt to change through developmental or genetic mechanisms (Chevin et al. 2010). For example, species may be unable to physiologically adapt through increasing their CT_{max} at a fast enough rate to keep pace with warming environmental temperatures (Muñoz et al. 2014). Thus, body temperatures will likely rise and approach CT_{max} . This is most likely to be the case for species whose climatic preferences are already close to their upper thermal limits (Arajo et al. 2013). These species are unlikely to evolve tolerances to higher temperatures, as physiological boundaries constrain their evolution, hence could be the most greatly affected by climate warming (Arajo et al. 2013).

Warming environmental temperatures will likely cause lizards to use refuges (e.g. shade) more extensively, in order to maintain body temperatures within their preferred range. This may limit activity time, and reduce opportunities for foraging, mating and population growth (Logan et al. 2013). Therefore global warming may lead to demographic collapse and extinctions (Sinervo et al. 2010).

1.1.2 Global scale patterns

Tropical ectotherms are particularly vulnerable to climate change. This has been attributed to a number of factors. Firstly, tropical ectotherms already live in environments where operative temperatures, i.e. temperatures that lizards would reach if they did not regulate their body temperature, are near or above T_{opt} for most of the year (Tewksbury et al. 2008; Gunderson and Leal, 2012). Secondly, many tropical species are intolerant of high temperatures (Tewksbury et al. 2008; Huey et al. 2009). CT_{max} is highly conserved with latitude (Ghalambor et al. 2006; Deutsch et al 2008; Sunday et al. 2014). Therefore tropical species are no more tolerant to increasing temperatures than temperate species, despite being adapted to warmer environments (Tewksbury et al. 2008). Thirdly, tropical species tend to have limited acclimation capacities compared to temperate species, as they are more thermally specialised having evolved in warmer, aseasonal environments (Janzen, 1967). Narrow thermal tolerance breadths of tropical species may also mean low genetic variation, and hence limited potential for evolution (Grigg and Buckley, 2013). Therefore, despite lower rates of warming in the tropics, body temperatures are predicted to reach critical levels faster, resulting in extinctions (Deutsch et al. 2008). This is concerning, as ectotherm biodiversity is greatest in the tropics, and many tropical lizards are occupying disappearing climatic regimes (Deutsch et al. 2008; Huey et al. 2009).

Overall, climate warming may be advantageous for temperate lizard species. Warmer temperatures will enable increased opportunities to bask. This will allow species to spend more time at their optimal body temperatures (Kearney et al. 2009; Hare and Cree, 2010), and will also increase growth rates and the duration of activity times (Huey et al. 2009). Warming temperatures could also result in earlier births, enabling longer growth periods before winter (Hare and Cree, 2010). However, the benefits of increased temperatures for temperate species may be offset by other climatic changes associated with warming. For example, increased cloud cover may prevent species from reaching optimal body temperatures, as basking ability is reduced (Hare and Cree, 2010). Shifts in vegetation cover

and humidity in temperate regions will also affect species responses to warming (Hare and Cree, 2010).

For montane species, lizard populations at high altitudes may benefit from warming temperatures, as environmental temperatures will match lizard preferred body temperature more closely. This will reduce the need to regulate body temperatures (Muñoz et al. 2014). However, as with latitude, maximum heat tolerance limits of species vary little with elevation (Sunday et al. 2014; Muñoz et al. 2014). Hence, as temperatures warm further, habitat will become thermally unsuitable. Therefore climate change is likely to increase extinctions for species at high elevations as the thermal quality of the environment declines (Pincheira-Donoso et al. 2013).

Viviparous lizards, which are largely restricted to cold environments, are particularly threatened by warming temperatures (Pincheira-Donoso et al. 2013). *Liolaemus* lizards, found in the colder environments of South America, including the Andes Mountain range, are a key example. As temperatures warm, the availability of cold environments for viviparous species will decline, significantly reducing their distribution (Pincheira-Donoso et al. 2013). With the current rate of warming, nearly half of the habitat of *Liolaemus* may become unsuitable in the next 50 years (Pincheira-Donoso et al. 2013). It is believed that viviparity evolved from oviparity as an evolutionary response to enable lizards to survive in cold climates. This evolutionary process will unlikely be reversed, and as viviparity is less viable in warmer climates, species will likely remain adaptively confined to colder climates. Hence viviparous species will be forced to higher elevations and latitudes, with increased risks of extinction (Pincheira-Donoso et al. 2013).

Species previously constrained to low elevations by heat tolerances may also expand to higher elevations as temperatures warm (Sinervo et al. 2010). This could be the case for oviparous species, which are constrained to lower elevations due to their minimum temperature requirements for nesting (Shine et al. 2002). Movement of species to higher elevations will lead to increased competition, and potentially competitive exclusion, which will further increase extinction risks (Sinervo et al. 2010). Although oviparity is more successful in warmer climates than viviparity, oviparous species also face challenges with climate change. For example, warmer nest temperatures will likely influence development rates and incubation periods, and may also shift the sex ratios to produce more female hatchlings (Lewis-Winokur and Winokur, 1995; Shine et al. 1997). This suggests that climate warming could have influences on population dynamics of oviparous species, and potentially also increase the risk of extinction.

1.1.3 Climate change and habitat

Understanding relationships between thermal biology and environmental conditions, and how relationships vary with habitat, is key to understanding the relative vulnerability of species to climate change (Sunday et al. 2011; 2014). Thermal biology and habitat type are interrelated, as habitats differ in mean climatic conditions, climatic variability and availability of microhabitats and thermal microclimates (Adolph, 1990; Shine et al. 2002; Ibanez et al. 2013). Habitat therefore influences the susceptibility of individuals to warming (Sunday et al. 2014). For example, species in habitats with greater climatic variability generally have broader thermal tolerances; hence can withstand more extreme temperatures (Sunday et al. 2011). The ability of species to modify their behaviour in response to warming, such as switching activity time and selecting cool microhabitats, and the associated costs such as altered predation risks and foraging opportunities, also vary with habitat (Kearney et al. 2009; Huey et al. 2009). Therefore habitat may be more important than physiological tolerances for warming alone in enabling species to survive climate change (Sunday et al. 2014).

Tropical forest species are particularly vulnerable to warming. This is because they live in cool, shaded environments, and are therefore not well adapted to higher temperatures that result from climate change (Huey et al. 2009). For many forest species, thermal tolerance limits are little above the lowest operative temperatures possible in deep shade (Sunday et al. 2014). Therefore species will likely see decreases in performance as operative temperatures rise (Tewksbury et al. 2008). This is largely unavoidable, as forest lizards already occupy the coolest habitat in the tropics, and opportunities for behaviourally avoiding increasing temperatures are limited (Deutsch et al. 2008; Logan et al. 2013). Within Costa Rica, heat stress from warming summer temperatures has been affecting forest lizards for decades, and as a result populations there are already in decline (Whitfield et al. 2007). As well as heat stress, it is thought that forest lizards will be subjected to biotic pressures as warm adapted, open habitat species invade the forests (Huey et al. 2012). It is predicted that warming temperatures will make tropical forests increasingly suitable for open habitat species (Huey et al. 2009). Forest lizards will therefore experience increased predation and competition, as open habitat species can forage in the forests for longer periods of time before body temperatures cool and they have to return to open habitats to bask (Vitt et al. 1998). Global analysis has shown that most ectotherms are incapable of surviving in open habitats due to thermal tolerance limits, and must have access to cooler refugia to survive. This is critical for lowland tropical species, which are dependent on cool microsites to avoid stress (Sunday et al. 2014). Therefore, open habitat species may permanently remain in the forests as warming continues, and hence displace tropical forest species (Huey et al. 2009).

Climate warming will also affect vegetation productivity and growth. This may cause canopies to open, changing the canopy structure (Huey et al. 2012). Increasing canopy gaps will increase temperatures associated with more solar radiation, and will also decrease humidity and increase wind speeds. This will likely increase the sensitivity of lizards to desiccation, and thereby increase extinction risks (Huey et al. 2009). This effect may be exacerbated if deforestation and habitat fragmentation act in combination with climate change to open forest canopies (Feeley et al. 2007; Whitfield et al. 2007; Munguia-Vega et al. 2013). Changes in canopy structure and forest macroclimates will also alter the suitability of microhabitats within the forest. This may reduce the ability of forest species to use microhabitats and their associated microclimates to buffer against rising temperatures (Adolph, 1990).

Although tropical forest species as a whole are under threat, there are likely to be fine scale spatial variations in their vulnerability related to forest type (Gunderson and Leal, 2012). Therefore, different populations of a single species may have different vulnerabilities to warming. For example, for *Anolis cristatellus* in Puerto Rico, populations living within the xeric forests are most likely to suffer as the habitat becomes too warm. However, for the mesic forests, the thermal suitability of the habitat is less likely to change, and populations here may even experience physiological benefits, such as increased physiological performance capacity (Gunderson and Leal, 2012). Overall, species living in cool montane forests should initially benefit from warming (Huey et al. 2009). Lowland species may also benefit during the cool seasons when operative and body temperatures are slightly lower (Huey et al. 2009). Such local scale variation complicates global trends.

Species within desert habitats are also highly vulnerable to climate warming. Due to high temperatures and extended droughts, ectotherms living within desert habitats may already have body temperatures at or near their physiological limits (Barrows, 2011). Barrows (2011) used niche modeling to assess how habitat suitability will be affected by climate change for 2 species of desert tortoise. Results show that under moderate predictions of climate change, 2°C warming and 50 mm reduction in precipitation, the suitability of habitat in the Sonoran and Mojave deserts will decrease by 88% and 66% respectively. This study highlights the susceptibility of desert ectotherms to climate change. Greater than average levels of warming are also expected in desert regions, as well as large reductions in precipitation and cloud cover (Clusella-Trullas et al. 2011). Therefore, increased drought frequencies and intensities are predicted for desert environments. These are thought to be the greatest challenges for desert species, as droughts minimize resources, and hence limit food and water availability (Bell, 1979; MacMahon, 1979; Parmesan et al. 2000).

Analysis of local population extinction records from North and South America, Africa, Europe and Australasia showed that, as of 2009, lizard extinctions had been greatest in tropical forest and desert habitats (Sinervo et al. 2010). This is consistent with the hypothesis that closed forest and desert species are particularly vulnerable to climate warming.

1.2 Body temperature and climate

Strong positive correlations between body temperature and air temperature are often reported at local scales (Ballinger et al. 1970; Al-Sadoon et al. 1998; Andrews, 1998; 2008; Hare and Cree, 2010). However, global trends have little been addressed. Meiri et al. (2013) were the first to address the global relationship between body temperature and air temperature in lizards. For 861 species, body temperatures obtained from various literature sources were averaged, and correlated with mean annual temperatures (BioClim, Hijmans et al. 2005), averaged across each species' range. Alone, body temperature and mean annual temperature were uncorrelated, however, a weak, positive correlation emerged after accounting for phylogenetic relationships ($R^2 = 0.03$, $P < 0.0001$). When Meiri et al (2013) considered additional predictors, the best model explained 57.1% of the variation in body temperature, and included mean annual temperature, phylogeny by family affiliation, activity time, and insularity. Exclusion of annual temperature from this model reduced the percentage of variation explained to 53.9%. However, averaging annual temperatures and body temperatures across a species' range smooths out spatial heterogeneity associated with latitude, altitude, habitat and climate (Huey and Webster, 1976), which could influence the correlations. Studying body temperatures in terms of only mean air temperatures may also have little physiological relevance, as mean temperatures can be poor indicators of thermal conditions actually experienced by organisms (Huey et al. 2012; Buckley et al. 2013).

Clusella-Trullas et al. (2011) correlated 19 climatic variables (BioClim, Hijmans et al. 2005), including mean annual temperature, mean annual precipitation and indicators of temperature and precipitation variability against preferred body temperature (T_{pref}) and CT_{max} at a global scale. T_{pref} refers to a body temperature that lizards aim to maintain to maximise performance, and is measured in a lab under a thermal gradient (Raske et al. 2012; Grigg and Buckley, 2013). T_{pref} is generally higher than body temperature, however, the scaling of this relationship is habitat dependent (Huey and Slatkin, 1976). Clusells-Trullas et al. (2011) found that precipitation, specifically precipitation of the driest month, and temperature variability, specifically diurnal temperature range, were the strongest predictors of T_{pref} and

CT_{max} respectively. Mean annual temperature, as used by Meiri et al. (2013), was less strongly correlated to T_{pref} and CT_{max} . However, correlations between BioClim variables and body temperature were not investigated.

Precipitation of the driest month correlated negatively to T_{pref} at a global scale (Clusella-Trullas et al. 2011). To an extent, precipitation is hypothesized to correlate negatively with body temperature, as high precipitation reduces the availability of optimal operative temperatures in a habitat, and therefore constrains individuals to sub-optimal conditions (Clusella-Trullas et al. 2011). The capacity for microhabitats to buffer air temperatures and further reduce body temperature is also directly linked to rainfall, as greater moisture availability increases heat capacities (Scheffers et al. 2014). Low body temperatures may therefore be expected in tropical forests and some temperate habitats related to higher rainfall. However, the relationship between precipitation and body temperature has been little studied (but see Kingsbury, 1994 and Clusella-Trullas et al. 2009). Precipitation also affects lizard performance through its effect on resource availability, and hence energy intake, and on hydration status. If precipitation is too low, lizards may select lower body temperatures to minimize dehydration risks. Low body temperatures may also be selected in resource poor areas, where low precipitation has reduced food and water availability, in order to minimize metabolic costs (Clusella-Trullas et al. 2011). Precipitation variability has been shown to affect lizard performance across latitudes at a global scale (Bonebrake and Mastandrea, 2010). Diurnal temperature range was positively correlated to CT_{max} (Clusella-Trullas et al. 2011). As with temperature means, temperature variability causes strong selection on thermal physiology (Huey et al. 2009; Deutsch et al. 2008; Sunday et al. 2011), and is therefore a strong predictor of warming tolerances and thermal safety margins. For example, seasonal temperature variation is believed to have an adaptive influence on the range of temperatures species can physiologically tolerate with latitude (Sunday et al. 2011). Lower seasonal temperature variation in the tropics is therefore a potential explanation for narrower thermal tolerance breadths in tropical species compared with higher latitude species (Sunday et al. 2011). The link between latitude and thermal tolerance breadth is highlighted through comparing data from Northern and Southern latitudes (Sunday et al. 2011). In the Northern Hemisphere, temperature variability increases with latitude at a greater rate compared to the Southern Hemisphere. This is mirrored by a greater rate of increase in thermal tolerance breadths with latitude in the Northern Hemisphere compared to in Southern Hemisphere species (Sunday et al. 2011).

For various ectotherms, including lizards, insects, turtles and frogs, warming tolerances and acclimatization capacities have been shown to increase with seasonal temperature variability

of habitats (Deutsch et al. 2008; Tewkesbury et al. 2008; Huey et al. 2009; Sunday et al. 2011; Buckley et al. 2013). As temperature seasonality affects physiological sensitivity, strong correlations between temperature seasonality and body temperature may also exist. However, this is yet to be investigated.

1.3 Body temperature and habitat

Research into the effect of habitat type on lizard body temperatures has predominantly focused at local scales (Huey and Webster, 1976; Gunderson and Leal, 2012; Logan et al. 2013). For example, body temperatures of forest populations of *Anolis* on the Bay Islands of Honduras were found to be lower and less variable than populations in open habitat (Logan et al. 2013). On Puerto Rico, Gunderson and Leal (2012) showed that body temperatures of *Anolis cristatellus* were on average 3.5°C lower in the mesic forests compared to xeric forests. However, work has thus far not been extended to examine global trends in body temperatures related to habitat type. As different habitats vary in their availability and variability of microhabitats and microclimates, habitat also affects the ability of individuals to regulate their body temperatures. Within spatially thermally variable habitats, individuals are more readily able to thermoregulate to maintain their body temperature within an optimal range to maximise performance (Bashey and Dunham, 1997; Bakken 1989). Therefore body temperatures are more likely to diverge from ambient conditions (Gunderson and Leal, 2012). In contrast, in thermally invariable environments such as closed forests, opportunities for thermoregulation are more limited (Huey and Slatkin, 1976). Hence species shift towards thermoconformity and body temperatures more closely track environmental conditions. Again, analysis of how habitat type relates to the degree of thermoregulation by individuals has not been examined beyond local scale studies.

1.4 Body temperature and vegetation

Ectotherm thermoregulation occurs through behavioural mechanisms. These include movement between habitat types (Huey et al. 2009), and shuttling between sunny and shaded patches of a habitat to exploit various microclimates (Al-Sadoon et al. 1998). Vegetation structure and quantity in a habitat are therefore important factors in influencing body temperatures, as they affect shade availability, the intensity of solar radiation to which lizards are exposed, the availability of microhabitats, and the costs of exploiting them for thermoregulation (Shine et al. 2002; Kearney et al. 2009). Increasing vegetation cover should

correlate negatively with body temperature. This is because increasing vegetation increases shade levels, and also increases the distance between sunny and shaded patches, raising the cost of thermoregulation (Gunderson and Leal, 2012). Optimal densities of vegetation not only provide optimum shade levels, but also minimize the distance lizards have to shuttle between sun and shaded patches. This enables lizards to more actively thermoregulate without experiencing trade offs due to costs associated with time and energy expenditure required to move between patches (Huey and Slatkin, 1976; Huey and Webster, 1976; Scheers and Van Damme, 2002).

1.5 Body temperature and substrate

Habitat type affects the types of substrate that lizards can access. Substrates may include ground, rocks, tree branches and water. Within forests, lizards would be expected to be (semi-) arboreal or completely ground dwelling, whereas within barren environments, lizards would be expected to have a greater degree of fossoriality (Porter et al. 1973). Preferred substrate is a strong determinant of available operative temperatures, the quality of the thermal environment, and also microclimatic conditions (Bakken, 1989; Adolph, 1990; Scheers and Van Damme, 2002). Substrate therefore affects thermoregulatory opportunities and hence influences body temperatures.

Fossorial, semi-aquatic and arboreal lizards have been shown to have lower body temperatures relative to ground dwelling species (Bakken, 1989; Shine and Madsen, 1996; López et al. 1998). However, little is known about the relative importance of different substrates in determining body temperatures or influencing thermoregulation (Bakken, 1989). Scheers and Van Damme (2002) aimed to assess how the thermal quality of substrate affects body temperature and thermoregulatory behaviour. The study compared *Lacerta oxycephala*, a saxicolous species found on rocks and stonewalls, to *Podacris meliscellensis*, a ground dwelling species found amongst vegetation, on the islands of Vis, Croatia. Both species were identified to be effective thermoregulators. However, body temperatures of *L. oxycephala* were lower than *P. meliscellensis*, as *L. oxycephala* occupied substrates of lower thermal quality. This highlights that even at a microgeographical scale, choice of substrate can significantly alter body temperatures. However, as Scheers and Van Damme (2002) pointed out, further work is needed to identify general trends in how substrate and its thermal quality affects lizard thermal biology.

For ground dwelling lizards, body temperatures are generally strongly correlated to land surface temperatures (LST), at least at local scales. For example, Waldschmidt and Tracy (1983) correlated surface temperatures of rocky substrates with body temperatures of *Uta stansburiana* in Colorado. Results showed that when lizards adopted the prostrate posture, body temperatures were nearly identical to the temperature of the substrate beneath them. Similar observations have been made for psammophilous (sand-loving) species in desert environments. For example, in the Arabian sand dunes, *Scincus mitranus* used thigmothermy (heat exchange by conduction) as a dominant method of thermoregulation; scraping away hot layers of sand and pressing their bodies against the cooler layers underneath to reduce body temperatures (Al-Sadoon et al. 1998). Strong correlations between land surface temperatures and body temperatures are a result of conductive heat exchange between the body and ground surface, and are also due to convection via the boundary layer (Heath, 1965; Norris, 1967). It is also thought that ground dwelling species absorb similar amounts of solar radiation to the ground surface, and also experience similar air temperatures, contributing to the strong correlation (Bakken, 1989).

Muth (1977) argued that for most lizards under most conditions, conduction is of minor importance in determining body temperatures. Hence radiation and convective coupling are the strongest determinants of correlations between LST and body temperature (Belluire and Carrascal, 2002). However, this may not be the case for saxicolous species, which are dependent upon conduction from the rock surface to maintain high body temperatures for activity. This is particularly true during morning periods, when absorption of solar radiation alone is insufficient to raise body temperatures (Al-Johany, 1995). Conduction is also a dominant heat transfer mechanism for fossorial lizards; and so body temperatures of fossorial species are strongly correlated to substrate temperatures (Martin et al. 1990; Gil et al, 1993; López et al. 1998; 2002). For fossorial species, moving vertically in the substrate to select warmer and colder layers at different times of day is a dominant thermoregulatory mechanism, and likely results in the greatest changes in body temperature (Meiri et al. 2013). Temperatures of upper soil layers can be highly variable, dependent upon soil properties, the degree of insolation and, in particular, meteorological conditions (López et al. 1998). Therefore, through its effect on substrate temperature, climate can indirectly affect body temperatures of fossorial species (López et al. 1998). Within deserts, soil temperatures 0.6 m below the surface can approximately equal mean monthly air temperatures (Porter et al. 1973). Therefore, body temperatures of fossorial lizards at shallow depths may be correlated with ambient temperatures. The strengths of correlations are expected to reduce as lizards retreat to greater depths and soil layers get cooler, resulting in cooler body temperatures.

Generally, fossorial species have lower body temperatures than surface dwelling lizards (Avery, 1982; López et al. 1998). This is because fossorial lizards can't readily bask to raise their body temperatures, and temperatures within burrows are generally cooler than surface air temperatures (Meiri et al. 2013). Soil type may also hinder thermoregulation through thigmothermy if the soil has a shallow thermal gradient (López et al. 1998). Therefore, subterranean conditions are thought to encourage thermoconformism (Martin et al. 1990). However, as observations under natural conditions are difficult, the thermal ecology of fossorial lizards is poorly known (López et al. 2002). Additionally, studies appear to have been limited to localized observations of Amphisbaenian worm lizards (Martin et al. 1990; Gil et al. 1993; Hailey and Elliot, 1995; López et al. 1998; López et al. 2002), with no analysis of broader scale trends (but see Meiri et al. 2013).

Arboreal lizards are also expected to have low body temperatures relative to ground dwelling species. This could be related to a combination of factors, including the thermal quality of the substrate, microhabitats, microclimates, and thermoregulatory mechanisms. Arboreal lizards have access to a range of cool microhabitats, including tree hole phytotelmata and arboreal epiphytes (Watson and Gough, 2012). These microhabitats reduce both air and substrate temperatures relative to the ground, resulting in a cooler thermal environment and lower body temperatures. Postural adjustments on tree branches also expose lizards to greater changes in operative temperatures compared to similar adjustments on the ground. This is related to large changes in air temperatures and wind speeds that can occur within only a few mm of a branch surface (Nobel, 1974). This may further explain why arboreal species have lower body temperatures compared to ground dwelling species. However, body temperatures are also expected to be highly variable within individual trees and bushes, related to variability in microclimates and thermal qualities of perches. For example, increasing perch height results in lower air temperatures, higher wind speeds and increased shade (Bakken, 1989). Therefore body temperatures are generally warmer closer to the ground where operative temperatures are higher (Adolph, 1990). Operative temperatures also increase with increasing perch diameter, decreasing heat capacity of perches, and increasing absorption of solar radiation (Bakken, 1989). Densely shaded perches can reduce average operative temperatures by up to 18°C compared to sunlit perches. Therefore, movement from sunlit to shaded perches within an individual tree, or selecting perches of varying thermal quality can have a large effect on body temperature (Bakken, 1989). Although body temperatures of arboreal species are expected to be low, it is hypothesized that arboreal species are effective thermoregulators due to high variability in microclimates (Huey and Slatkin, 1976).

Semi-aquatic lizards also have low body temperatures compared to ground dwelling species, as the high thermal conductivity and heat capacity of water results in a cooler medium than air (Angiletta, 2009). Low thermal heterogeneity also limits opportunities for behavioural thermoregulation; hence body temperatures are expected to closely follow water temperature as species shift to thermoconformity (Rummary et al. 1995). Although aquatic lizards are generally thought to be thermoconformers (Shine and Madsen, 1996; Angiletta, 2009), some species also display thermoregulatory strategies (Seebacher and Grigg, 1997). For example, both thermoconformity and thermoregulatory strategies were observed in a population of *Crocodylus johnstoni* (Seebacher and Grigg, 1997). Individuals either remained in the water throughout the day so that body temperature always approximated water temperature, or alternated between basking on land and cooling in water, so that body temperature formed a plateau above water temperatures. However, preferred body temperatures of thermoregulators paralleled seasonal changes in water temperatures; suggesting that even amongst thermoregulators, body temperatures of aquatic species will largely track environmental conditions.

1.6 Body temperature and insularity

Insularity may significantly affect lizard body temperatures and thermoregulatory strategies as islands differ substantially in environmental conditions compared to the mainland (Weigelt et al. 2013). For example, islands are generally more thermally benign due to buffering of temperatures by oceans; hence lizards are exposed to milder and less variable environments compared to the mainland (Sagonas et al. 2013).

Thus far, direct comparisons of lizard body temperatures and thermoregulation between mainland and island species have been limited (Meiri et al. 2013; Sagonas et al. 2013). At a localized scale, Sagonas et al. (2013) compared body temperatures of 2 populations of *Lacerta trilineata* on mainland Greece to 2 populations on Greek islands. Body temperatures were slightly lower and less variable on the islands compared to the mainland, although the results were insignificant. However, mainland populations were significantly more effective at thermoregulation (Sagonas et al. 2013). Globally, Meiri et al. (2013) found body temperatures to be 2.4°C cooler on islands than on the mainland, with insularity explaining 32.6% of the variation in global body temperatures. This is the only study to examine mainland-island body temperature differences at a global scale. However, Meiri et al. (2013)

did not consider the underlying causes of these differences in mean body temperatures, such as climatic differences or thermoregulatory strategies.

As well as variations in the thermal environment, lower body temperatures on islands may be related to biotic factors such as predation pressure and population size. As predation pressure is generally relaxed on islands (Perez-Mellado et al. 1997; Pafilis et al. 2008), insular species can afford to be active at lower body temperatures and thermoregulate less effectively, hence have sub-optimal performance (Meiri et al. 2013). This compares to mainland populations, where harsher climates and higher predation pressure requires more effective thermoregulation (Sagonas et al. 2013). Due to predator and competitor release, population sizes are greater on islands (Buckley and Jetz, 2007; Novosolov et al. 2012; Sagonas et al. 2013). This may also contribute to lower body temperatures as high population sizes reduce predation risk, reducing the need to maintain optimal body temperatures for performance (Downes and Hofer, 2004; Meiri et al. 2013).

1.7 Study aims

In this study, I assess the influence of environmental variables on body temperatures at a global scale. Firstly, I compare whether the relationships between body temperature and environmental variables vary consistently between 5 major land cover types, or habitats. This expands on the work of Clusella-Trullas et al. (2011) and Meiri et al. (2013), investigating the effect of climatic variables on body temperature, including temperature, precipitation and seasonality, whilst maintaining spatial heterogeneity of global location and controlling for habitat type. I also test whether remotely sensed indicators of vegetation structure such as leaf area index (LAI) can capture the effects of shade on operative temperatures and improve model fit, and likely predictions of body temperatures. I hypothesize that LAI will be unimportant for nocturnal species. This is because environments are cooler and more thermally homogenous at night, with no direct solar radiation and limited opportunities to raise body temperatures (Huey and Slatkin, 1976; Muñoz et al. 2014). Therefore nocturnal species do not need to seek shade from solar radiation to behaviourally thermoregulate, and should have lower body temperatures which more closely approximate environmental temperatures (Huey and Slatkin, 1976). In contrast, LAI should be important for diurnal species, as they are more dependent upon shade for thermoregulation.

Following recommendations of Scheers and Van Damme (2002), I then consider 6 substrate types to identify global trends in how substrate affects body temperatures and relationships between body temperature and the environment. I also assess how insularity affects body

temperature ~ environmental variable relationships. This furthers Meiri et al. (2013), who compared body temperatures of surface dwelling, fossorial and semi-aquatic species, and body temperatures of insular and mainland species at a global scale.

I examine relationships between climatic variables and body temperature using linear regression. I then use multiple regression to investigate how climatic variables interact to influence body temperature; and how this varies with land cover, substrate type and insularity. I predict that the relative importance of environmental variables in predicting body temperature will vary with land cover due to differing thermal complexity. Specifically, I expect that more of the variation in body temperatures will be explained by environmental variables in more homogenous environments such as closed vegetation, where species are expected to be largely thermoconformers, compared to semi-open environments where thermal heterogeneity should allow greater scope for thermoregulation. For substrate, I expect that more variation in body temperatures will be explained for arboreal species, as they would largely occupy closed vegetation environments. Although there is microclimatic variation in individual trees allowing for thermoregulation (Huey and Slatkin, 1976), I predict that the broadscale homogeneity of closed environments will dominate model predictions. In heterogeneous habitats, I predict that less variation in body temperature would be explained for species in rocky substrates due to high microclimatic variation for thermoregulation. Body temperatures should also be more predictable with environmental variables on islands than on the mainland, as insular species are thought to have a greater degree of thermoconformity.

2 METHODOLOGY

2.1 Data collection

2.1.1 Lizard data

Body temperature data were collected from the literature for lizards worldwide (Figure 1). 544 papers were searched for data, obtained from the reference lists of Huey et al. (2009), Clusella-Trullas et al. (2011), Sunday et al. (2011) and Meiri et al. (2013). All body temperatures were means of active lizards of any species recorded in field-based studies (Meiri et al. 2013). Most papers presented mean body temperatures of a population, and did not specify the proportion of adults or juveniles present. These means were taken for this study, however it should be noted that average body temperatures of juveniles and adults generally differ, hence their proportions will affect the population mean (Bauwens et al. 1999; Adamopoulou and Valakos, 2005; Ibarregüengoytía et al. 2008). This is related to lower heat capacities and higher surface-area:volume ratios associated with smaller body sizes, which reduce the costs of raising body temperatures and enables small lizards to equilibrate their body temperatures quicker with the environment (Huey and Slatkin, 1976; Seebacher and Shine, 2004). For studies that specified age categories, only the mean body temperatures of adults were selected.

For most cases, the study sample size was not given, however, this ranged from 1 (e.g. *Microlophus atacamensis*; Sepúlveda et al. 2008) to 1070 (*Cnemidophorus murinus*; Schall and Dearing, 1994) when reported. Data for all sample sizes were taken, as data are unlikely to be systematically biased even if sample sizes are small (Meiri et al. 2013).

Body temperatures were excluded if individuals were inactive when measured, e.g. nocturnal species studied during the day (Meiri et al. 2013). Body temperatures were also excluded if they were taken from gravid females. Gravid female snakes are known to thermoregulate more carefully than non-gravid females and males (Charland and Gregory, 1990; Tu and Hutchison, 1994; Brown and Weatherhead, 2000, Isaac and Gregory, 2004), and also exploit their habitat differently to gain the best opportunities for thermoregulation (Reinert, 1993). Although these studies considered only snakes, results may also apply to lizard populations. If so, average body temperatures of gravid female lizards may significantly differ from the population mean.

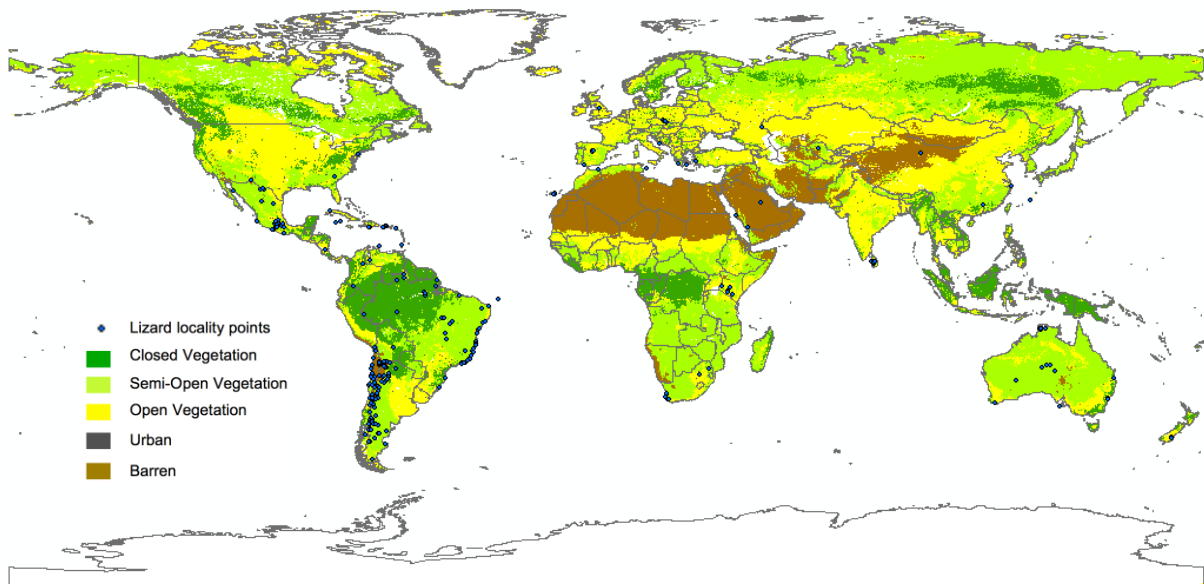


Figure 1: Global map showing land cover type and locations of lizard locality points from where body temperatures were obtained. The numbers of lizard locality points located within each continent and land cover are indicated in Table 1. The global land cover map was downloaded from MODIS2005 (MCD12C1, version 051), https://lpdaac.usgs.gov/dataset_discovery/modis/modis_products_table/mcd12c1.

Table 1: The number of lizard locality points located within each continent and land cover.

<i>Continent</i>	<i>Number of Lizard data points</i>	<i>Land Cover</i>	<i>Number of Lizard data points</i>
<i>Africa</i>	19	<i>Closed Vegetation</i>	64
<i>Asia</i>	29	<i>Semi-Open Vegetation</i>	152
<i>Australasia</i>	40	<i>Open Vegetation</i>	114
<i>Europe</i>	26	<i>Urban</i>	31
<i>North America</i>	76	<i>Barren</i>	41
<i>South America</i>	212		

Activity times of species (diurnal, nocturnal) were obtained from Meiri et al. (2013) if not reported in the original paper. As I was interested in how activity time affects thermoregulation, cathemeral species were classified as diurnal or nocturnal corresponding to the time of day their body temperature was recorded. Preferred substrate types of species were obtained from Meiri et al. (2013) for fossorial and semi-aquatic species, and from the literature and web sources including the reptile database (<http://www.reptile-database.org/>) and IUCN red list (<http://www.iucnredlist.org/>) for saxicolous, arboreal, psammophilous and non-specialised ground dwelling species. Semi-fossorial and semi-arboreal species were classified as fossorial and arboreal respectively.

The latitude and longitude of study sites were obtained from papers if reported. Coordinates were often reported using degrees and minutes. These were translated to decimal degrees for use in GIS software, using place names and altitudes reported where applicable to maintain accuracy. If not reported, coordinates were geo-referenced as accurately as possible in decimal degrees using locality information. It should be noted that geo-referencing points based on locality information, or translating from degrees and minutes to decimal degrees, which requires a finer level of precision than reported by the paper, introduces error. However, this was acceptable given the coarser resolutions of climatic and satellite data.

2.1.2 Environmental data

Global climatic data were obtained from BioClim (Hijmans et al. 2005), at approximately 1 km resolution for 1950-2000 (Appendix D). Bio 1 – Bio 19 were downloaded to capture trends in mean annual temperature and precipitation values, and temperature and precipitation extremes. Isothermality (Bio 3) was excluded, as it is simply a ratio of diurnal temperature range (Bio 2), and annual temperature range (Bio 7), quantifying the extent of day to night temperature oscillations relative to summer to winter oscillations (O'Donnell and Ignizio, 2012).

Annual precipitation range (Bio 14.5) was calculated through subtracting Bio 14 (mean precipitation of the driest month) from Bio 13 (mean precipitation of the wettest month). Global potential evapotranspiration (PET) and global aridity datasets were obtained from the Consultative Group for International Agricultural Research (CGIAR), at approximately 1 km resolution for 1950-2000 (Zorner et al. 2007; 2008). Altitude was not downloaded as

temperature and precipitation datasets from BioClim are modeled as functions of latitude, longitude and elevation (Hijmans et al. 2005).

Global land cover data were obtained from the Global Land Cover Consensus dataset (Tuanmu and Jetz, 2014) at approximately 1 km resolution, available from EarthEnv (<http://www.earthenv.org/>). The dataset was produced using a generalized classification scheme and an accuracy based integration approach to integrate data from four global land cover products: GlobCover2005, MODIS2005, GLC2000 and DISCover. Despite availability from 2001-2012 for MODIS, and 2005-2009 for GlobCover, datasets from 2005 were acquired to match their acquisition time and to minimize differences in their acquisition times with DISCover and GLC2000, which acquire data from 1992-1993 and 1999-2000 respectively (Tuanmu and Jetz, 2014) (Appendix A). For each 1 km square, the dataset presents the consensus prevalence for each of 12 generalized land cover classes (Appendix B).

Global LAI was obtained from the Glass LAI product (Liang and Xiao, 2012) available from the Global Land Cover Facility (GLCF, 2012). The dataset is derived from the MODIS Land Surface Reflectance product (MOD90A1) and is projected at approximately 5.6 km resolution over 8 days. LAI was downloaded from 2005 to match the acquisition times of GlobCover2005 and MODIS2005 used within the Global Land Cover Consensus dataset. Data from 12th-19th July 2005 and 9th-16th January 2005 were obtained for the northern hemisphere and southern hemisphere respectively. These were combined into a single measure, summer LAI. This ensured that LAI data corresponded to when lizards were thermoregulating the most in both hemispheres. Global land surface temperature (LST) were obtained from the MODIS Land Surface Temperature and Emissivity product (MOD11C3) for July and January 2005 at approximately 5.6 km resolution, and combined to produce summer day LST and summer night LST. Within forested environments, remotely sensed LST data reflect the temperature at the top of the canopy. However, in the tropical forests of Costa Rica, Bohlman et al. (1995) noted that the temperature of organic matter in the upper canopy and in the soil horizon remained within 1°C of each other over a 42 month period, despite yearly fluctuations between 11.5 – 21°C. Therefore, for tropical forests at least, LST data are likely representative of LST conditions at the forest floor.

Aridity and night LST were later excluded from analysis due to high collinearity (Pearson's $r > 0.7$) with precipitation for aridity, and day LST and environmental temperature (T_{env}) for night LST (Appendix C).

2.2 Data Processing and analysis

For each lizard locality point, environmental data were extracted from global maps using ArcMap10.2. The dominant land cover class was determined for each locality, defined as the land cover class with the greatest percentage prevalence. The land covers for each locality were then re-classified as closed vegetation, semi-open vegetation, open vegetation, urban and barren (Appendix D), with the vegetation classes grouped into the above as deemed appropriate using the Global Land Cover product class descriptions (Appendix B). Lizard data collected prior to 1990 were excluded to ensure temporal consistency with the land cover data, which uses only post 1990 data (Tuanmu and Jetz, 2014). The distribution of lizard points with land cover and per continent is reported in Table 1.

Due to high collinearity amongst many BioClim variables, the data were reduced dimensionally using principal components correlation analysis (PCA) to identify the major axes of variation (Muñoz et al. 2014). PCA was done using Community Analysis Package (CAP) 4.0. The temperature PCA (Bio 1 – Bio 11), indicated a gradient of cool, seasonal environments to warm, aseasonal environments along axis 1, and a gradient of aseasonal environments with cool summers, to seasonal environments with hot summers along axis 2. The precipitation PCA (Bio 12 – Bio 19) showed similar trends (Appendix E). For simplicity during analysis, the scores for both temperature axes and precipitation axis 1 for each locality point were multiplied by -1. Therefore, increasing axis 1 scores represented increasing mean and extreme environmental temperatures (T_{env}) and precipitation, and increasing axis 2 scores represented increasing temperature seasonality and precipitation seasonality. Pearson's correlations between each original BioClim variable and body temperature, and between BioClim variables indicating collinearity are reported in Appendix F.

All further analysis was conducted using R 3.2.1 (R Development Core Team).

Linear regressions were used to assess relationships between body temperature and environmental variables globally, and for each land cover class, activity time, substrate, and for islands and the mainland. Slopes of relationships are reported \pm standard error.

Kruskal-Wallis analysis, with Kruskal-Wallis post hoc, and ANOVA with Tukey's HSD post hoc tests, were used to assess whether mean body temperature varied significantly between land cover types, activity times, substrates, and with insularity. Kruskal-Wallis was used to compare land covers and substrates due to significant heteroscedasticity of residuals

between classes. ANCOVA, with Bonferroni post hoc corrections, was used to test whether the slopes of the relationships between body temperature and environmental temperature (T_{env}) varied with land cover, activity time, substrates and insularity. Mean body temperatures are reported ± 1 standard deviation.

Multiple regression analysis was used to assess the importance of environmental variables – T_{env} , temperature seasonality, precipitation, precipitation seasonality, PET, LAI, LST – in accounting for variance in body temperature at a global scale, and to assess whether their relative importance varies with land cover, substrate, insularity and activity time. The response variable, body temperature (T_b), was transformed to $-\text{Log}(k-T_b)$, where $k = \text{maximum } T_b + 1$, for all multiple regression models to reduce heteroscedasticity and increase normality of residuals. A backwards step-wise procedure was used to select the final models. A full model was fitted that included all terms and pairwise interactions. Terms with the highest P-values were then removed in turn and the model refitted until all terms were significant ($P < 0.05$), with interactions removed prior to main effects. Main effects were retained if they were included in a significant interaction term. In turn, climatic variables were dropped along with all their significant interactions from the model. New R^2 values were then subtracted from the R^2 of the final model to find the percentage of unique variation explained by each variable. Due to the contribution of pairwise interactions, the sum of the unique variation explained by all climatic variables in the final model may not total the final model R^2 .

Final models were run again whilst controlling for spatial autocorrelation and phylogeny using GLS and PGLS respectively. The phylogenetic tree used for PGLS was obtained from Pyron and Burbrink (2013). This is a time-calibrated tree containing 4161 squamate species out of an approximate 9400 total, constructed using molecular data. Pyron and Burbrink (2013) calibrated the 6 higher nodes using fixed ages according to the existing temporal frameworks for squamate evolution. The root age was fixed at 228 Ma in accordance with previous studies. They then used Penalised likelihood in the treePL program to estimate divergence times for the other nodes (Pyron and Burbrink, 2013). The tree shows close agreement with recent estimates of squamate divergence times, and is concordant with fossil and molecular estimates of squamate origins (Pyron and Burbrink, 2013). Before PGLS, the tree was trimmed to include species only in my dataset. Species in the dataset but not in the phylogeny were also removed. For species in the dataset with more than one entry, a single value was chosen for inclusion in the PGLS.

As points from South America dominated lizard T_b data, South America data were randomly reduced from 212 to 100 points, and a global multiple regression analysis conducted on the

reduced data as above. This was repeated 3 times. This was to reduce the likelihood that results were being biased by the South American climate (Sunday et al. 2011). Multiple regression models were also fitted as above globally and for each land cover type without LAI, LST and their pairwise interactions included. This aimed to assess to what extent including remotely sensed variables can improve $T_b \sim$ environmental models.

2.3 Methodological limitations

Stepwise multiple regression analysis is a widely employed technique used in ecology and evolutionary biology to identify which combination of predictor variables best describe a system, and to test their contributions (see Whittingham et al. 2006 for a review). This technique however has recognized limitations, in that it can result in biases in parameter estimation, interactions between main effect variables may hinder interpretations, and that it ignores model uncertainty (Grueber et al. 2011). In this study, I select the single “best” model for each land cover, substrate, insularity and activity time category, which has the highest R^2 value. As single models are studied, inferences made should be treated with a degree of caution, as other models may exist which include different parameters and fit the data almost as well (Whittingham et al. 2006). Information theoretic ‘IT’ approaches to model selection can account for this uncertainty through ‘model averaging’, where models with similar fit are averaged to obtain a final model with more robust parameter estimates. This technique is still in its infancy, however is now being used in many areas of ecology (Grueber et al. 2011). In future, analysis should be conducted using IT approaches to reduce model uncertainty and hence strengthen inferences and conclusions drawn in this study.

Within this study, sample size was not controlled for, as this would have been impractical and would have severely reduced the number of studies from which body temperature records could be taken. This resulted in a large range of sample sizes within the data, from 1 to 1070. Down weighting sample sizes above or below a set threshold would help account for the range of sample sizes used. This was not done here for simplicity; however, this would be recommended for future analysis. This is important, as population size and resultant population dynamics may have affected average body temperature measurements. For example, with larger group sizes, perceived predation risks by individuals decrease, hence individuals spend less time on anti-predatory behaviour and thermoregulate more effectively (Downes and Hofer, 2004). The influence of population size on effectiveness of thermoregulation and hence body temperature may also be habitat dependent. Within open habitats, basking and movement between sun and shade makes individuals more

conspicuous to predators, increasing predation risk. Therefore, small populations in open habitats would have body temperatures more affected by predator effects than in closed habitats. Body temperatures of juveniles were excluded where possible, however, in studies that reported the mean body temperature of a population, it is likely that body temperatures of both juveniles and adults were included. To account for this, down weighting cases that may include juveniles would be recommended for future analysis.

Ideally, body temperatures should all be collected from the same season. This would be summer in temperate latitudes and in the warm, wet season in tropical latitudes, where opportunities for thermoregulation are greatest. Again, collection of data from a single season would have reduced sample sizes, and would have largely been impractical due to the methods used by authors from whom data was collected. For example, some studies collected body temperatures within just month (e.g. Andrews et al. 2008), whereas others averaged body temperatures collected throughout one season (e.g. Kiefer et al. 2005), many seasons (e.g. Andrews et al. 1999) or over a whole year (Anaya-Rojas et al. 2010). Mean body temperatures for a given location would vary dependent upon the seasons they were collected, and across how many months or seasons they were averaged. A number of studies have documented the effect of seasonality on body temperature. For example, Christian and Bedford (1995) found that body temperatures of *Chlamydosaura kingii* in tropical Australia were significantly lower in the dry season. Lower body temperatures in the dry season could be an adaptation to conserve water and energy, as resources are relatively scarce, and there is increased risk of desiccation due to lower cloud cover, and reduced humidity and moisture content of substrates (Ballinger et al. 1970; Christian and Bedford, 1995). In the dry season, costs of thermoregulation are also greater due to reduced availability of warm operative temperatures (Christian and Bedford, 1995). Seasonality has a greater impact on mean body temperatures for species at temperate latitudes, where air temperature and solar radiation are more variable (Stevenson, 1985).

3 RESULTS

3.1 Global

Global body temperatures ranged from 10.9 – 39.6 °C, mean $31.5 \pm 5.2^\circ\text{C}$ (Figure 2; Table G1). The lowest body temperature belonged to *Tarentola boettgeri*, a nocturnal species whose body temperature was collected in winter in the Canary Islands (Brown, 1996). The highest belonged to *Cnemidophorus mumbuca*, a diurnal species collected in the summer in tropical Brazil (Mesquita et al. 2006).

All climatic variables showed significant, positive correlations with body temperature, except precipitation and LAI, which were negatively correlated (Figure 3; Table H1). The global OLS multiple regression model explained 33.7% of the variation in body temperature ($R^2 = 0.337$, adjusted $R^2 = 0.317$) (Table I1). Apart from precipitation seasonality, all main effect variables remained in the model, including 5 interactions – T_{env} x precipitation, temperature seasonality x LAI, precipitation x PET, precipitation x LAI, PET x LST. Precipitation and LAI explained the most unique variation: 11% and 9% respectively. This was largely attributable to their interaction, which explained 6% of the variation (Table 2; Table I1)

Globally there was minimal spatial autocorrelation (GLS) (Moran's $I = 0.218$, Distance Class = 0, $P < 0.01$), with less phylogenetic signal (PGLS) than expected under Brownian motion (Blomberg's $K = 0.177$, $P < 0.001$; Pagel's $\Lambda = 0.622$, $P < 0.001$) (Table J2). For GLS, the significance of all variables did not change. For PGLS, all variables except the precipitation x LAI interaction became non-significant.

Fitting the global OLS model without LAI and LST reduced the proportion of variation in body temperature explained to 26% ($R^2 = 0.260$, adjusted $R^2 = 0.243$) (Table 3; Table K1). Fitting the global OLS model with a reduced number of South America data points produced the same model in each of 3 repetitions (Appendix L). With reduced data, all main effect variables remained in the final models apart from precipitation seasonality, as in the final global model with all data. The interactions that remained in the models were T_{env} x LAI, temperature seasonality x LAI, precipitation x LAI and PET x LAI. These differed from the interactions remaining in the global OLS model with all data.

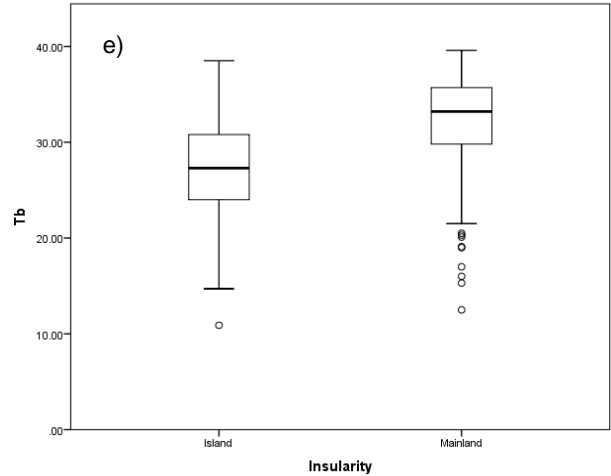
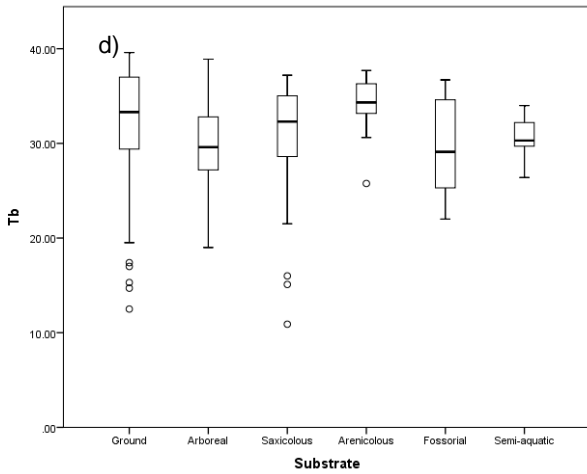
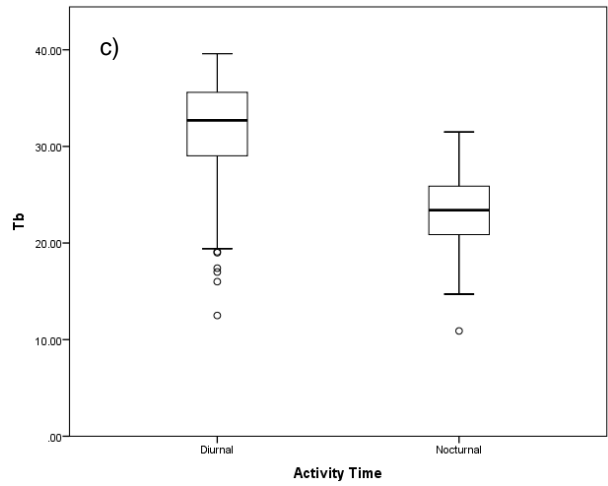
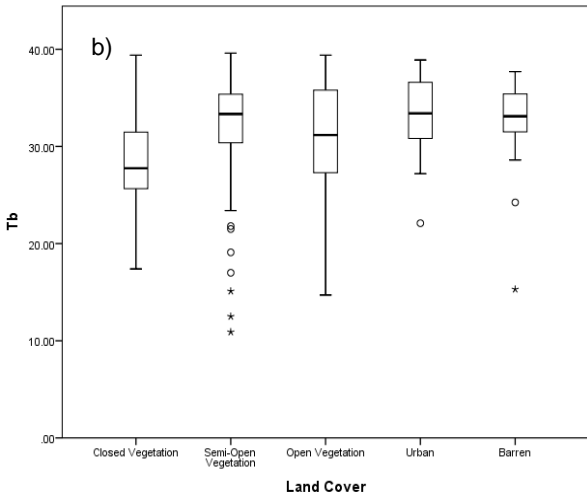
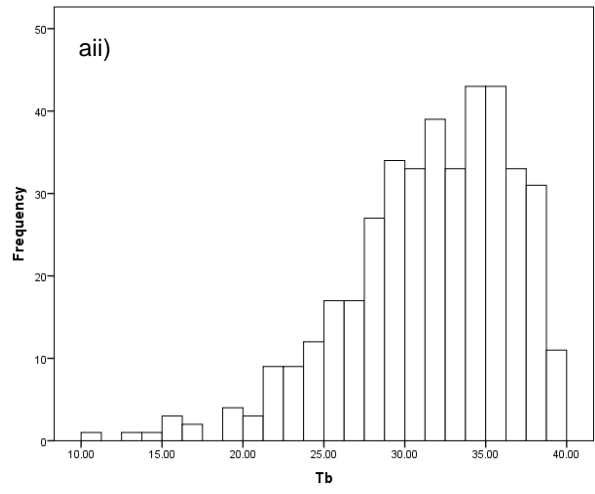
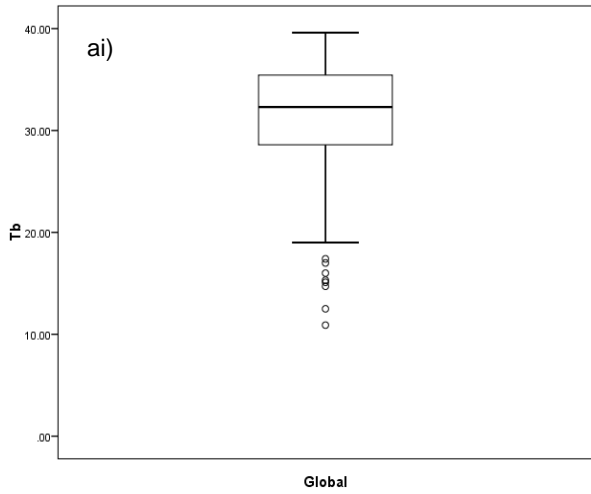


Figure 2: ai) Box plot of lizard body temperatures (T_b ; °C) at a global scale. aii) Frequency-distribution graph of lizard body temperatures across all species at a global scale. Box plots of lizard body temperatures with b) land cover, c) activity time, d) substrate and e) insularity.

Table 2: Summary of multiple regression models at a global scale, and for each land cover, activity time, substrate and insularity. The contribution of variables to the model indicates the percentage of unique variation explained by each variable. Contributions were obtained by dropping each variable and their significant interactions in turn from the model, and then subtracting new R^2 values from the R^2 of the complete model. 0 = 0% contribution, 1 = 100% contribution. For main effect variables, the percentage contribution is a total contribution, and hence includes the contribution of all their significant pair-wise interactions. All pairwise interactions are significant at $P < 0.05$. P values are not included in the table. * denotes main effect variables which are non-significant ($P > 0.05$) but are held in the model through significant pairwise interactions. The dependent variable, body temperature (T_b ; °C) was transformed to $-\text{Log}(k-T_b)$ for all multiple regressions to reduce heteroscedasticity and increase normality of residuals. $K = \text{Maximum } T_b + 1$. Full details of all multiple regression models are reported in Appendix I. T_{env} = Environmental Temperature. PET = Potential Evapotranspiration. LAI = Leaf Area Index. LST = Land Surface Temperature.

	Land Cover				Activity Time			Substrate			Insularity			
	Global	Closed Vegetation	Semi-Open Vegetation	Open Vegetation	Urban	Barren	Diurnal	Nocturnal	Terrestrial	Ground	Arboreal	Saxicolous	Island	Mainland
Dependent variable: $-\text{Log}(k-T_b)$														
R^2	0.337	0.698	0.434	0.494	0.821	0.696	0.364	0.718	0.370	0.526	0.712	0.254	0.834	0.325
Adjusted R^2	0.317	0.648	0.397	0.442	0.744	0.630	0.343	0.612	0.349	0.495	0.639	0.205	0.768	0.301
df	382	54	141	97	21	32	359	16	362	180	67	76	48	314
Residual SE	0.215	0.139	0.184	0.217	0.119	0.115	0.200	0.073	0.209	0.205	0.120	0.182	0.109	0.204
Percentage contribution of variables to R^2 (% / 100)														
T_{env}	0.044	0.167	0.038	0.175	0.250*	0.088	0.072	0.447	0.062	0.171	0.036	0.117	0.426*	0.070*
Temperature Seasonality	0.010	0.104	0.079	0.035	0.426*	0.297	0.008*	0.241	0.009*	0.042	0.145		0.304	0.014
Precipitation	0.092	0.127		0.067		0.432	0.085		0.071	0.143	0.111		0.233	0.061
Precipitation Seasonality		0.168	0.033	0.093*	0.126	0.063		0.113*		0.048*	0.114		0.173	
PET	0.050	0.086	0.110	0.061*	0.054		0.024*		0.039		0.138	0.193	0.473*	0.065
LAI	0.114*	0.084*		0.133*	0.059*		0.075*		0.116	0.066*	0.071		0.181	0.110

	Land Cover				Activity Time			Substrate			Insularity			
	Global	Closed Vegetation	Semi-Open Vegetation	Open Vegetation	Urban	Barren	Diurnal	Nocturnal	Terrestrial	Ground	Arboreal	Saxicolous	Island	Mainland
<i>LST</i>	0.029*		0.099		0.047	0.139	0.031	0.142*	0.028	0.070	0.066	0.108	0.148*	0.032
<i>T_{env} x Temperature Seasonality</i>					0.073		0.008				0.030		0.096	
<i>T_{env} x Precipitation</i>	0.043	0.120					0.041		0.020	0.084				0.022
<i>T_{env} x Precipitation Seasonality</i>				0.081						0.019			0.033	
<i>T_{env} x PET</i>			0.027	0.059			0.008							
<i>T_{env} x LAI</i>									0.007					0.011
<i>T_{env} x LST</i>						0.077	0.013		0.008	0.040		0.104		
<i>Temperature Seasonality x Precipitation</i>		0.045					0.280			0.025	0.021		0.155	
<i>Temperature Seasonality x Precipitation Seasonality</i>					0.068			0.100		0.020	0.061		0.076	
<i>Temperature Seasonality x PET</i>			0.076								0.047		0.093	
<i>Temperature Seasonality x LAI</i>	0.008								0.009		0.018			0.010
<i>Temperature Seasonality x LST</i>			0.053					0.142			0.023		0.082	
<i>Precipitation x Precipitation Seasonality</i>				0.029									0.030	
<i>Precipitation x PET</i>	0.014						0.017				0.064			
<i>Precipitation x LAI</i>	0.058			0.055			0.055		0.055	0.065			0.015	0.031
<i>Precipitation x LST</i>													0.089	
<i>Precipitation Seasonality x PET</i>											0.042			
<i>Precipitation Seasonality x LAI</i>		0.083			0.057						0.025		0.024	
<i>Precipitation Seasonality x LST</i>			0.033										0.129	
<i>PET x LAI</i>	0.009								0.027		0.059			0.055
<i>PET x LST</i>												0.072		
<i>LAI x LST</i>													0.079	

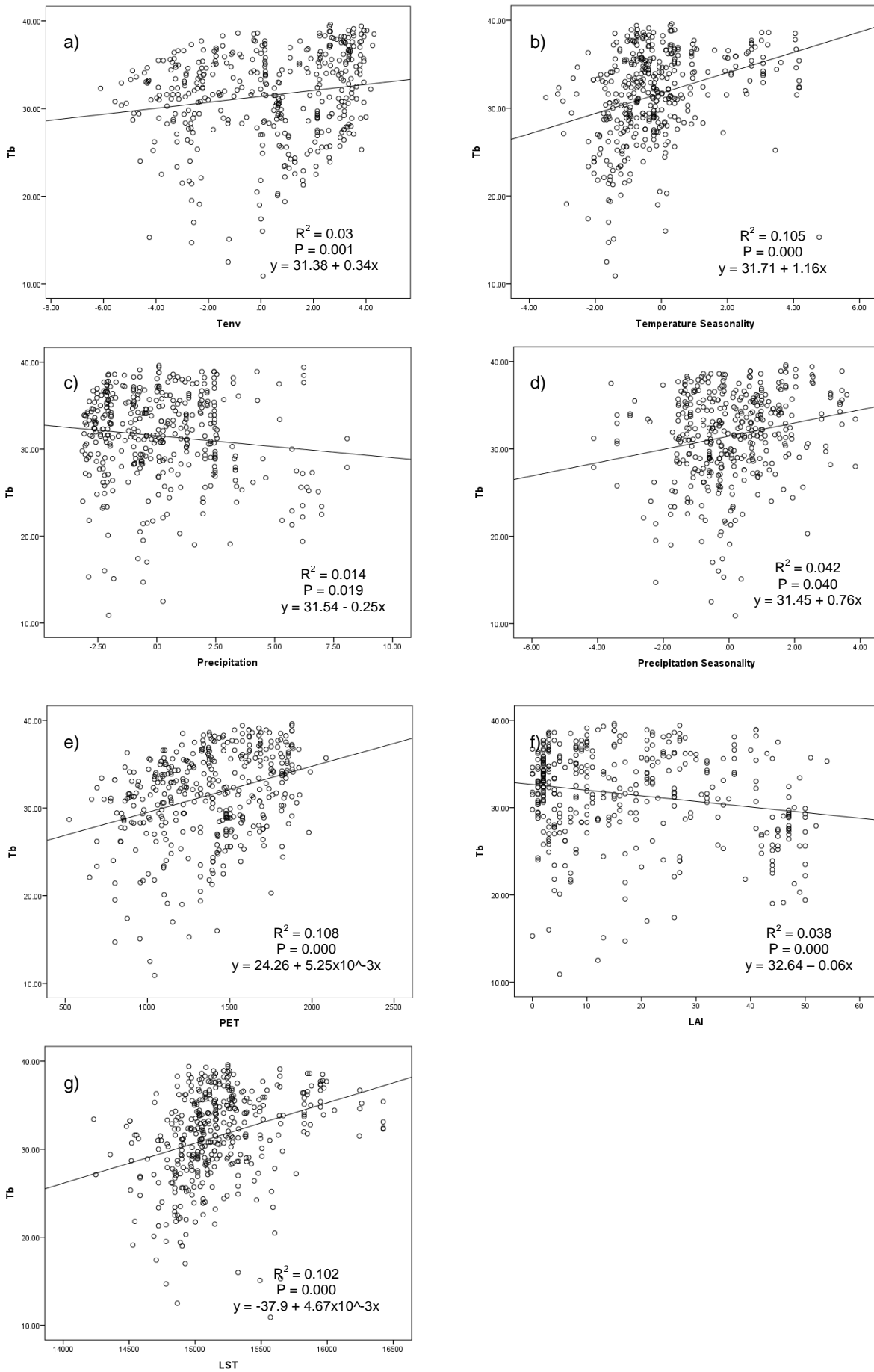


Figure 3: Global scale correlations between body temperature (T_b ; °C) and a) Environmental Temperature (T_{env} ; Temperature PCA axis 1 scores), b) Temperature Seasonality (Temperature PCA axis 2 scores), c) Precipitation (Precipitation PCA axis 1 scores), d) Precipitation Seasonality (Precipitation PCA axis 2 scores), e) Potential Evapotranspiration (PET; mm/month), f) Leaf Area Index (LAI), (g) Land Surface Temperature (LST; Kelvin, scaling factor 0.02).

Table 3: Final OLS multiple regression models at a global scale and with land cover.

a) Results of models which were fitted with all environmental data (T_{env} , temperature seasonality, precipitation, precipitation seasonality, PET, LAI, LST and all pairwise interactions).

b) Results of models fitted without including remotely sensed data, LAI and LST and their pairwise interactions.

T_{env} = Environmental Temperature. PET = Potential Evapotranspiration. LAI = Leaf Area Index. LST = Land Surface Temperature.

	<i>Land Cover</i>					
	<i>Global</i>	<i>Closed Vegetation</i>	<i>Semi-Open Vegetation</i>	<i>Open Vegetation</i>	<i>Urban</i>	<i>Barren</i>
a)						
Dependent variable: -Log(k-T_b)						
<i>R</i> ²	0.337	0.698	0.434	0.494	0.821	0.696
<i>Adjusted R</i> ²	0.317	0.648	0.397	0.442	0.744	0.630
<i>df</i>	382	54	141	97	21	32
<i>Residual SE</i>	0.215	0.139	0.184	0.217	0.119	0.115
b)						
Dependent variable: -Log(k-T_b)						
<i>R</i> ²	0.260	0.656	0.370	0.361	0.630	0.711
<i>Adjusted R</i> ²	0.243	0.606	0.339	0.324	0.573	0.624
<i>df</i>	389	55	143	105	26	30
<i>Residual SE</i>	0.221	0.147	0.193	0.235	0.154	0.115

3.2 Differences with land cover

Within closed vegetation, average body temperature was 2.8°C lower than the global mean (Table G1). This was significantly lower than the average body temperature within all other land covers, which otherwise did not significantly differ, based on Kruskal-Wallis tests (Table G2). The slope of the $T_b \sim T_{env}$ relationship for open vegetation (slope = 1.27 ± 0.20) was significantly steeper than for closed vegetation ($P < 0.05$), semi-open vegetation ($P < 0.001$) and barren land covers ($P < 0.05$) (slopes = 0.46 ± 0.39 ; 0.44 ± 0.15 ; 0.38 ± 0.28 respectively) (Figure G1; Table G3).

The final OLS multiple regression model for closed vegetation explained 69.8% of the variation in body temperature ($R^2 = 0.698$, adjusted $R^2 = 0.648$) (Table 2; Table I2). LST did not remain in the final model. LAI, held in the model through its interaction with precipitation seasonality, uniquely explained 8% of the variation. LAI and precipitation were negatively correlated with body temperature (Figure 4; Table H2). Temperature seasonality and LAI were correlated most strongly with body temperature through linear regression, temperature seasonality displaying a positive relationship with body temperature ($r = 0.409$, $P < 0.001$; $r = 0.408$, $P < 0.001$ respectively) (Table H2).

For semi-open vegetation, the final OLS multiple regression model explained 43.4% of the variation ($R^2 = 0.434$, adjusted $R^2 = 0.397$) (Table I3). LAI and precipitation did not remain in the final model. Temperature seasonality, PET and LST explained the most unique variation: 7.9%, 11% and 9.9% respectively.

For open vegetation, the final OLS multiple regression model explained 49.4% of the variation in body temperature ($R^2 = 0.494$, adjusted $R^2 = 0.442$) (Table I4). LST did not remain in the final model. T_{env} and LAI explained the most unique variation: 17.5% and 13.3% respectively. T_{env} was the most strongly correlated with body temperature by linear regression, showing a positive correlation ($r = 0.509$, $P < 0.001$) (Table H2). LAI was held in the model through the pairwise interaction, precipitation x LAI. LAI was otherwise non-significant in the OLS multiple regression, and had no significant correlation with body temperature by linear regression.

Within urban landscapes, the final OLS multiple regression model explained 82% of the variation in body temperature ($R^2 = 0.821$, adjusted $R^2 = 0.744$) (Table I5). Precipitation did not remain in the final model. T_{env} and temperature seasonality explained the most unique

variation: 25% and 42.6% respectively. Despite explaining the most variation, temperature seasonality was only held in the model through its interactions.

Within barren landscapes, the final OLS multiple regression explained 69.6% of the variation in T_b ($R^2 = 0.696$, adjusted $R^2 = 0.630$) (Table I6). Temperature seasonality and precipitation explained the most unique variation: 29.7% and 43.2% respectively. LAI and PET did not remain in the final model.

There was no significant spatial autocorrelation or phylogenetic signal amongst the model residuals for any land cover type (Appendix J). Fitting the OLS multiple regression models without LAI and LST data reduced the proportion of variation in body temperatures explained for all land covers, except for within barren landscapes (Appendix K).

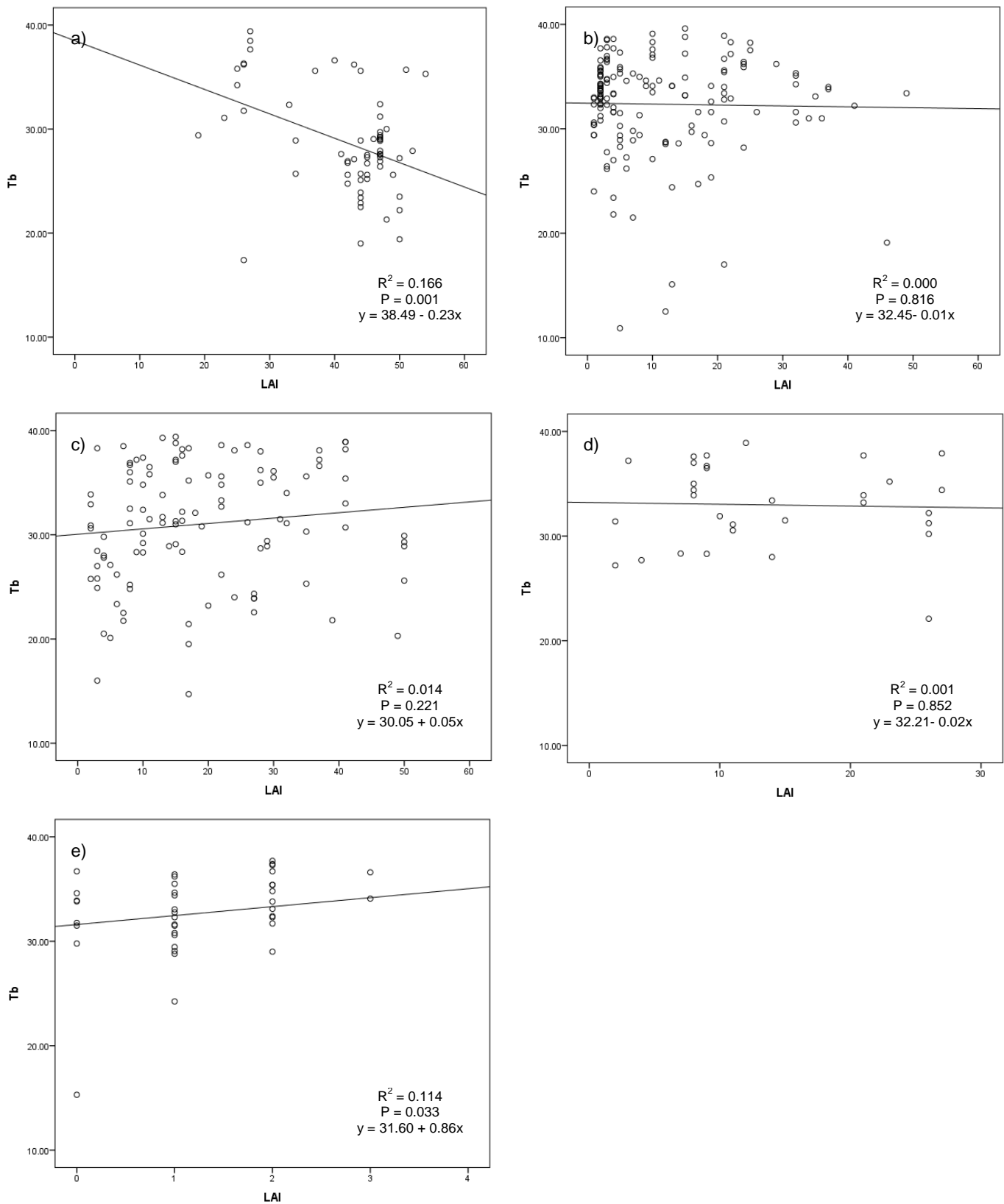


Figure 4: Correlations between body temperature (T_b ; °C) and Leaf Area Index (LAI) by land cover. a) Closed Vegetation, b) Semi-Open Vegetation, c) Open Vegetation, d) Urban, e) Barren

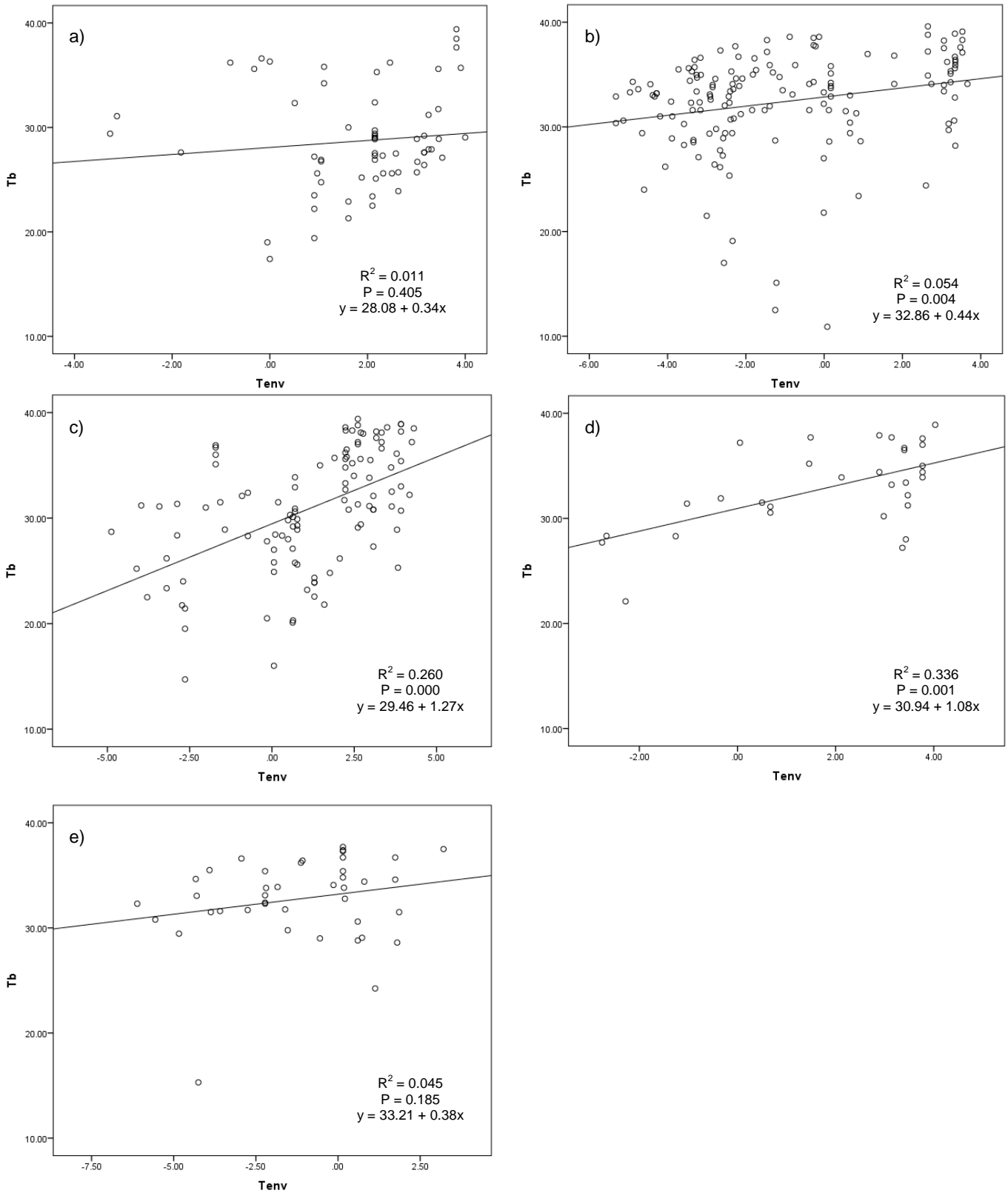


Figure 5: Correlations between body temperature (T_b ; °C) and Environmental Temperature (T_{env} ; Temperature PCA axis 1 scores) by land cover. a) Closed Vegetation, b) Semi-Open Vegetation, c) Open Vegetation, d) Urban, e) Barren

3.3 Differences with activity time

As predicted, the average body temperature of nocturnal species was significantly lower than for diurnal species ($P < 0.001$), with means of $22.8 \pm 5.0^\circ\text{C}$ and $32.0 \pm 4.7^\circ\text{C}$ respectively (Figure 2). The slope of the $T_b \sim T_{\text{env}}$ relationship was significantly steeper for nocturnal than diurnal species ($P < 0.05$) (slopes = 1.19 ± 0.35 and 0.29 ± 0.09 respectively) (Figure G1; Table G3). The final diurnal OLS multiple regression model explained 36.4% of the variation in body temperature ($R^2 = 0.364$, adjusted $R^2 = 0.343$) (Table 2; Table I7). All main effect variables remained in the model apart from precipitation seasonality. This was the same as in the global model, however the remaining interactions differed. The final OLS multiple regression for nocturnal species explained 71.8% of the variation in body temperature ($R^2 = 0.718$, adjusted $R^2 = 0.612$) (Table I8). T_{env} and temperature seasonality explained the most unique variation: 44.7% and 24.1% respectively. LAI, precipitation and PET did not remain in the final model.

There was no significant spatial autocorrelation amongst the model residuals for both the nocturnal and diurnal models (Table J1). The diurnal model showed phylogenetic signal, however, this was less than expected under Brownian motion (Blomberg's $K = 0.186$, $P < 0.001$; Pagel's $\Lambda = 0.609$, $P < 0.001$) (Table J2). For the diurnal PGLS model, all variables except LST and precipitation x LAI became non-significant.

3.4 Differences with substrate

My final database included only 9 data points for fossorial species, and 9 for semi-aquatic species. Therefore, multiple regression and linear regression models were not produced for these lizards due to low sample sizes. Linear regression and multiple regression models were conducted with only terrestrial species to see the effect of excluding fossorial and semi-aquatic species on the global model.

The final terrestrial OLS multiple regression model explained 37% of the variation in body temperature ($R^2 = 0.370$, adjusted $R^2 = 0.349$) (Table 2; Table I9). This was 3.3% increase in the variation explained compared to the global model ($R^2 = 0.337$, adjusted $R^2 = 0.317$) (Table I1). As with the global model, all main effect climatic variables remained in the final terrestrial model apart from precipitation seasonality. The terrestrial model showed minimal spatial autocorrelation amongst the residuals (Moran's $I = 0.129$, distance class = 0, $P < 0.01$) (Table J1), and less phylogenetic signal than expected under Brownian motion

(Blomberg's $K = 0.167$ $P < 0.001$; Pagel's $\Lambda = 0.561$, $P < 0.001$) (Table J2). For GLS, T_{env} , temperature seasonality, $T_{env} \times LAI$ and $T_{env} \times LST$ changed significance. Temperature seasonality, held in the final terrestrial OLS model through interactions, became significant; whereas T_{env} and its LAI and LST interactions became non-significant. For PGLS, half the terms in the model became non-significant.

The mean body temperature of all terrestrial species was $31.5 \pm 5.2^\circ\text{C}$, equaling the global mean (Table G1). Fossorial species had the lowest mean body temperature of $29.5 \pm 5.5^\circ\text{C}$, with semi-aquatic species averaging $30.5 \pm 2.5^\circ\text{C}$ (Figure 2). Although, as expected, mean body temperatures for fossorial and semi-aquatic species were lower than for terrestrial species, the difference was not significant (Table G2). There was also no significant difference in the slopes of the relationship between body temperature and T_{env} for terrestrial, fossorial and semi-aquatic species (Table G3). Excluding fossorial and semi-aquatic species from analysis did not alter the significance of correlations between body temperature and climatic variables by linear regression, and had minimal effect on Pearson's r values.

The terrestrial group was further sub-divided into arboreal, psammophilous, saxicolous, and general ground-dwelling species. General ground dwelling species were those that appeared to have no preference for a specialised substrate. The average body temperatures for psammophilous and ground dwelling species were higher than the overall terrestrial mean: $34.1^\circ \pm 3.0^\circ\text{C}$ and $32.4 \pm 5.5^\circ\text{C}$ respectively (Table G1). The average body temperature for arboreal species, $29.8 \pm 4.4^\circ\text{C}$, was lower than the terrestrial mean, and statistically similar to that of fossorial species. Arboreal body temperatures were significantly lower than body temperatures of saxicolous ($P < 0.05$), psammophilous ($P < 0.01$) and ground dwelling ($P < 0.001$) species. Mean body temperatures did not differ significantly between the other groups (Table G2). For general ground dwelling species, the slope of the relationship between body temperature and T_{env} differed significantly to the slopes of saxicolous ($P < 0.01$), psammophilous ($P < 0.05$) and arboreal ($P < 0.001$) species. There was no significant difference in the slope of the relationship between any other groups (Table G3).

Multiple regression models were fitted for arboreal, saxicolous and ground-dwelling species. As with semi-aquatic and fossorial species, psammophilous species were excluded from this analysis due to low sample size ($n = 16$). For ground dwelling species, the final OLS multiple regression model explained 52.6% of the variation in body temperature ($R^2 = 0.526$, adjusted $R^2 = 0.495$) (Table I10). All main effect variables apart from PET remained in the final model. T_{env} and precipitation explained the most unique variation: 17.1% and 14.3% respectively. The final OLS arboreal model explained 71.2% of the variation in body temperature ($R^2 =$

0.712, adjusted $R^2 = 0.639$) (Table I11). All main effect variables remained in the final model, plus 10 pairwise interactions. Temperature seasonality and PET explained the most unique variation: 14.5% and 13.8% respectively. For saxicolous species, the final OLS model explained 25.4% of the variation in body temperature ($R^2 = 0.254$ adjusted $R^2 = 0.205$) (Table I12). Only 3 climatic variables, T_{env} , PET and LST remained in the final model, plus 2 pairwise interactions.

None of the arboreal, ground or saxicolous models showed significant spatial autocorrelation amongst residuals (Table J1). There was phylogenetic signal amongst the saxicolous model residuals, however, less than expected under Brownian motion (Blomberg's $K = 0.478$, $P < 0.001$; Pagel's $\Lambda = 0.803$, $P < 0.001$) (Table J2). For saxicolous PGLS, all variables became non-significant.

3.5 Differences with Insularity

As expected, the average body temperature of insular species was significantly lower than for mainland species, with means of $27.4 \pm 5.5^\circ\text{C}$ and $32.4 \pm 4.6^\circ\text{C}$ respectively ($P < 0.001$) (Figure 2; Table G1). The slope of the relationship between body temperature and T_{env} was much steeper for island species compared to mainland species ($P < 0.001$) (slopes = 1.84 ± 0.33 and 0.46 ± 0.09 respectively) (Figure G1; Table G3).

For island species, the final OLS multiple regression explained 83.4% of the variation in body temperature ($R^2 = 0.834$, adjusted $R^2 = 0.768$) (Table I13). The model showed no significant spatial autocorrelation. All climatic variables remained in the final model, along with 12 interactions. PET, T_{env} and Temperature Seasonality explained the most unique variation: 47.3%, 42.6% and 30.4% respectively.

The final mainland OLS multiple regression model explained 32.5% of the variation in body temperature ($R^2 = 0.325$, adjusted $R^2 = 0.301$) (Table I14). Similar to the global OLS model, all main effect variables remained in the final model apart from precipitation seasonality, although the global and mainland models showed small differences in the significance of interactions.

The mainland model showed limited spatial autocorrelation amongst residuals (Moran's $I = 0.179$, Distance Class = 0, $P < 0.05$) (Table J1), and less phylogenetic signal than expected under Brownian motion (Blomberg's $K = 0.178$, $P < 0.001$; Pagel's $\Lambda = 0.679$, $P <$

0.001) (Table J2). Controlling for spatial autocorrelation using GLS did not affect the significance of variables, except for $T_{env} \times LAI$, which became marginally non-significant. For mainland PGLS, all variables except PET, LST and precipitation \times LAI became non-significant (Table I14).

There was no significant spatial autocorrelation or phylogenetic signal amongst the island model residua

4 DISCUSSION

Quantifying global relationships between habitat, climate and thermal biology is important for understanding the vulnerability of species to climate change (Sunday et al. 2011; 2014). Here, I build upon studies examining the effect of habitat on body temperature at local scales (Huey and Webster, 1976; Seebacher and Grigg, 1997; Gunderson and Leal, 2012; Ibanez et al. 2013), by expanding to a global scale to investigate broad-scale trends. I also build upon the work of Scheers and Van Damme (2002), Clusella-Trullas et al. (2011) and Meiri et al. (2013) by incorporating a range of climatic variables into global models, whilst accounting for habitat, substrate and insularity, to further understanding of how environmental variables interact to influence body temperature. Results suggest that habitat, substrate type and insularity affect body temperature, opportunities for behavioural thermoregulation, and also relationships between body temperature and climatic conditions. Additionally, remotely sensed LAI can capture the effect of shade on microclimatic variability within a habitat. Incorporating LAI in to models as a quantitative measure of shade availability can be used to improve T_b ~ environmental model predictions, and will reduce the requirement to use qualitative estimates of shade availability in future studies.

Previous studies, which have assessed relationships between environmental variables and lizard thermal biology, have generally only considered single climatic variables in their analysis, such as environmental temperature or precipitation (Clusella-Trullas et al. 2011; Meiri et al. 2013). This approach is perhaps over-simplistic, as models indicate that across all habitats, a range of environmental variables interact to influence lizard body temperatures. For example, even the simplest multiple regression model, which was for barren environments, used 5 environmental variables plus 2 interactions to explain the most variance in lizard body temperature. With climate change, lizard body temperatures will respond to changes in a combination of environmental variables. As environmental variables interact, these responses will also not be independent. This highlights that, in future, studies should ideally consider a range of environmental variables when studying lizard thermal biology. This is particularly important in making predictions as to how lizards will respond to climate change.

4.1 Evaluation of the global model

Meiri et al. (2013) studied the global relationship between mean annual temperature and T_b . The variables alone were uncorrelated, with a weak positive correlation emerging only after

phylogenetic relationships had been accounted for by family affiliation ($R^2 = 0.03$, $P < 0.0001$). I found that T_{env} and T_b were significantly correlated without accounting for other variables ($R^2 = 0.03$, $P < 0.001$). This significant relationship, in contrast to Meiri et al. (2013) may be related to my use of T_{env} (created by dimensionally reducing BioClim temperature variables (Bio 1 – Bio 11, Bio 3 excluded) using PCA by correlation, and obtaining axis 1 scores) in the model, rather than using simply mean annual temperature (Bio 1). Meiri et al. (2013) averaged temperatures across a species range, and thus did not consider temperature variability within species ranges or among populations. In contrast, my model maintained spatial heterogeneity of temperatures. However, as the R^2 values of both models are the same, results suggest that spatial averaging by Meiri et al. (2013) had little effect on model fit.

Meiri et al.'s (2013) best model for body temperature included phylogeny, annual temperature, activity time and insularity, and explained 57.1% of the variation in global body temperature. Here, the global model explained 33.7% of the variation in T_b ($R^2 = 0.337$, adjusted $R^2 = 0.317$), considering only climate. However, when also accounting for land cover, up to 82.1% of the variation in T_b could be explained without controlling for additional variables such as insularity and activity time. The proportion of variation in T_b explained also varied greatly with land cover. This indicates that habitat strongly influences thermal biology (Deutsch et al. 2008; Sunday et al. 2014), even at broad spatial scales.

Weak phylogenetic signal was observed in the global OLS multiple regression model (Blomberg's $K = 0.189$, $P < 0.001$, Pagel's $\Lambda = 0.630$, $P < 0.001$). 7 terms in the model lost their significance after phylogeny was accounted for (Table I1). This shows that there is shared variation explained between the phylogenetic structure of the data and climatic predictors. As many terms did not remain significant with phylogeny accounted for, the model should be interpreted with caution. However, some phylogenetic signal was expected for the global model. This is because phylogenetic conservatism of body temperatures tends to account for much of the variation in body temperature patterns (Seebacher and Shine, 2004; Tewksbury et al. 2008; Grigg and Buckley, 2013). Climatic variables that influence body temperature, such as environmental temperature, exhibit geographical gradients (Grigg and Buckley, 2013). It is likely that closely related species inhabit similar habitats and climates, and hence experience similar environmental pressures on body temperature; accounting for the phylogenetic signal. This explanation is consistent with my finding that there is no phylogenetic signal in residuals of models after accounting for land cover. Refitting the global OLS multiple regression model with a reduced number of South America points did not

change which main effect variables remained in the model. This confirms that the model is not biased by a preponderance of South America body temperature and climate data.

4.2 Global scale environmental correlations with T_b , and the effects of habitat

Globally, increasing precipitation correlated negatively with T_b . Previous studies have hypothesized that increasing precipitation should reduce lizard body temperatures (Clusella-Trullas et al. 2009; 2011). This is because high rainfall reduces the availability of optimal operative temperatures for thermoregulation within a habitat, constraining individuals to cooler and more homogenous thermal conditions, with limited thermoregulatory opportunities (Clusella-Trullas et al. 2011). The global, negative correlation between T_b and precipitation identified in this study is consistent with these predictions.

As predicted, LAI also correlated negatively with T_b at a global scale. This is likely due to the effect of increased vegetation on shade availability. For thermoregulators, increased vegetation provides greater opportunity to shuttle between sun and shaded patches, and thereby access cool microclimates to behaviourally reduce body temperatures (Sunday et al. 2014). Sun patches may also be eliminated in high vegetation levels, such as in closed canopies. This would prevent species from behaviourally increasing their body temperatures by basking in areas of high solar radiation, restricting them to lower body temperatures. For thermoconformers, increased vegetation, resulting in reduced exposure to solar radiation and lower operative temperatures, would also reduce warming of body temperatures. Complex ecosystems such as rainforests also contain an array of microhabitats, with microclimatic temperatures that are cooler and less variable than ambient conditions (Scheffers et al. 2014). For example, microhabitats such as epiphytic plant cover on tree branches can reduce local ambient air temperatures by up to 5°C (Freiberg, 2001), and reduce the time lizards are exposed to lethal air temperatures by up to 31 fold (Scheffers et al. 2014). Increasing vegetation cover increases the availability of such microhabitats. This may further explain the decrease in T_b associated with increased LAI.

As predicted, LAI did not remain in the final OLS multiple regression for nocturnal species, as there is no requirement for nocturnal species to find shade. In contrast, LAI was second strongest contributor to the diurnal species model, explaining 7.5% of the unique variation. This was also expected, as diurnal species have greater scope to behaviourally thermoregulate by shifting between shaded and sunny habitats and microhabitats (Huey and Webster, 1976; Stevenson, 1985; Huey et al. 2009). These results are consistent with the

hypothesis that the effect of LAI on body temperature is related to shade availability, and potentially subsequent effects of microhabitats, as shade availability is a major difference between night and day time habitats. This also suggests that remote sensing data such as LAI can contribute to estimates of shade at broad, global scales, and by extension, changes in shade under future land cover and climate change scenarios, allowing for improved predictions of ectotherm body temperatures.

Reductions in vegetation and hence shade availability are predicted in the future, as deforestation and global warming are likely to act in combination to cause vegetation dieback (Whitfield et al. 2007; Huey et al. 2012). Reductions in shade availability are predicted to increase thermal stress, as lizards are less able to access cool thermal refugia, resulting in extinctions (Kearney et al. 2009; Sunday et al. 2014). Results here bolster this prediction, suggesting that global reductions in vegetation cover will cause body temperatures to rise.

Globally, and for all habitats except open vegetation, temperature seasonality was one of the strongest predictors in the OLS multiple regression models, explaining a large proportion of the unique variation in T_b ; or was otherwise correlated most strongly to T_b through simple linear regression. This result is consistent with the hypothesis that the degree of temperature seasonality within a habitat poses strong selection on lizard thermal biology (Deutsch et al. 2008; Sunday et al. 2011). Therefore, changes in temperature variability with climate change will likely have a strong impact on lizard body temperatures worldwide, irrespective of habitat type.

Although a global influence of precipitation variability on lizard performance curves has been noted (Bonebrake and Mastrandrea, 2010), precipitation seasonality was not retained in the final global multiple regression model for body temperature. However, precipitation seasonality did remain in the models for each individual land cover. Its contribution to the models varied greatly between land cover types, suggesting a stronger influence on body temperature in some habitats than others. In the closed vegetation model, precipitation seasonality explained the most unique variation in T_b . This may be because lizards within closed vegetation generally inhabit tropical forests, where high precipitation reduces thermal heterogeneity and hence body temperatures (Clusella-Trullas et al. 2011). Increasing precipitation seasonality would cause seasonal increases in operative temperatures related to precipitation levels, and would therefore affect opportunities for thermoregulation, and body temperatures, at different times of year.

Multiple regression models with higher R^2 values may suggest a greater degree of thermoconformity within a habitat. It has been suggested that thermoconforming lizards are more vulnerable than thermoregulators to climate change (Huey et al. 2009), although vulnerability may be more related to low T_b and a low number of hours where T_b is above T_{pref} rather than thermoconformity (Sinervo et al. 2010). Recent work on the Bogert effect also suggests that thermoregulation may prevent species from adapting to higher temperatures, thus increasing thermal vulnerability (Muñoz et al. 2014; Buckley et al. 2015). Huey et al. (1993) suggest that using regression based analyses to measure thermoconformity may be inappropriate, as many biophysical variables (e.g. solar radiation) in addition to environmental temperature influence T_b . The use of multiple climatic variables in my regression models may partially overcome this criticism of temperature-only models. However, inferences of thermoconformity and thermoregulation from the models should still be treated with caution, as not all environmental variables that influence T_b (e.g. wind speed), have been accounted for.

My results suggest that urban species show more thermoconformity than individuals within any other habitat. This could be because individuals, which occupy urban environments, are more likely to be generalists and can tolerate a wider range of environmental conditions (Huey and Slatkin, 1976). For generalists, effective thermoregulation is hence unnecessary and not advantageous, as it reduces time and energy available for other activities such as finding food, defending territories and attracting a mate (Angiletta, 2009).

To the extent that the regression approach is reliable, results show that individuals within closed vegetation and barren environments are also largely thermoconformers, at least relative to broad scale climate conditions, with models explaining approximately 70% of the variation in T_b for both habitats. For closed environments, this result supports other studies, which state that species in closed tropical forests largely shift towards thermoconformity (Huey and Webster, 1976; Gunderson and Leal, 2012). This is because intense shade results in low thermal heterogeneity, which increases the cost of, and limits the opportunities for, thermoregulation (Huey and Webster, 1976; Shine and Madsen, 1996; Mann and Meek, 2004; Sagonas et al. 2013).

Within barren environments, opportunities for behavioural thermoregulation are limited due to lack of vegetation. Therefore individuals are largely restricted to selecting above or belowground environments to regulate their body temperature (Stevenson, 1985). LAI did not remain in the final barren multiple regression model. This likely reflects the lack of opportunity for barren species to exploit cooler microclimates due to limited vegetation, and

further reinforces that LAI can be used as an estimate of shade availability. The strong influence of temperature seasonality and precipitation in the barren model, which both explained the most unique variation, supports inferences that drought frequency and intensity are the greatest threats for species in barren environments (MacMahon, 1979; Parmesan et al. 2000; Barrows, 2011). For barren environments, precipitation was positively correlated to body temperature, which goes against global trends. However, it should be noted that precipitation only varied here by 1.2 units (PCA scores). The positive association may reflect the influence of precipitation on resource availability. Increasing precipitation in barren environments, which are expected to be poor in resources, would decrease dehydration risk as well as increase food and water availability. Therefore body temperatures would rise, as lizards do not need to reduce their metabolism in order to survive (Ballinger et al. 1970; Christian and Bedford, 1995; Clusella-Trullas et al. 2011).

The final multiple regression model for semi-open vegetation explained 43% of the variation in T_b , which was the lowest proportion compared to all other land cover types. This implies that there are greater opportunities for thermoregulation in semi-open vegetation; hence body temperatures are less easily predicted by environmental variables. For example, amongst semi-open vegetation, short distances would be expected between shaded and sunny patches of the landscape, compared to within closed and open habitats, where lizards would have to travel long distances to find sun and shade respectively. This would enable lizards to thermoregulate more, as costs of thermoregulation such as time and energy expenditure for shuttling between sun and shade are reduced (Huey and Webster, 1976). Short distances between sun and shade may also reduce predation risk (Herczeg et al. 2008). Temperature regulation and predation risk exhibit a trade off, as basking in open areas with more intense solar radiation can draw the attention of predators (Webb and Whiting, 2005). However, in semi-open areas, risk may be reduced as individuals can more easily take refuge from predators amongst vegetation, allowing for more efficient thermoregulation (Herczeg et al. 2008).

As LAI did not remain in the final multiple regression model for semi-open vegetation, it could be inferred that shade levels in this habitat approximate optimal levels for thermoregulation. Therefore, as long as habitat remains as semi-open, increasing or decreasing vegetation levels may not significantly affect opportunities for thermoregulation, since both shade and sun remain reasonably available, and thus would not affect predictions of body temperatures. In contrast, with intense shade amongst closed vegetation, small reductions in vegetation levels would increase solar radiation and raise operative temperatures, and hence have larger effects on T_b (Huey et al. 2012). The opposite effect would occur in open vegetation,

with small increases in vegetation enabling more shade for thermoregulation. This could explain why LAI is not included in the final semi-open model, whereas it remains in the model for the other vegetation types.

4.3 Variability in T_b with activity time

Overall, average body temperatures of nocturnal species were 9.2°C lower than diurnal species. This compares to a maximum difference in mean body temperature of 4.3°C between land cover types. This is consistent with the hypothesis that activity time has a greater effect on body temperature than habitat type (Stevenson, 1985). For example, within some habitats such as deserts, the daily temperature ranges could raise lizard body temperatures above lethal limits. Therefore lizards must behaviourally restrict activity times or shift between microhabitats to remain cool (Stevenson, 1985). However, the variation between night and day time body temperatures may be habitat dependent. Within closed, shaded habitats, air temperatures would be slow to cool at night; and heat radiation would be trapped by vegetation rather than lost to the atmosphere (Stevenson, 1985). Therefore, in closed environments, warmer nighttime air temperatures would likely permit smaller changes in body temperature with activity time compared to within open habitat. The effect of habitat type on body temperatures of nocturnal species was not investigated here due to limited sample size; this topic requires further research.

4.4 The effect of substrate on T_b and model predictions

Localized studies have suggested that fossorial and semi-aquatic species have lower body temperatures than ground-dwelling species (Avery, 1982; Shine and Madsen 1996; Seebacher and Grigg, 1997; López et al. 1998). I found no significant difference between body temperatures of these groups, suggesting this pattern may not be generalized beyond local scales. However, my sample size for fossorial and semi-aquatic species was low, so I may have lacked sufficient power to detect a difference. Indeed, the non-significant trend was for ground-dwelling species to have higher T_b ($32.4 \pm 0.39^\circ\text{C}$) than both fossorial ($29.5 \pm 1.85^\circ\text{C}$) and semi-aquatic species ($30.5 \pm 0.84^\circ\text{C}$).

The terrestrial multiple regression model explained more of the variation in body temperature than the global model. Although the increase in variation explained was small, it shows that excluding fossorial and semi-aquatic species can improve model fit. The increase in variation

explained was expected. This is because, for fossorial species, body temperatures are most strongly influenced by subterranean substrate temperature (López et al. 1998). Therefore, unless a fossorial lizard is residing close to the surface (Porter et al. 1973), average climatic conditions such as those used in these models would be less representative of the environments these lizards experience. That said, for a fossorial lizard to be captured and its body temperature measured, it would likely be residing at the surface but under rocks, rather than in burrows underground (Martin et al. 1990; López et al. 1998). In this case, the thickness of the rock rather than substrate temperature would have the greatest effect on operative temperatures, and hence lizard body temperatures (Huey et al. 1989; López et al. 1998). Similarly for semi-aquatic species, species are thought to largely thermoconform to water temperatures (Angilletta, 2009). Again, temperatures of this substrate are unlikely to be reflected accurately in average temperature measures such as T_{env} and temperature seasonality. Therefore, with fossorial and semi-aquatic species excluded, species were removed from the model whose environments are less well represented by the climatic variables in the model. Hence the proportion of variation in T_b explained by the model was expected to increase.

The multiple regression model for arboreal species explained 71.2% of the variation in body temperature. This was a similar proportion to the closed vegetation model, which explained 69.8%. The two models would be expected to be similar in the proportion variation explained, as many arboreal species would be expected to live amongst closed vegetation. Within this dataset, the greatest number of arboreal species did live amongst closed vegetation. However, this was equaled by the sum of arboreal species living amongst semi-open and open vegetation. Two arboreal species also lived in barren environments. These were *Varanus gilleni*, an arboreal pigmy monitor lizard associated with the desert oak (Casuarinae), whose body temperature was recorded in the Red Sands of the Great Victoria Desert, Australia (Pianka, 1994); and *Trapelus sanguinolentus*, a semi-arboreal agamid lizard whose body temperature was recorded at the Kyzylkum Desert, Uzbekistan (Clemann et al. 2008). This suggests that the similarity in variation explained between closed vegetation and arboreal models is not entirely a product of shared data, and increases confidence that body temperatures of arboreal species can largely be predicted by broadscale environmental data. However, body temperatures of arboreal species are strongly influenced by microclimatic conditions, such as changes in air temperature and wind speeds with vegetation height (Bakken, 1989). Such micro-scale environmental conditions cannot be captured by the broader scale climatic variables of these multiple regression models. This should be taken into consideration when interpreting model results, though the

high R^2 of our models suggest that at least across large spatial extents and climatic gradients, much of the variation in T_b is captured by macro-climatic conditions.

Although saxicolous species occupy specialist microhabitats, body temperatures are largely affected by surface temperature of the substrate and to a lesser extent by air temperatures and solar radiation (Al-Johany, 1995). It was hence expected that a large proportion of variation in body temperatures of these species would be explained by LST and T_{env} variables alone. This prediction was partially consistent with my multiple regression results, as LST and T_{env} were two of the three remaining main effect variables in the final model. Unlike arboreal, fossorial and semi-aquatic species, saxicolous species are surface dwelling and hence more exposed to ambient conditions. However, the model explained only 25.4% of the variation in body temperature ($R^2 = 0.254$, adjusted $R^2 = 0.205$). Therefore, although saxicolous species are known to be dependent on thigmothermy, and hence body temperatures are generally strongly correlated to rock temperatures, results suggest that other factors aside from environmental temperatures may play a large role in affecting saxicolous body temperatures. For saxicolous lizards, the combined effect of microclimatic variation and thermoregulatory behaviour may contribute to the low proportion of variation explained. For example, climbing onto higher rocks exposes lizards to cooler microclimates, with cooler air temperatures and higher wind regimes. Raising the body off the rock rather than flattening it to the rock surface reduces heat conduction and increases exposure to winds, whereas sitting on shaded sides of rocks increases convective heat loss and minimizes radiation absorbed (Al-Johany, 1995; Sabo, 2003). Therefore, lizards can use postural adjustments and rock height to behaviourally reduce their body temperatures (Porter and Gates, 1969). Additionally, saxicolous lizards also exploit crevices to regulate their body temperature, as crevices provide microclimates which are cooler than ambient temperatures at the surface (Schwarzkopf et al. 2010). Saxicolous lizards also use crevices as a means of predator avoidance, and retreat to them when threatened or injured by predators to avoid capture (Al-Johany, 1995; Schwarzkopf et al. 2010). Due to their high value for thermoregulation and predator avoidance, saxicolous lizards are often found in close proximity of crevices (Al-Johany, 1995). If an individual has just emerged from a crevice before capture, body temperatures would be lower than if it had been spending time on the rock surface due to the specialised microclimate. This would decouple relationships between body temperatures and broadscale climatic variables, contributing to the lower proportion of variation explained by the model.

The final multiple regression model for ground dwelling species explained 52.6% of the variation in body temperature ($R^2 = 0.526$, adjusted $R^2 = 0.495$). This was more variation

explained than for the model with all terrestrial species combined ($R^2 = 0.370$, adjusted $R^2 = 0.349$). Again, the increase in percentage variance explained is expected. This is because removing arboreal, saxicolous, fossorial, psammophilous and semi-aquatic species from the model excludes species whose body temperatures are more dependent on fine-scale microclimatic variables such as changes in wind speeds and air temperatures with height. It is likely that of all substrates, the environments of ground dwelling species are the best represented by broadscale environmental conditions. Hence models for ground dwelling species are able to explain more variation in body temperature through these variables.

Overall, broad-scale environmental data can be used to infer general trends about substrate and thermoregulatory abilities. However, such data cannot account for fine-scale microclimatic variation that influences body temperatures of species using different substrates. Recently, Kearney et al. (2014) simulated global estimates of microclimates based on monthly averages of macroclimate data. The dataset provides estimates for air temperature, wind speed, humidity, solar radiation, and substrate temperature at approximately 15 km resolution, which can be extracted for different locations. Different heights above and below ground, substrate type and shading levels can also be accounted for in microclimate estimates. This dataset could be applied to models to try to predict body temperatures of arboreal, fossorial, semi-aquatic and saxicolous species, whose body temperatures are more dependent on microclimatic conditions.

4.5 Model predictions with insularity

Sagonas et al. (2013) showed that insular lizards on Greece were less effective thermoregulators than the mainland species, as they inhabit more thermally benign environments. Therefore insular lizards showed a greater degree of thermoconformity (Sagonas et al. 2013). Results here indicate that this localized observation can be extrapolated to a global scale. The final insular multiple regression model explained 83.4% of the variation in body temperature through climatic variables, suggesting that island lizards are strong thermoconformers. In contrast, the final multiple regression model for mainland species explained only 32.5% of the variation. Although results here are a good indicator of broadscale patterns, relationships between body temperature and climatic variables may differ between islands, as islands vary greatly in biotic and abiotic characteristics (Meiri et al. 2013). For example, variability in habitat type between islands and on individual islands has been shown to influence the thermal biology of insular species (Foufopoulos et al 2011; Logan et al. 2013). Inclusion of habitat into studies conducted at fine spatial scales has

indicated that even on islands in close proximity with similar broad-scale temperatures, lizards could vary markedly in their vulnerability to global warming. Knowledge as to the effect of habitat on body temperatures should therefore also be applied when considering island systems.

5.0 CONCLUSION

Results here further our understanding of relationships between body temperatures and environmental variables at a global scale, and how they vary with habitat, substrate and insularity. Habitat affects the relative importance of environmental variables in models fitted to body temperature data worldwide. Therefore, species in different habitats face different threats with changing climate. Threats may vary from reduced canopy cover increasing the rate of warming in tropical forests, or changing precipitation and temperature seasonality affecting drought frequency and intensity in barren environments. Lizards in these habitats are predicted to be particularly sensitive to global warming (Sinervo et al. 2010), as body temperatures here are already approaching physiological limits, and these habitats will provide limited thermoregulatory opportunity with climate warming to remain cool (Huey et al. 2009; Kearney et al. 2009; Barrows, 2011). Incorporating climate and habitat data into models, including remotely sensed LAI, which can capture patterns shade availability, could significantly improve the ability of models to predict lizard body temperatures. Extending models to include future climates and shade levels from land cover and climate change scenarios may therefore provide more accurate predictions about which species and habitats are most vulnerable to climate change.

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Appendix A

Characteristics of the four global land-cover products use to derive the global 1 km consensus land cover dataset (Tuanmu and Jetz, 2014).

	<i>DISCover</i>	<i>GLC2000</i>	<i>MODIS2005</i>	<i>GlobCover</i>
<i>Sensor</i>	AVHRR	VEGETATION	MODIS2005	MERIS
<i>Satellite</i>	NOAA	SPOT	Aqua, Terra	ENVISAT
<i>Image acquisition time</i>	April 1992 - March 1993	November 1999 - December 2000	2005	December 2004 - June 2006
<i>Input data</i>	Monthly NDVI composites	Diverse composites of reflectance in four spectral bands, NDVI and/or derived metrics	32-day composites and annual metrics of nadir BRDF-adjusted reflectance in bands 1-7, EVI and LST	Bi-monthly surface reflectance composites of 13 spectral bands
<i>Classification technique</i>	Unsupervised classification	Flexible classification depending on the responsible institutions	Supervised classification decision tree	Per-pixel supervised and unsupervised classification; per-cluster unsupervised classification
<i>Processing sequence</i>	Continent-by-continent	Region-by-region	Global	Region-by-region
<i>Classification scheme</i>	IGBP, 17 classes	LCCS-based, 22 classes	IGBP, 17 classes	LCCS-based, 22 classes
<i>Spatial resolution</i>	1 km	1 km	500 m	300 m
<i>Overall accuracy</i>	66.9% (Scepan, 1999)	68.8% (Mayaux et al. 2006)	75% (Friedl et al. 2010)	73.1% (Bicheron et al. 2008)

NDVI, normalised difference vegetation index; LCCS, UN Land Cover Classification Scheme; BRDF, bidirectional reflectance distribution function; LST, Land Surface Temperature.

Data Source: DISCover (GLCC, version 2), <http://edc2.usgs.gov/glcc/glcc.php>; GCG2000 (Global Product, version 1.1), <http://bioval.jrc.ec.europa.eu/products/glc2000/products.php>; MODIS2005 (MCD12Q1, version 051), https://lpdaac.usgs.gov/products/modis_products_table/mcd12q1; GlobCover (2005-06, version 2.2), <http://due.esrin.esa.int/globcover>

Appendix B

Generalised land cover classes for harmonising the classification schemes of the four global land cover products. The numbers refer to the class codes for individual products (Tuanmu and Jetz, 2014).

Generalised land cover class	DISCover/MODIS2005	GLC2000	GlobCover
1. Evergreen/deciduous needleleaf trees	1. Evergreen needleleaf forest 3. Deciduous needleleaf forest	4. Tree cover, needle-leaved, evergreen 5. Tree cover, needle-leaved, deciduous	70. Closed needleleaved evergreen forest 90. Open needleleaved deciduous or evergreen forest
2. Evergreen broadleaf trees	2. Evergreen broadleaf forest	1. Tree cover, broadleaved, evergreen 7. Tree cover, regularly flooded, fresh and brackish water 8. Tree cover, regularly flooded, saline water	40. Closed to open broadleaved evergreen and/or semi-deciduous forest 160. Closed broadleaved forest regularly flooded - fresh water 170. Closed broadleaved semi-deciduous and/or evergreen forest regularly flooded, saline water
3. Deciduous broadleaf trees	4. Deciduous broadleaf forest	2. Tree cover, broadleaved, deciduous, closed 3. Tree cover, broadleaved, deciduous, open	50. Closed broadleaved deciduous forest 60. Open broadleaved deciduous forest
4. Mixed/other trees	5. Mixed forest 8. Woody savannah 9. Savannah	6. Tree cover, mixed leaf type 9. Mosaic: tree cover/other natural vegetation 10. Tree cover, burnt	100. Closed to open mixed broadleaved and needleleaved forest 110. Mosaic forest/shrubland (50-70%)/grassland (20-50%) 120. Mosaic grassland (50-70%)/forest/shrubland (20-50%)
5. Shrubs	6. Closed shrubland 7. Open shrubland	11. Shrub cover, closed-open, evergreen 12. Shrub cover, closed-open, deciduous	130. Closed to open shrubland
6. Herbaceous vegetation	10. Grasslands	13. Herbaceous cover, closed-open	140. Closed to open grassland
7. Cultivated and managed vegetation (including a mixture with natural vegetation)	12. Cropland 14. Cropland/natural vegetation	16. Cultivated and managed areas 17. Mosaic: cropland/tree cover/natural vegetation 18. Mosaic: cropland/shrub or grass cover	11. Post-flooding or irrigated croplands 14. Rain-fed croplands 20. Mosaic cropland (50-70%)/vegetation (grassland, shrubland, forest (20-50%)) 30. Mosaic vegetation (grassland, shrubland, forest) (50-70%)/cropland (20-50%)
8. Regularly flooded vegetation	11. Permanent wetlands	15. Regularly flooded shrub and/or herbaceous cover	180. Closed to open vegetation (grassland, shrubland, woody vegetation) on regularly flooded or waterlogged soil - fresh, brackish or saline water
9. Urban/built-up	13. Urban and built-up	22. Urban and built-up areas	190. Artificial surfaces and associated areas
10. Snow/ice	15. Snow and ice	21. Snow and ice	220. Permanent snow and ice
11. Barren	16. Barren	14. Sparse herbaceous or sparse shrub cover 19. Bare areas	150. Sparse vegetation (woody vegetation, shrubs, grassland) 200. Bare areas
12. Open water	17. Water	20. Water bodies	210. Water bodies

Appendix C

Pearson's r correlations between main effect variables. Highly collinear variables ($r > 0.7$) are in bold.

Environmental Temperature (T_{env} ; Temperature PCA axis 1 scores). Temperature Seasonality (Temperature PCA axis 2 scores). Precipitation (Precipitation PCA axis 1 scores). Precipitation Seasonality (Precipitation PCA axis 2 scores). Potential Evapotranspiration (PET; mm/month). Leaf Area Index (LAI). Land Surface Temperature (LST; Kelvin).

		<i>Pearson's r Correlations</i>								
		T_{env}	Temperature Seasonality	Precipitation	Precipitation Seasonality	Aridity	PET	LAI	LST (Day)	LST (Night)
T_{env}	<i>Pearson's r</i>	1.000	0.000	0.533	0.263	0.328	0.674	0.332	0.593	0.781
	<i>P</i>		1.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000
	<i>N</i>	564	564	563	563	564	564	564	564	562
Temperature Seasonality	<i>Pearson's r</i>	0.000	1.000	-0.310	-0.015	-0.388	0.497	-0.179	0.391	0.216
	<i>P</i>	1.000		0.000	0.726	0.000	0.000	0.000	0.000	0.000
	<i>N</i>	564	564	563	563	564	564	564	564	562
Precipitation	<i>Pearson's r</i>	0.533	-0.310	1.000	0.000	0.922	0.194	0.413	0.183	0.431
	<i>P</i>	0.000	0.000		1.000	0.000	0.000	0.000	0.000	0.000
	<i>N</i>	563	563	563	563	563	563	563	563	561
Precipitation Seasonality	<i>Pearson's r</i>	0.263	-0.015	0.000	1.000	-0.056	0.435	-0.061	0.261	0.158
	<i>P</i>	0.000	0.726	1.000		0.188	0.000	0.149	0.000	0.000
	<i>N</i>	563	563	563	563	563	563	563	563	561
Aridity	<i>Pearson's r</i>	0.328	-0.388	0.922	-0.056	1.000	-0.049	0.358	0.082	0.313
	<i>P</i>	0.000	0.000	0.000	0.188		0.247	0.000	0.052	0.000
	<i>N</i>	564	564	563	563	564	564	564	564	562
PET	<i>Pearson's r</i>	0.674	0.497	0.194	0.435	-0.049	1.000	0.129	0.554	0.508
	<i>P</i>	0.000	0.000	0.000	0.000	0.247		0.002	0.000	0.000
	<i>N</i>	564	564	563	563	564	564	564	564	562

<i>LAI</i>	<i>Pearson's r</i>	0.332	-0.179	0.413	-0.061	0.358	0.129	1.000	0.159	0.321
	<i>P</i>	0.000	0.000	0.000	0.149	0.000	0.002		0.000	0.000
	<i>N</i>	564	564	563	563	564	564	570	570	568
<i>Day LST</i>	<i>Pearson's r</i>	0.593	0.391	0.183	0.261	0.082	0.554	0.159	1.000	0.876
	<i>P</i>	0.000	0.000	0.000	0.000	0.052	0.000	0.000		0.000
	<i>N</i>	564	564	563	563	564	564	570	570	568
<i>Night LST</i>	<i>Pearson's r</i>	0.781	0.216	0.431	0.158	0.313	0.508	0.321	0.876	1.000
	<i>P</i>	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000	
	<i>N</i>	562	562	561	561	562	562	568	568	568

Appendix D

Data source, acquisition date and spatial resolution of raw and processed satellite and climate data.

	Name	Data Source	Acquisition Date	Spatial Resolution (km)
Raw Data				
<i>Bio 1</i>	Annual Mean Temperature	Bioclim	1950 - 2000	1
<i>Bio 2</i>	Mean Diurnal Range	Bioclim	1950 - 2000	1
<i>Bio 4</i>	Temperature Seasonality	Bioclim	1950 - 2000	1
<i>Bio 5</i>	Maximum Temperature Warmest Month	Bioclim	1950 - 2000	1
<i>Bio 6</i>	Minimum Temperature Coldest Month	Bioclim	1950 - 2000	1
<i>Bio 7</i>	Temperature Annual Range (Bio 5 - Bio 6)	Bioclim	1950 - 2000	1
<i>Bio 8</i>	Mean Temperature Wettest Quarter	Bioclim	1950 - 2000	1
<i>Bio 9</i>	Mean Temperature Driest Quarter	Bioclim	1950 - 2000	1
<i>Bio 10</i>	Mean Temperature Warmest Quarter	Bioclim	1950 - 2000	1
<i>Bio 11</i>	Mean Temperature Coldest Quarter	Bioclim	1950 - 2000	1
<i>Bio 12</i>	Annual Precipitation	Bioclim	1950 - 2000	1
<i>Bio 13</i>	Precipitation Wettest Month	Bioclim	1950 - 2000	1
<i>Bio 14</i>	Precipitation Driest Month	Bioclim	1950 - 2000	1
<i>Bio 14.5</i>	Precipitation Annual Range (Bio 13-Bio 14)	Bioclim	1950 - 2000	1
<i>Bio 15</i>	Precipitation Seasonality	Bioclim	1950 - 2000	1
<i>Bio 16</i>	Precipitation Wettest Quarter	Bioclim	1950 - 2000	1
<i>Bio 17</i>	Precipitation Driest Quarter	Bioclim	1950 - 2000	1
<i>Bio 18</i>	Precipitation Warmest Quarter	Bioclim	1950 - 2000	1
<i>Bio 19</i>	Precipitation Coldest Quarter	Bioclim	1950 - 2000	1
<i>Aridity</i>	Global Aridity	CGIAR	1950 - 2000	1
<i>PET</i>	Global Potential-Evapotranspiration	CGIAR	1950 - 2000	1
<i>LAI</i>	Glass Leaf Area Index	GLCF	January 2005, July 2005	5.6
<i>Day LST</i>	Day Land Surface Temperature	MODIS2005 (MOD11C3)	January 2005, July 2005	5.6
<i>Night LST</i>	Night Land Surface Temperature	MODIS2005 (MOD11C3)	January 2005, July 2005	5.6

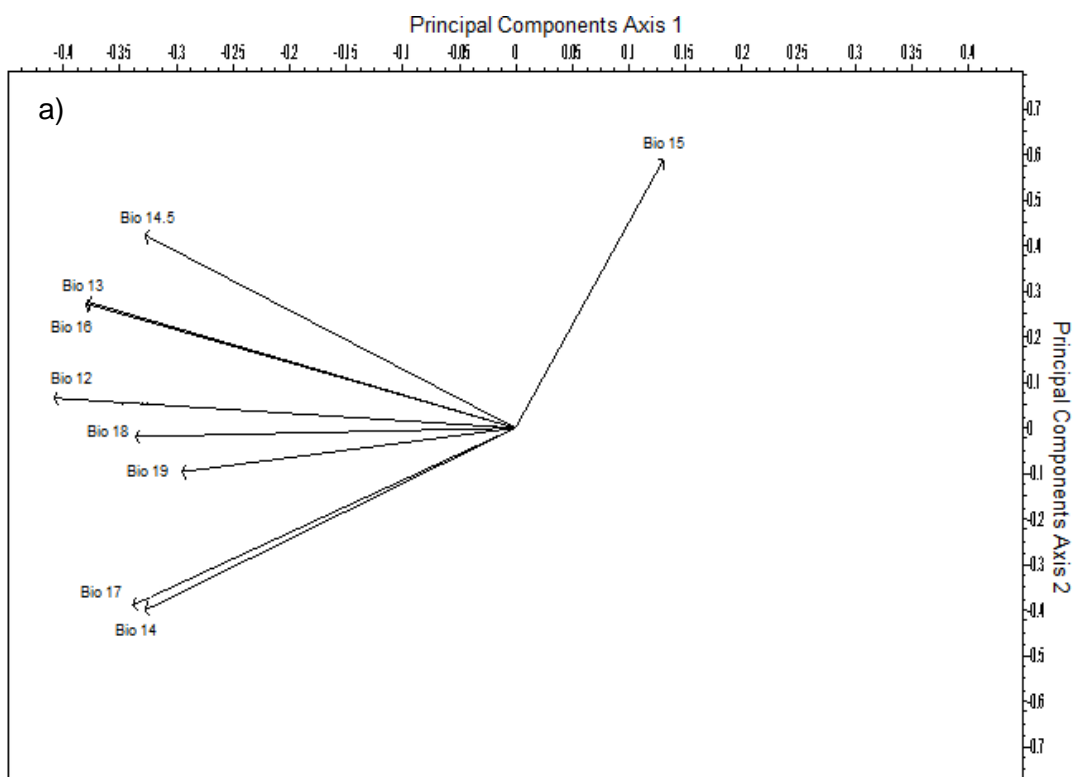
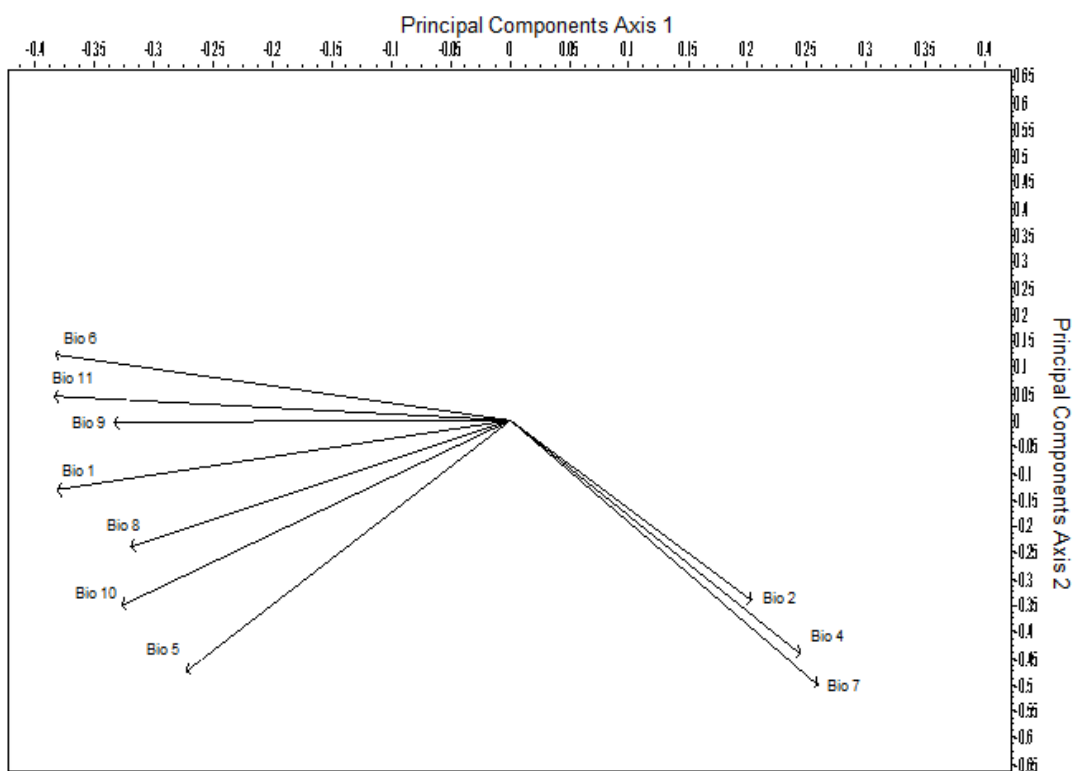
<i>Land Cover 1</i>	Evergreen/deciduous needle-leaf trees	EarthEnv	1992 - 2005	1
<i>Land Cover 2</i>	Evergreen broadleaf trees	EarthEnv	1992 - 2005	1
<i>Land Cover 3</i>	Deciduous broadleaf trees	EarthEnv	1992 - 2005	1
<i>Land Cover 4</i>	Mixed/Other trees	EarthEnv	1992 - 2005	1
<i>Land Cover 5</i>	Shrubs	EarthEnv	1992 - 2005	1
<i>Land Cover 6</i>	Herbaceous Vegetation	EarthEnv	1992 - 2005	1
<i>Land Cover 7</i>	Cultivated/Managed Vegetation	EarthEnv	1992 - 2005	1
<i>Land Cover 8</i>	Regularly flooded vegetation	EarthEnv	1992 - 2005	1
<i>Land Cover 9</i>	Urban	EarthEnv	1992 - 2005	1
<i>Land Cover 11</i>	Barren	EarthEnv	1992 - 2005	1
<i>Land Cover 12</i>	Water	EarthEnv	1992 - 2005	1

Processed Data

T_{env}	Environmental Temperature	Bio 1 - Bio 11 PC1 Scores	1950 - 2000	1
<i>Temperature Seasonality</i>	Temperature Seasonality	Bio 1 - Bio 11 PC2 Scores	1950 - 2000	1
<i>Precipitation</i>	Precipitation	Bio 12 - Bio 19 PC1 Scores	1950 - 2000	1
<i>Precipitation Seasonality</i>	Precipitation Seasonality	Bio 12 - Bio 19 PC2 Scores	1950 - 2000	1
<i>LAI</i>	Summer Leaf Area Index	LAI July 2005 (NH) and LAI January 2005 (SH)	2005	5.6
<i>LST</i>	Summer Land Surface Temperature	Day LST July 2005 (NH) and Day LST January 2005 (SH)	2005	5.6
<i>Closed Vegetation</i>	Closed Vegetation	Land Cover 1 - 3	1992 - 2005	1
<i>Semi-Open Vegetation</i>	Semi-Open Vegetation	Land Cover 4 - 5	1992 - 2005	1
<i>Open Vegetation</i>	Open Vegetation	Land Cover 6 - 8	1992 - 2005	1
<i>Urban</i>	Urban	Land Cover 9	1992 - 2005	1
<i>Barren</i>	Barren	Land Cover 11	1992 - 2005	1

Data source: Bioclim, <http://www.worldclim.org/bioclim>; CGIAR, <http://www.cgiar-csi.org/data/global-aridity-and-pet-database>; GLCF, <http://glcf.umd.edu/data/lai>; MODIS2005 (MOD11C3, version 004), https://www.lpdaac.usgs.gov/products/modis_products_table/mod11c3; EarthEnv, <http://www.earthenv.org/landcover.html>

Appendix E



Principal Components Correlation matrices of a) BioClim temperature variables (Bio 1- Bio 11, Bio 3 excluded), and b) BioClim precipitation variables (Bio 12 – Bio 19). Refer to Appendix D for descriptions of BioClim variables.

Appendix F

Table F1: Pearson's *r* correlations between BioClim variables and lizard body temperature.

		Pearson's <i>r</i> correlations		
		<i>Pearson's r</i>	<i>P</i>	<i>n</i>
<i>Bio 1</i>	Annual Mean Temperature	0.254	0.000	426
<i>Bio 2</i>	Mean Diurnal Range	0.198	0.000	426
<i>Bio 4</i>	Temperature Seasonality	0.014	0.773	426
<i>Bio 5</i>	Maximum Temperature Warmest Month	0.361	0.000	426
<i>Bio 6</i>	Minimum Temperature Coldest Month	0.139	0.004	426
<i>Bio 7</i>	Temperature Annual Range (Bio 5 - Bio 6)	0.112	0.021	426
<i>Bio 8</i>	Mean Temperature Wettest Quarter	0.262	0.000	426
<i>Bio 9</i>	Mean Temperature Driest Quarter	0.18	0.000	426
<i>Bio 10</i>	Mean Temperature Warmest Quarter	0.3	0.000	426
<i>Bio 11</i>	Mean Temperature Coldest Quarter	0.198	0.000	426
<i>Bio 12</i>	Annual Precipitation	-0.063	0.197	426
<i>Bio 13</i>	Precipitation Wettest Month	0.014	0.767	426
<i>Bio 14</i>	Precipitation Driest Month	-0.236	0.000	426
<i>Bio 14.5</i>	Precipitation Annual Range (Bio 13-Bio 14)	0.084	0.085	426
<i>Bio 15</i>	Precipitation Seasonality	0.169	0.000	426
<i>Bio 16</i>	Precipitation Wettest Quarter	0.019	0.699	426
<i>Bio 17</i>	Precipitation Driest Quarter	-0.224	0.000	426
<i>Bio 18</i>	Precipitation Warmest Quarter	-0.157	0.001	426
<i>Bio 19</i>	Precipitation Coldest Quarter	-0.066	0.174	426

Table F2: Pearson's Correlations between BioClim variables. Highly collinear variables ($r > 0.7$) are in bold.

		Pearson's r Correlations																		
		Bio 1	Bio 2	Bio 4	Bio 5	Bio 6	Bio 7	Bio 8	Bio 9	Bio 10	Bio 11	Bio 12	Bio 13	Bio 14	Bio 14.5	Bio 15	Bio 16	Bio 17	Bio 18	Bio 19
Bio 1	Pearson's r	1.000	-0.352	-0.522	0.849	0.932	-0.511	0.915	0.851	0.929	0.964	0.545	0.587	0.191	0.589	0.017	0.589	0.218	0.434	0.189
	P		0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000	.721	0.000	0.000	0.000	0.000
	N	426	426	426	426	426	426	426	426	426	426	426	426	426	426	426	426	426	426	426
Bio 2	Pearson's r	-0.352	1.000	0.330	-0.034	-0.563	0.694	-0.207	-0.441	-0.281	-0.396	-0.436	-0.334	-0.478	-0.228	0.426	-0.328	-0.493	-0.314	-0.378
	P			0.000	.490	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000
	N	426	426	426	426	426	426	426	426	426	426	426	426	426	426	426	426	426	426	426
Bio 4	Pearson's r	-0.522	0.330	1.000	-0.047	-0.731	0.899	-0.389	-0.466	-0.171	-0.730	-0.600	-0.647	-0.230	-0.644	-0.166	-0.645	-0.285	-0.436	-0.293
	P				.336	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000	.001	0.000	0.000	0.000	0.000
	N	426	426	426	426	426	426	426	426	426	426	426	426	426	426	426	426	426	426	426
Bio 5	Pearson's r	0.849	-0.034	-0.047	1.000	0.625	0.003	0.819	0.725	0.961	0.695	0.272	0.326	-0.005	0.359	0.002	0.332	0.012	0.194	0.025
	P		.490	.336		0.000	.959	0.000	0.000	0.000	0.000	0.000	0.000	.924	0.000	.649	0.000	.803	0.000	.614
	N	426	426	426	426	426	426	426	426	426	426	426	426	426	426	426	426	426	426	426
Bio 6	Pearson's r	0.932	-0.563	-0.731	0.625	1.000	-0.779	0.782	0.861	0.765	0.978	0.657	0.677	0.311	0.654	-0.045	0.676	0.343	0.473	0.346
	P		0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000	.357	0.000	0.000	0.000	0.000
	N	426	426	426	426	426	426	426	426	426	426	426	426	426	426	426	426	426	426	426
Bio 7	Pearson's r	-0.511	0.694	0.899	0.003	-0.779	1.000	-0.344	-0.520	-0.209	-0.695	-0.624	-0.606	-4.020	-0.549	0.075	-0.599	-0.429	-0.450	-0.423
	P		0.000	0.000	.959	0.000		0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000	.122	0.000	0.000	0.000	0.000
	N	426	426	426	426	426	426	426	426	426	426	426	426	426	426	426	426	426	426	426
Bio 8	Pearson's r	0.915	-0.207	-0.389	-0.819	0.782	-0.344	1.000	0.597	0.881	0.849	0.455	0.481	0.171	0.478	0.003	0.483	0.193	0.485	0.049
	P		0.000	0.000	0.000	0.000	0.000		0.000	0.000	0.000	0.000	0.000	0.000	0.000	.956	0.000	0.000	0.000	.311
	N	426	426	426	426	426	426	426	426	426	426	426	426	426	426	426	426	426	426	426

Bio 9	Pearson's <i>r</i>	0.851	-0.441	-0.466	0.725	0.861	-0.520	0.597	1.000	0.793	0.835	0.475	0.519	0.141	0.528	0.010	0.519	0.171	0.204	0.315
	<i>P</i>	0.000	0.000	0.000	0.000	0.000	0.000	0.000		0.000	0.000	0.000	0.000	.004	0.000	.840	0.000	0.000	0.000	0.000
	<i>N</i>	426	426	426	426	426	426	426	426	426	426	426	426	426	426	426	426	426	426	426
Bio 10	Pearson's <i>r</i>	0.929	-0.281	-0.171	0.961	0.765	-0.209	0.881	0.793	1.000	0.798	0.373	0.399	0.126	0.402	-0.065	0.402	0.145	0.305	0.102
	<i>P</i>	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000		0.000	0.000	0.000	.009	0.000	.184	0.000	.003	0.000	.035
	<i>N</i>	426	426	426	426	426	426	426	426	426	426	426	426	426	426	426	426	426	426	426
Bio 11	Pearson's <i>r</i>	0.964	-0.393	-0.730	0.695	0.978	-0.695	0.849	0.835	0.789	1.000	0.626	0.671	0.227	0.671	0.056	0.673	0.258	0.478	0.249
	<i>P</i>	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000		0.000	0.000	0.000	0.000	.247	0.000	0.000	0.000	0.000
	<i>N</i>	426	426	426	426	426	426	426	426	426	426	426	426	426	426	426	426	426	426	426
Bio 12	Pearson's <i>r</i>	0.545	-0.436	-0.600	0.272	0.657	-0.624	0.455	0.475	0.373	0.625	1.000	0.929	0.693	0.820	-0.230	0.938	0.726	0.754	0.660
	<i>P</i>	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000		0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000
	<i>N</i>	426	426	426	426	426	426	426	426	426	426	426	426	426	426	426	426	426	426	426
Bio 13	Pearson's <i>r</i>	0.587	-0.334	-0.647	0.326	0.677	-0.606	0.481	0.519	0.399	0.671	0.929	1.000	0.453	0.967	0.040	0.996	0.486	0.660	0.580
	<i>P</i>	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000	.415	0.000	0.000	0.000	0.000
	<i>N</i>	426	426	426	426	426	426	426	426	426	426	426	426	426	426	426	426	426	426	426
Bio 14	Pearson's <i>r</i>	0.191	-0.478	-0.230	-0.005	0.311	-0.402	0.171	0.141	0.126	0.228	0.693	0.453	1.000	0.209	-0.596	0.456	0.991	0.676	0.601
	<i>P</i>	0.000	0.000	0.000	.924	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000		0.000	0.000	0.000	0.000	0.000	0.000
	<i>N</i>	426	426	426	426	426	426	426	426	426	426	426	426	426	426	426	426	426	426	426
Bio 14.5	Pearson's <i>r</i>	0.589	-0.228	-0.644	0.359	0.654	-0.549	0.478	0.528	0.402	0.671	0.820	0.976	0.209	1.000	0.215	0.961	0.248	0.529	0.464
	<i>P</i>	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000
	<i>N</i>	426	426	426	426	426	426	426	426	426	426	426	426	426	426	426	426	426	426	426
Bio 15	Pearson's <i>r</i>	0.017	0.426	-0.166	0.022	-0.045	0.075	0.003	0.010	-0.065	0.056	-0.230	0.040	-0.596	0.215	1.000	0.027	-0.605	-0.254	-0.254
	<i>P</i>	.721	0.000	.001	.649	.357	.122	.956	.840	.184	.247	0.000	.415	0.000	0.000		.579	0.000	0.000	0.000
	<i>N</i>	426	426	426	426	426	426	426	426	426	426	426	426	426	426	426	426	426	426	426

Bio 16	Pearson's <i>r</i>	0.589	-0.328	-0.545	0.332	0.676	-0.599	0.483	0.519	0.402	0.673	0.938	0.996	0.456	0.961	0.027	1.000	0.486	0.661	0.576
	<i>P</i>	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000	.579		0.000	0.000	0.000
	<i>N</i>	426	426	426	426	426	426	426	426	426	426	426	426	426	426	426	426	426	426	426
Bio 17	Pearson's <i>r</i>	0.218	-0.493	-0.258	0.012	0.343	-0.429	0.193	0.171	0.145	0.258	0.726	0.486	0.991	0.248	-0.605	0.486	1.000	0.678	0.630
	<i>P</i>	0.000	0.000	0.000	.803	0.000	0.000	0.000	0.000	.003	0.000	0.000	0.000	0.000	0.000	0.000	0.000		0.000	0.000
	<i>N</i>	426	426	426	426	426	426	426	426	426	426	426	426	426	426	426	426	426	426	426
Bio 18	Pearson's <i>r</i>	0.434	-0.314	-0.436	0.194	0.473	-0.450	0.485	0.204	0.305	0.478	0.754	0.660	0.676	0.529	-0.254	0.661	0.687	1.000	0.198
	<i>P</i>	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000
	<i>N</i>	426	426	426	426	426	426	426	426	426	426	426	426	426	426	426	426	426	426	426
Bio 19	Pearson's <i>r</i>	0.189	-0.387	-0.293	0.025	0.346	-0.423	0.049	0.315	0.102	0.249	0.660	0.580	0.601	0.464	-0.254	0.576	0.630	0.198	1.000
	<i>P</i>	0.000	0.000	0.000	0.614	0.000	0.000	0.311	0.000	0.035	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000	
	<i>N</i>	426	426	426	426	426	426	426	426	426	426	426	426	426	426	426	426	426	426	426

Appendix G

Table G1: Summary of lizard body temperatures (°C) globally, and by land cover, activity time, substrate and insularity.

Category	Lizard Body Temperature (°C) Summary						
	<i>N</i>	<i>Mean</i>	<i>SE</i>	<i>Min</i>	<i>Max</i>	<i>Range</i>	<i>SD</i>
Global	406	31.5	0.257	10.9	39.6	28.7	5.176
Land Cover							
<i>Closed Vegetation</i>	64	28.7	0.615	17.4	39.4	22.0	4.917
<i>Semi-Open Vegetation</i>	152	32.4	0.398	10.9	39.6	28.7	4.907
<i>Open Vegetation</i>	114	31.0	0.532	14.7	39.4	24.7	5.676
<i>Urban</i>	31	33.0	0.715	22.1	38.9	16.8	3.989
<i>Barren</i>	41	32.7	0.641	15.3	37.7	22.4	4.106
Activity Time							
<i>Diurnal</i>	383	32.0	0.240	12.5	39.6	27.1	4.704
<i>Nocturnal</i>	23	22.8	1.043	10.9	31.5	20.6	5.000
Substrate							
Terrestrial	386	31.5	0.266	10.9	39.6	28.7	5.224
Ground	197	32.4	0.390	12.5	39.6	27.1	5.476
Arboreal	90	29.8	0.460	19.0	38.9	19.9	4.368
Saxicolous	83	30.9	0.571	10.9	37.2	26.3	5.200
<i>Psammophilous</i>	16	34.1	0.758	25.8	37.7	11.9	3.033
Fossorial	9	29.5	1.848	22.0	36.7	14.7	5.543
Semi-aquatic	9	30.5	0.838	26.4	34.0	7.6	2.515
Insularity							
<i>Island</i>	77	27.4	0.624	10.9	38.5	27.6	5.475
<i>Mainland</i>	329	32.4	0.255	12.5	39.6	27.1	4.618

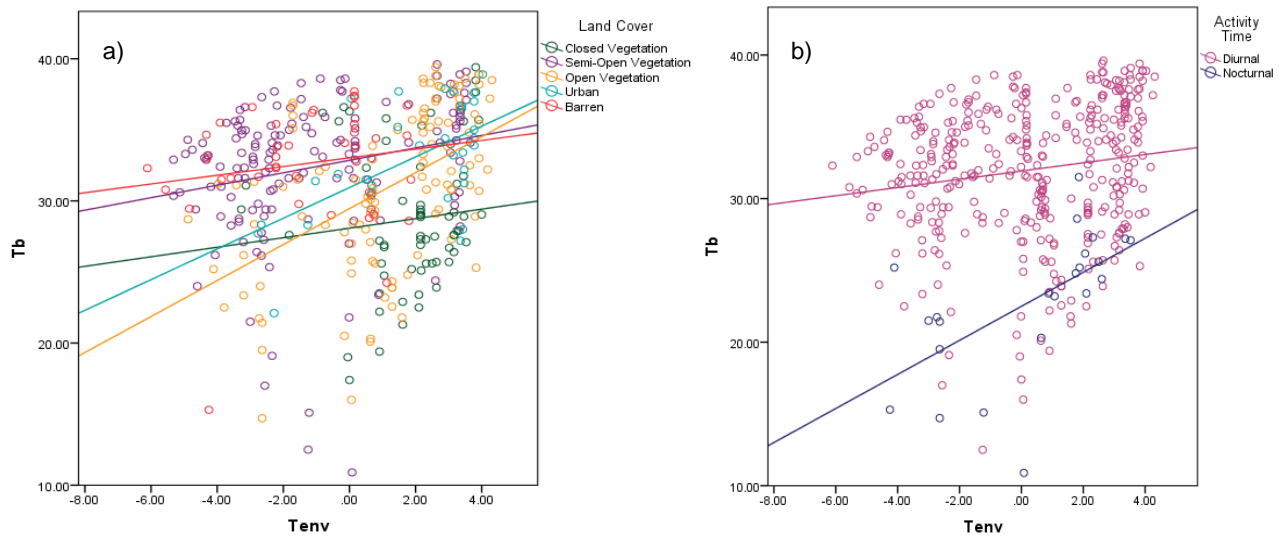
Table G2: Kruskal-Wallis and Kruskal Wallis post-hoc tests comparing body temperatures of lizards with a) land cover and b) substrate. Kruskal-Wallis is used to compare groups as Levene's test indicates significant heterogeneity of variances. $P < 0.05$ = Significant difference in average body temperatures between groups.

a) Land Cover

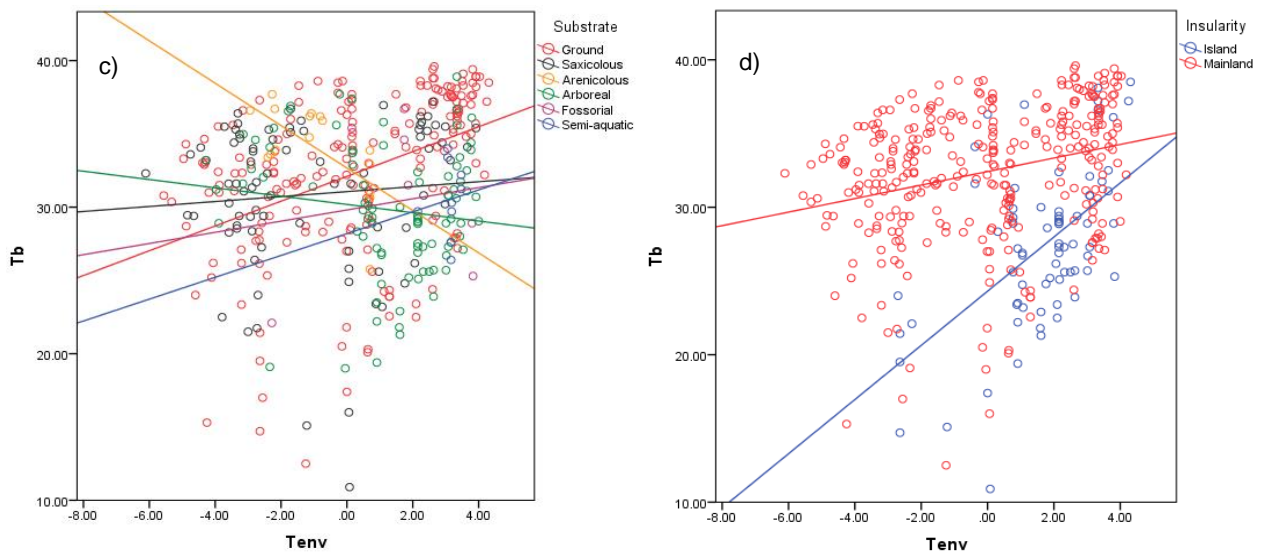
Variable	Test	Test Statistic	df	P
Land Cover	<i>Levene's</i>	3.039	4	0.017
	<i>Kruskal-Wallis</i>	34.145	4	0.000
Land Cover 1	Land Cover 2	Std. Test Statistic	SE	P
<i>Closed Vegetation</i>	<i>Semi-Open Vegetation</i>	-5.474	17.765	0.000
<i>Closed Vegetation</i>	<i>Open Vegetation</i>	-3.807	18.746	0.000
<i>Closed Vegetation</i>	<i>Urban</i>	-3.729	25.204	0.000
<i>Closed Vegetation</i>	<i>Barren</i>	-4.335	24.391	0.000
<i>Semi-Open Vegetation</i>	<i>Barren</i>	-0.393	21.611	0.695
<i>Open Vegetation</i>	<i>Semi-Open Vegetation</i>	1.731	14.951	0.083
<i>Open Vegetation</i>	<i>Urban</i>	-0.97	23.306	0.332
<i>Open Vegetation</i>	<i>Barren</i>	-1.533	22.242	0.125
<i>Urban</i>	<i>Semi-Open Vegetation</i>	0.145	22.525	0.885
<i>Urban</i>	<i>Barren</i>	-0.419	28.048	0.675

b) Substrate

Variable	Test	Test Statistic	df	P
Substrate	<i>Levene's</i>	2.604	5	0.025
	<i>Kruskal-Wallis</i>	34.239	5	0.000
Substrate 1	Substrate 2	Std. Test Statistic	SE	P
<i>Ground</i>	<i>Saxicolous</i>	2.562	15.280	0.156
<i>Ground</i>	<i>Psammophilous</i>	-1.111	30.354	0.266
<i>Ground</i>	<i>Arboreal</i>	5.126	14.856	0.000
<i>Ground</i>	<i>Fossorial</i>	1.784	39.801	0.074
<i>Ground</i>	<i>Semi-aquatic</i>	1.775	39.801	0.076
<i>Saxicolous</i>	<i>Psammophilous</i>	-2.286	31.881	0.334
<i>Saxicolous</i>	<i>Arboreal</i>	2.082	17.770	0.037
<i>Saxicolous</i>	<i>Fossorial</i>	0.777	40.978	0.437
<i>Saxicolous</i>	<i>Semi-aquatic</i>	0.769	40.978	0.442
<i>Psammophilous</i>	<i>Arboreal</i>	3.469	31.680	0.008
<i>Psammophilous</i>	<i>Fossorial</i>	2.153	48.653	0.470
<i>Psammophilous</i>	<i>Semi-aquatic</i>	2.146	48.653	0.478
<i>Arboreal</i>	<i>Fossorial</i>	-0.126	40.822	0.899
<i>Arboreal</i>	<i>Semi-aquatic</i>	-0.134	40.822	0.892
<i>Fossorial</i>	<i>Semi-aquatic</i>	-0.003	55.044	0.995



Land Cover	Equation	Activity Time	Equation
<i>Closed Vegetation</i>	$y = 28.08 + 0.34x$	<i>Diurnal</i>	$y = 31.93 + 0.29x$
<i>Semi-Open Vegetation</i>	$y = 32.86 + 0.44x$	<i>Nocturnal</i>	$y = 22.50 + 1.19x$
<i>Open Vegetation</i>	$y = 29.46 + 1.27x$		
<i>Urban</i>	$y = 30.94 + 1.08x$		
<i>Barren</i>	$y = 33.21 + 0.38x$		



Substrate	Equation	Insularity	Equation
<i>Terrestrial</i>	$y = 31.50 + 0.37x$	<i>Island</i>	$y = 24.31 + 1.84x$
<i>Ground</i>	$y = 32.10 + 0.85x$	<i>Mainland</i>	$y = 32.42 + 0.46x$
<i>Arboreal</i>	$y = 30.18 - 0.28x$		
<i>Saxicolous</i>	$y = 31.06 + 0.17x$		
<i>Psammophilous</i>	$y = 32.67 - 1.45x$		
<i>Fossorial</i>	$y = 29.81 + 0.38x$		
<i>Semi-aquatic</i>	$y = 28.20 + 0.75x$		

Figure G1: Relationships between body temperature (T_b ; °C) and Environmental Temperature (T_{env} ; Temperature PCA axis 1 scores) by a) land cover, b) activity time, c) substrate and d) insularity.

Table G3: ANCOVA post-hoc with Bonferroni adjustment comparing how the slope of the relationship between body temperature (T_b ; °C) and Environmental Temperature (T_{env}) varies between land covers, activity times, substrates and with insularity. $P < 0.05$ = Significant difference in the slope of the relationship between the two indicated groups.

Land Cover		P	Activity Time		P
Closed Vegetation	Semi-Open Vegetation	0.800	Diurnal	Nocturnal	0.026
Closed Vegetation	Open Vegetation	0.029			
Closed Vegetation	Urban	0.176			
Closed Vegetation	Barren	0.927			
Semi-Open Vegetation	Open Vegetation	0.001			
Semi-Open Vegetation	Urban	0.132			
Semi-Open Vegetation	Barren	0.873			
Open Vegetation	Urban	0.676			
Open Vegetation	Barren	0.020			
Urban	Barren	0.132			
Substrate		P	Insularity		P
Ground	Saxicolous	0.006	Island	Mainland	0.000
Ground	Psammophilous	0.016			
Ground	Arboreal	0.000			
Ground	Fossorial	0.614			
Ground	Semi-aquatic	0.982			
Saxicolous	Psammophilous	0.627			
Saxicolous	Arboreal	0.160			
Saxicolous	Fossorial	0.820			
Saxicolous	Semi-aquatic	0.627			
Psammophilous	Arboreal	0.230			
Psammophilous	Fossorial	0.163			
Psammophilous	Semi-aquatic	0.627			
Arboreal	Fossorial	0.481			
Arboreal	Semi-aquatic	0.816			
Fossorial	Semi-aquatic	0.936			

Appendix H

Table H1: Linear regressions between environmental variables and body temperature (T_b ; °C) at a global scale.

Environmental Temperature (T_{env} ; Temperature PCA axis 1 scores). Temperature Seasonality (Temperature PCA axis 2 scores).

Precipitation (Precipitation PCA axis 1 scores). Precipitation Seasonality (Precipitation PCA axis 2 scores). Potential Evapotranspiration

(PET; mm/month). Leaf Area Index (LAI). Land Surface Temperature (LST; Kelvin).

Category	Variable	df	<i>r</i>	R^2	Adjusted R^2	Residual SE	SE	<i>t</i>	<i>P</i>	Equation
Global	T_{env}	398	0.173	0.030	0.027	5.086	0.097	3.503	0.001	$y = 31.38 + 0.34x$
	Temperature Seasonality	398	0.324	0.105	0.103	4.884	0.169	6.843	0.000	$y = 31.71 + 1.16x$
	Precipitation	397	0.117	0.014	0.011	5.122	0.107	-2.347	0.019	$y = 31.54 - 0.25x$
	Precipitation Seasonality	397	0.206	0.042	0.040	5.047	0.180	4.190	0.040	$y = 31.45 + 0.76x$
	PET	398	0.328	0.108	0.105	4.877	0.001	6.930	0.000	$y = 24.26 + 5.25 \times 10^{-3}x$
	LAI	396	0.194	0.038	0.035	5.105	0.016	-3.838	0.000	$y = 32.64 - 0.06x$
	LST	404	0.319	0.102	0.100	4.912	0.001	6.764	0.000	$y = -37.9 + 4.57 \times 10^{-3}x$

Table H2: Linear regressions between environmental variables and body temperature (T_b ; °C) with land cover.

Environmental Temperature (T_{env} ; Temperature PCA axis 1 scores). Temperature Seasonality (Temperature PCA axis 2 scores). Precipitation (Precipitation PCA axis 1 scores). Precipitation Seasonality (Precipitation PCA axis 2 scores). Potential Evapotranspiration (PET; mm/month). Leaf Area Index (LAI). Land Surface Temperature (LST; Kelvin).

Category	Variable	df	r	R ²	Adjusted R ²	Residual SE	SE	t	P	Equation
Closed Vegetation	T_{env}	62	0.106	0.011	-0.005	4.929	0.399	0.839	0.405	$y = 28.08 + 0.34x$
	Temperature Seasonality	62	0.409	0.168	0.154	4.523	0.697	3.533	0.001	$y = 30.34 + 2.46x$
	Precipitation	62	0.277	0.077	0.062	4.763	0.219	-2.271	0.027	$y = 30.23 - 0.50x$
	Precipitation Seasonality	62	0.337	0.114	0.100	4.666	0.461	2.821	0.006	$y = 29.01 + 1.30x$
	PET	62	0.135	0.018	0.002	4.911	0.003	1.074	0.287	$y = 24.01 + 3.20 \times 10^{-3}x$
	LAI	62	0.408	0.166	0.153	4.527	0.067	-3.514	0.001	$y = 38.49 - 0.23x$
	LST	62	0.329	0.108	0.094	4.681	0.004	2.745	0.008	$y = -132.40 + 0.01x$
Semi-Open Vegetation	T_{env}	149	0.233	0.054	0.048	0.054	0.150	2.921	0.004	$y = 32.86 + 0.44x$
	Temperature Seasonality	149	0.468	0.219	0.214	4.329	0.235	6.471	0.000	$y = 32.42 + 1.52x$
	Precipitation	149	0.047	0.002	-0.005	4.894	0.252	0.570	0.569	$y = 32.51 + 0.14x$
	Precipitation Seasonality	149	0.139	0.019	0.013	4.852	0.270	1.710	0.089	$y = 32.17 + 0.46x$
	PET	149	0.435	0.190	0.184	4.411	0.001	5.904	0.000	$y = 24.52 + 5.89 \times 10^{-3}x$
	LAI	150	0.019	0.000	-0.006	4.922	0.037	-0.234	0.816	$y = 32.45 - 0.01x$
	LST	150	0.313	0.098	0.092	4.675	0.001	4.041	0.000	$y = -29.46 + 4.06 \times 10^{-3}x$

Open Vegetation	T _{env}	110	0.509	0.260	0.253	4.874	0.204	6.209	0.000	y = 29.46 + 1.27x
	Temperature Seasonality	110	0.212	0.045	0.036	5.535	0.562	2.274	0.025	y = 31.50 + 1.28x
	Precipitation	110	0.223	0.050	0.041	5.522	0.318	2.394	0.018	y = 30.50 + 0.76x
	Precipitation Seasonality	110	0.264	0.070	0.061	5.463	0.400	2.874	0.005	y = 31.21 + 1.15x
	PET	110	0.425	0.180	0.173	5.128	0.002	4.920	0.000	y = 20.26 + 7.77x10 ⁻³
	LAI	108	0.118	0.014	0.005	5.754	0.042	1.231	0.221	y = 30.05 + 0.05x
	LST	112	0.265	0.070	0.062	5.498	0.002	2.905	0.004	y = -74.89 + 7.02x10 ⁻³ x
	Urban	T _{env}	29	0.580	0.336	0.313	3.298	0.282	3.830	0.001
	Temperature Seasonality	29	0.063	0.004	-0.030	4.039	0.726	-0.339	0.737	y = 32.92 - 0.25x
	Precipitation	29	0.444	0.197	0.170	3.626	0.396	2.670	0.012	y = 31.77 + 1.06x
	Precipitation Seasonality	29	0.055	0.003	-0.031	4.041	0.453	0.298	0.768	y = 32.95 + 0.13x
	PET	29	0.344	0.119	0.088	3.800	0.002	1.974	0.058	y = 20.28 + 4.53x10 ⁻³ x
	LAI	29	0.035	0.001	-0.033	4.045	0.090	-0.188	0.852	y = 32.21 - 0.02x
	LST	29	0.054	0.003	-0.011	4.000	0.003	0.825	0.416	y = -10.31 + 2.86x10 ⁻³ x
Barren	T _{env}	39	0.211	0.045	0.020	4.064	0.282	1.350	0.185	y = 33.21 + 0.38x
	Temperature Seasonality	39	0.152	0.023	-0.002	4.110	0.253	0.959	0.343	y = 32.59 + 0.24x
	Precipitation	38	0.335	0.112	0.089	3.745	0.818	2.193	0.035	y = 37.43 + 1.79x
	Precipitation Seasonality	38	0.168	0.028	0.003	3.918	0.793	-1.052	0.299	y = 32.74 - 0.83x
	PET	39	0.354	0.126	0.103	3.889	0.002	2.366	0.023	y = 27.14 + 4.25x10 ⁻³ x
	LAI	38	0.337	0.114	0.091	3.914	0.388	2.209	0.033	y = 31.60 + 0.86x
	LST	39	0.306	0.093	0.070	3.959	0.001	2.005	0.052	y = -10.53 + 2.76x10 ⁻³ x

Table H3: Linear regressions between environmental variables and body temperature (T_b , °C) with activity time.

Environmental Temperature (T_{env} ; Temperature PCA axis 1 scores). Temperature Seasonality (Temperature PCA axis 2 scores). Precipitation (Precipitation PCA axis 1 scores). Precipitation Seasonality (Precipitation PCA axis 2 scores). Potential Evapotranspiration (PET; mm/month). Leaf Area Index (LAI). Land Surface Temperature (LST; Kelvin).

Category	Variable	df	r	R ²	Adjusted R ²	Residual SE	SE	t	P	Equation
Diurnal	T_{env}	375	0.165	0.027	0.025	4.615	0.090	3.242	0.001	$y = 31.93 + 0.29x$
	Temperature Seasonality	375	0.368	0.136	0.133	4.350	0.159	7.671	0.000	$y = 32.25 + 1.22x$
	Precipitation	374	0.156	0.024	0.022	4.610	0.103	-3.064	0.002	$y = 32.08 - 0.31x$
	Precipitation Seasonality	374	0.202	0.041	0.038	4.572	0.168	3.982	0.000	$y = 31.98 + 0.67x$
	PET	375	0.309	0.095	0.093	4.450	0.001	6.283	0.000	$y = 2.58 + 4.53x$
	LAI	374	0.227	0.052	0.049	4.593	0.015	-4.512	0.000	$y = 33.23 - 0.07x$
	LST	381	0.375	0.141	0.138	4.366	0.001	7.898	0.000	$y = -42.32 + 4.90 \times 10^{-3}x$
Nocturnal	T_{env}	21	0.596	0.355	0.325	4.109	0.348	3.402	0.003	$y = 22.50 + 1.19x$
	Temperature Seasonality	21	0.203	0.041	-0.006	5.011	0.561	0.948	0.354	$y = 22.89 + 0.52x$
	Precipitation	21	0.251	0.063	0.018	4.954	0.312	1.186	0.249	$y = 22.64 + 0.37x$
	Precipitation Seasonality	21	0.080	0.006	-0.041	5.101	0.840	0.369	0.716	$y = 22.87 + 0.31x$
	PET	21	0.532	0.283	0.249	4.333	0.002	2.879	0.009	$y = 13.68 + 7.19 \times 10^{-3}x$
	LAI	20	0.229	0.052	0.006	4.934	0.063	1.062	0.301	$y = 21.19 + 0.07x$
	LST	21	0.115	0.013	-0.034	5.084	0.003	0.529	0.602	$y = 31.00 + 1.48 \times 10^{-3}x$

Table H4: Linear regressions between environmental variables and body temperature (T_b ; °C) with substrate.

Environmental Temperature (T_{env} ; Temperature PCA axis 1 scores). Temperature Seasonality (Temperature PCA axis 2 scores). Precipitation (Precipitation PCA axis 1 scores). Precipitation Seasonality (Precipitation PCA axis 2 scores). Potential Evapotranspiration (PET; mm/month). Leaf Area Index (LAI). Land Surface Temperature (LST; Kelvin).

Category	Variable	df	r	R ²	Adjusted R ²	Residual SE	SE	t	P	Equation
Terrestrial	T_{env}	379	0.187	0.035	0.032	5.136	0.101	3.701	0.000	$y = 31.50 + 0.37x$
	Temperature Seasonality	379	0.321	0.103	0.101	4.952	0.180	6.592	0.000	$y = 31.80 + 1.19x$
	Precipitation	378	0.101	0.010	0.008	5.194	0.111	-1.979	0.049	$y = 31.57 - 0.22x$
	Precipitation Seasonality	378	0.207	0.043	0.041	5.108	0.189	4.123	0.000	$y = 31.52 + 0.78x$
	PET	379	0.335	0.112	0.110	4.925	0.001	6.924	0.000	$y = 24.00 + 5.53x10^{-3}x$
	LAI	377	0.179	0.032	0.029	5.185	0.017	-3.524	0.000	$y = 32.60 - 0.06x$
	LST	384	0.310	0.096	0.093	4.974	0.001	6.380	0.000	$y = -37.69 + 4.57x10^{-3}x$
Ground	T_{env}	192	0.411	0.169	0.164	5.012	0.136	6.240	0.000	$y = 32.10 + 0.85x$
	Temperature Seasonality	192	0.251	0.063	0.058	5.320	0.252	3.600	0.000	$y = 32.55 + 0.91x$
	Precipitation	191	0.135	0.018	0.013	5.429	0.175	1.883	0.061	$y = 32.45 + 0.33x$
	Precipitation Seasonality	191	0.262	0.069	0.064	5.289	0.273	3.748	0.000	$y = 32.20 + 1.02x$
	PET	192	0.456	0.208	0.204	4.891	0.001	7.105	0.000	$y = 22.16 + 7.40x10^{-3}x$
	LAI	194	0.018	0.000	-0.005	5.502	0.030	0.246	0.806	$y = 32.31 + 7.31x$
	LST	195	0.293	0.086	0.081	5.249	0.001	4.277	0.000	$y = -32.37 + 4.2710^{-3}x$

Arboreal	T _{env}	87	0.137	0.019	0.008	4.343	0.219	-1.292	0.200	$y = 30.18 - 0.28x$
	Temperature Seasonality	87	0.552	0.305	0.297	3.655	0.292	6.177	0.000	$y = 30.40 + 1.80x$
	Precipitation	87	0.573	0.329	0.321	3.592	0.149	-6.529	0.000	$y = 31.63 - 0.97x$
	Precipitation Seasonality	87	0.341	0.117	0.106	4.121	0.327	3.386	0.001	$y = 29.62 + 1.12x$
	PET	87	0.200	0.040	0.029	4.296	0.002	1.901	0.061	$y = 24.51 + 3.59x10^{-3}x$
	LAI	84	0.639	0.408	0.401	3.446	0.021	-7.606	0.000	$y = 34.36 - 0.16x$
	LST	88	0.564	0.318	0.310	3.628	0.001	6.401	0.000	$y = -76.44 + 7.04x10^{-3}x$
Saxicolous	T _{env}	80	0.083	0.007	-0.006	5.242	0.228	0.742	0.460	$y = 31.06 + 0.17x$
	Temperature Seasonality	80	0.251	0.063	0.051	0.063	0.480	2.321	0.023	$y = 31.24 + 1.11x$
	Precipitation	80	0.212	0.045	0.033	5.140	0.392	1.943	0.056	$y = 31.48 + 0.76x$
	Precipitation Seasonality	80	0.017	0.000	-0.012	5.259	0.511	-0.153	0.879	$y = 30.86 - 0.08x$
	PET	80	0.289	0.083	0.072	5.036	0.002	2.696	0.009	$y = 24.51 + 5.24x10^{-3}x$
	LAI	79	0.169	0.029	0.016	5.211	0.047	1.527	0.131	$y = 29.96 + 0.07x$
	LST	81	0.006	0.000	-0.012	5.232	0.002	0.058	0.954	$y = 29.07 + 1.20x10^{-4}x$
Psammophilous	T _{env}	14	0.633	0.401	0.359	2.429	0.472	-3.063	0.008	$y = 32.67 - 1.45x$
	Temperature Seasonality	14	0.566	0.320	0.272	2.588	0.445	2.567	0.022	$y = 33.68 + 1.14x$
	Precipitation	14	0.670	0.448	0.409	2.332	0.233	-3.373	0.005	$y = 33.82 - 0.79x$
	Precipitation Seasonality	14	0.738	0.545	0.512	2.118	0.336	4.093	0.001	$y = 36.04 + 1.37x$
	PET	14	0.449	0.202	0.145	2.804	0.003	1.882	0.081	$y = 27.37 + 5.32x10^{-3}x$
	LAI	14	0.100	0.010	-0.061	3.123	0.053	0.377	0.712	$y = 33.93 + 0.02x$
	LST	14	0.475	0.226	0.170	2.762	0.002	2.020	0.063	$y = -20.72 + 3.59x10^{-3}x$

Fossorial	T _{env}	6	0.149	0.022	-0.141	5.451	1.029	0.370	0.724	$y = 29.81 + 0.38x$
	Temperature Seasonality	6	0.876	0.768	0.729	2.655	0.404	4.457	0.004	$y = 27.71 + 1.80x$
	Precipitation	6	0.711	0.505	0.423	3.879	0.388	-2.474	0.048	$y = 29.94 - 1.37x$
	Precipitation Seasonality	6	0.391	0.153	0.001	5.075	1.484	1.039	0.339	$y = 30.96 + 1.54x$
	PET	6	0.772	0.596	0.529	3.505	0.003	2.974	0.025	$y = 15.67 + 9.12x$
	LAI	6	0.854	0.730	0.685	2.867	0.073	-4.024	0.007	$y = 34.38 - 0.29x$
	LST	7	0.886	0.785	0.755	2.746	0.002	5.060	0.001	$y = -90.73 + 7.75x10^{-3}x$
Semi-aquatic	T _{env}	7	0.115	0.013	-0.128	2.671	2.439	0.305	0.769	$y = 28.20 + 0.75x$
	Temperature Seasonality	7	0.632	0.400	0.314	1.132	1.132	2.158	0.068	$y = 30.02 + 2.44x$
	Precipitation	7	0.691	0.477	0.402	1.944	0.766	-2.527	0.039	$y = 34.64 - 1.94x$
	Precipitation Seasonality	7	0.536	0.288	0.186	2.269	0.590	1.681	0.137	$y = 28.98 + 0.99x$
	PET	7	0.455	0.207	0.094	2.394	0.007	1.352	0.218	$y = 12.97 + 0.01x$
	LAI	7	0.685	0.470	0.394	1.958	0.051	-2.489	0.042	$y = 34.30 - 0.13x$
	LST	7	0.921	0.848	0.826	1.050	0.001	6.238	0.000	$y = -495.10 + 3.49x10^{-2}x$

Table H5: Linear regressions between environmental variables and body temperature (T_b ; °C) with insularity.

Environmental Temperature (T_{env} ; Temperature PCA axis 1 scores). Temperature Seasonality (Temperature PCA axis 2 scores). Precipitation (Precipitation PCA axis 1 scores). Precipitation Seasonality (Precipitation PCA axis 2 scores). Potential Evapotranspiration (PET; mm/month). Leaf Area Index (LAI). Land Surface Temperature (LST; Kelvin).

Category	Variable	df	r	R ²	Adjusted R ²	Residual SE	SE	t	P	Equation
Island	T_{env}	71	0.550	0.302	0.293	4.614	0.331	5.547	0.000	$y = 24.31 + 1.84x$
	Temperature Seasonality	71	0.482	0.232	0.221	4.841	0.726	4.633	0.000	$y = 30.22 + 3.36x$
	Precipitation	71	0.171	0.029	0.015	5.443	0.225	-1.460	0.149	$y = 27.98 - 0.33x$
	Precipitation Seasonality	71	0.268	0.072	0.059	5.322	0.761	2.343	0.022	$y = 28.29 + 1.78x$
	PET	71	0.386	0.149	0.137	5.097	0.002	3.522	0.001	$y = 16.72 + 0.01x$
	LAI	67	0.010	0.000	-0.014	5.625	0.045	-0.253	0.801	$y = 27.50 - 0.01x$
	LST	75	0.188	0.035	0.022	5.413	0.003	1.656	0.102	$y = -37.10 + 4.30 \times 10^{-3}x$
Mainland	T_{env}	325	0.270	0.073	0.070	4.445	0.091	5.046	0.000	$y = 32.42 + 0.46x$
	Temperature Seasonality	325	0.252	0.064	0.061	4.466	0.163	4.694	0.000	$y = 32.44 + 0.77x$
	Precipitation	324	0.082	0.007	0.004	4.585	0.121	1.484	0.139	$y = 32.46 + 0.18x$
	Precipitation Seasonality	324	0.133	0.018	0.015	4.559	0.172	2.413	0.016	$y = 32.35 + 0.41x$
	PET	325	0.337	0.114	0.111	4.345	0.001	6.454	0.000	$y = 25.96 + 4.67 \times 10^{-3}x$
	LAI	327	0.011	0.000	-0.003	4.625	0.019	-2.202	0.840	$y = 32.47 - 3.79 \times 10^{-3}x$
	LST	327	0.273	0.074	0.071	4.450	0.001	5.123	0.000	$y = -19.00 + 3.38 \times 10^{-3}x$

Appendix I

Final OLS multiple regression models for Table I1) Global; Land Cover - Table I2) Closed Vegetation, Table I3) Semi-Open Vegetation, Table I4) Open Vegetation, Table I5) Urban, Table I6) Barren; Activity Time – Table I7) Diurnal, Table I8) Nocturnal; Substrate – Table I9) Terrestrial, Table I10) Ground-dwelling, Table I11) Arboreal, Table I12), Saxicolous; Insularity – Table I13) Island, Table I14) Mainland.

The contribution of variable to the model indicates the percentage of unique variation explained by each variable. For main effect variables, the percentage contribution is a total contribution, and hence includes all their significant pairwise interactions. The percentage contribution was obtained by dropping each environmental variable with their interactions from the model, and subtracting the new R^2 value from the total R^2 of the complete model. The dependent variable, body temperature (T_b) ($^{\circ}\text{C}$) was transformed to $-\text{Log}(k-T_b)$ for all multiple regressions to reduce heteroscedasticity and increase normality of residuals.

Variables are significant at $P < 0.05$.

GLS = Generalized Least Squares, control for spatial autocorrelation. P values are reported.

PGLS = Partial Generalized Least Squares, control for phylogenetic signal. P values are reported.

GLS and PGLS are only reported if the OLS model residuals showed significant spatial autocorrelation and/or phylogenetic signal.

Table I1) Global

<i>Dependent variable: $-\text{Log}(k-T_b)$</i>	<i>r</i>	<i>R²</i>	<i>Adjusted R²</i>	<i>Residual SE</i>	<i>Contribution of variable to model</i>			
	<i>t</i>	<i>P</i>	<i>SE</i>	<i>GLS</i>	<i>PGLS</i>	<i>R²</i>	<i>Adjusted R²</i>	<i>Contribution</i>
<i>Pearson's r</i>	0.580	0.337	0.317	0.215				
<i>(Constant)</i>	0.415	0.678	0.002	0.682	0.352			
<i>T_{env}</i>	1.843	0.066	0.001	0.099	0.812	0.293	0.277	0.044
<i>Temperature Seasonality</i>	-2.224	0.027	0.017	0.021	0.087	0.326	0.310	0.010
<i>Precipitation</i>	3.764	0.000	0.004	0.000	0.258	0.244	0.023	0.092
<i>PET</i>	-2.199	0.029	0.000	0.026	0.483	0.286	0.271	0.050
<i>LAI</i>	0.740	0.460	0.000	0.493	0.834	0.223	0.207	0.114
<i>LST</i>	-0.928	0.354	0.000	0.365	0.676	0.307	0.291	0.029
<i>T_{env} x Precipitation</i>	4.981	0.000	0.004	0.000	0.009	0.293	0.275	0.043
<i>Temperature Seasonality x LAI</i>	2.180	0.030	0.001	0.042	0.388	0.328	0.311	0.008
<i>Precipitation x PET</i>	-2.823	0.005	0.000	0.005	0.450	0.323	0.305	0.014
<i>Precipitation x LAI</i>	-5.765	0.000	0.000	0.000	0.011	0.279	0.260	0.058
<i>PET x LST</i>	2.299	0.022	0.000	0.020	0.392	0.327	0.310	0.009

OLS AIC: -94.40, GLS AIC: -93.85, PGLS AIC: -90.70

Land Cover

Table I2) Closed Vegetation

<i>Dependent variable: -Log(k-T_b)</i>	<i>r</i>	<i>R²</i>	<i>Adjusted R²</i>	<i>Residual SE</i>	Contribution of variable to model		
	<i>t</i>	<i>P</i>	<i>SE</i>	<i>R²</i>	<i>Adjusted R²</i>	<i>Contribution</i>	
Pearson's r	0.836	0.698	0.648	0.139			
(Constant)	0.426	0.672	0.251				
<i>T_{env}</i>	2.896	0.005	0.027	0.531	0.473	0.167	
Temperature Seasonality	3.811	0.000	0.036	0.595	0.544	0.104	
Precipitation	-4.160	0.000	0.031	0.572	0.527	0.127	
Precipitation Seasonality	4.559	0.000	0.081	0.530	0.472	0.168	
PET	-3.916	0.000	0.000	0.613	0.556	0.086	
LAI	0.165	0.870	0.003	0.615	0.566	0.084	
T_{env} x Precipitation	4.633	0.000	0.006	0.578	0.517	0.120	
Temperature Seasonality x Precipitation	-2.824	0.007	0.015	0.654	0.603	0.045	
Precipitation Seasonality x LAI	-3.858	0.000	0.002	0.615	0.559	0.083	

Table I3) Semi-Open Vegetation

<i>Dependent variable: -Log(k-T_b)</i>	<i>r</i>	<i>R²</i>	<i>Adjusted R²</i>	<i>Residual SE</i>	Contribution of variable to model		
	<i>t</i>	<i>P</i>	<i>SE</i>	<i>R²</i>	<i>Adjusted R²</i>	<i>Contribution</i>	
Pearson's r	0.658	0.434	0.397	0.184			
(Constant)	-4.353	0.000	0.908				
<i>T_{env}</i>	-2.965	0.004	0.038	0.396	0.366	0.038	
Temperature Seasonality	-3.282	0.001	0.448	0.354	0.327	0.079	
Precipitation Seasonality	-2.870	0.005	0.616	0.4005	0.3711	0.033	
PET	2.951	0.004	0.000	0.323	0.295	0.110	
LST	2.899	0.004	0.000	0.334	0.307	0.099	
T_{env} x PET	2.597	0.010	0.000	0.407	0.373	0.027	
Temperature Seasonality x PET	-4.342	0.000	0.000	0.358	0.322	0.076	
Temperature Seasonality x LST	3.625	0.000	0.000	0.381	0.346	0.053	
Precipitation Seasonality x LST	2.869	0.005	0.000	0.401	0.367	0.033	

Table I4) Open Vegetation

<i>Dependent variable: -Log(k-T_b)</i>	<i>r</i>	<i>R²</i>	<i>Adjusted R²</i>	<i>Residual SE</i>	Contribution of variable to model		
	<i>t</i>	<i>P</i>	<i>SE</i>		<i>R²</i>	<i>Adjusted R²</i>	<i>Contribution</i>
Pearson's r	0.703	0.494	0.442	0.217			
(Constant)	-4.941	0.000	0.189				
<i>T_{env}</i>	-2.260	0.026	0.055		0.319	0.271	0.175
Temperature Seasonality	2.602	0.011	0.027		0.459	0.409	0.035
Precipitation	2.694	0.008	0.032		0.428	0.388	0.067
Precipitation Seasonality	0.330	0.742	0.028		0.401	0.360	0.093
PET	-0.111	0.912	0.000		0.433	0.388	0.061
LAI	0.103	0.918	0.003		0.362	0.312	0.133
T_{env} x Precipitation Seasonality	-3.934	0.000	0.114		0.413	0.359	0.081
T_{env} x PET	3.361	0.001	0.000		0.435	0.383	0.059
Precipitation x Precipitation seasonality	2.339	0.021	0.017		0.466	0.416	0.029
Precipitation x LAI	-3.235	0.002	0.001		0.440	0.388	0.055

Table I5) Urban

<i>Dependent variable: -Log(k-T_b)</i>	<i>r</i>	<i>R²</i>	<i>Adjusted R²</i>	<i>Residual SE</i>	Contribution of variable to model		
	<i>t</i>	<i>P</i>	<i>SE</i>		<i>R²</i>	<i>Adjusted R²</i>	<i>Contribution</i>
Pearson's r	0.906	0.821	0.744	0.119			
(Constant)	-2.408	0.253	4.260				
<i>T_{env}</i>	1.793	0.087	0.025		0.570	0.429	0.250
Temperature Seasonality	-0.933	0.362	0.045		0.395	0.244	0.426
Precipitation Seasonality	2.372	0.027	0.047		0.695	0.618	0.126
PET	-2.521	0.020	0.000		0.766	0.681	0.054
LAI	0.557	0.583	0.004		0.762	0.689	0.059
LST	2.339	0.029	0.000		0.774	0.692	0.047
T_{env} x Temperature Seasonality	-2.931	0.008	0.020		0.747	0.655	0.073
Temperature Seasonality x Precipitation Seasonality	-2.814	0.010	0.034		0.753	0.663	0.068
Precipitation Seasonality x LAI	-2.588	0.017	0.002		0.7634	0.6773	0.057

Table I6) Barren

<i>Dependent variable: -Log(k-T_b)</i>	<i>r</i>	<i>R²</i>	<i>Adjusted R²</i>	<i>Residual SE</i>	Contribution of variable to model		
	<i>t</i>	<i>P</i>	<i>SE</i>	<i>R²</i>	<i>Adjusted R²</i>	<i>Contribution</i>	
<i>Pearson's r</i>	0.834	0.696	0.630	0.115			
(Constant)	-3.452	0.002	1.181				
<i>T_{env}</i>	-2.875	0.007	0.307	0.608	0.550	0.088	
<i>Temperature Seasonality</i>	5.162	0.000	0.088	0.399	0.310	0.297	
<i>Precipitation</i>	6.679	0.000	0.040	0.264	0.156	0.432	
<i>Precipitation Seasonality</i>	2.579	0.015	0.033	0.633	0.566	0.063	
<i>LST</i>	3.219	0.003	0.000	0.557	0.492	0.139	
<i>T_{env} x LST</i>	2.837	0.008	0.000	0.620	0.551	0.077	
<i>Temperature Seasonality x Precipitation</i>	5.429	0.000	0.033	0.416	0.310	0.280	

Activity Time

Table I7) Diurnal

<i>Dependent variable: -Log(k-T_b)</i>	<i>r</i>	<i>R²</i>	<i>Adjusted R²</i>	<i>Residual SE</i>	<u>Contribution of variable to model</u>		
	<i>t</i>	<i>P</i>	<i>SE</i>	<i>PGLS</i>	<i>R²</i>	<i>Adjusted R²</i>	<i>Contribution</i>
<i>Pearson's r</i>	0.604	0.364	0.3431	0.200			
<i>(Constant)</i>	-5.164	0.000	0.870	0.000			
<i>T_{env}</i>	-2.896	0.004	0.293	0.166	0.292	0.279	0.072
<i>Temperature Seasonality</i>	-0.821	0.412	0.015	0.204	0.357	0.339	0.008
<i>Precipitation</i>	3.742	0.000	0.042	0.237	0.280	0.264	0.085
<i>PET</i>	1.586	0.114	0.000	0.125	0.341	0.324	0.024
<i>Summer LAI</i>	0.109	0.913	0.001	0.667	0.290	0.270	0.075
<i>Summer LST</i>	4.012	0.000	0.000	0.000	0.333	0.315	0.031
<i>T_{env} x Temperature Seasonality</i>	-2.066	0.040	0.006	0.973	0.357	0.337	0.008
<i>T_{env} x Precipitation</i>	4.824	0.000	0.004	0.080	0.323	0.302	0.041
<i>T_{env} x PET</i>	2.108	0.036	0.000	0.686	0.356	0.337	0.008
<i>T_{env} x LST</i>	2.690	0.007	0.000	0.183	0.352	0.332	0.013
<i>Precipitation x PET</i>	-3.075	0.002	0.000	0.772	0.348	0.328	0.017
<i>Precipitation x LAI</i>	-5.593	0.000	0.000	0.000	0.309	0.288	0.055

OLS AIC: -127.13, PGLS AIC: -180.34

Table I8) Nocturnal

<i>Dependent variable: -Log(k-T_b)</i>	<i>r</i>	<i>R²</i>	<i>Adjusted R²</i>	<i>Residual SE</i>	<u>Contribution of variable to model</u>		
	<i>t</i>	<i>P</i>	<i>SE</i>		<i>R²</i>	<i>Adjusted R²</i>	<i>Contribution</i>
<i>Pearson's r</i>	0.847	0.718	0.612	0.073			
<i>(Constant)</i>	-0.613	0.548	0.955				
<i>T_{env}</i>	5.037	0.000	0.007		0.271	0.057	0.447
<i>Temperature Seasonality</i>	-2.793	0.013	0.556		0.477	0.394	0.241
<i>Precipitation Seasonality</i>	-0.608	0.552	0.015		0.605	0.517	0.113
<i>LST</i>	-0.747	0.466	0.000		0.576	0.482	0.142
<i>Temperature Seasonality x Precipitation Seasonality</i>	-2.377	0.030	0.013		0.619	0.506	0.100
<i>Temperature Seasonality x LST</i>	2.839	0.012	0.000		0.576	0.451	0.142

Substrate

Table I9) Terrestrial

<i>Transformation -Log(k-T_b)</i>	<i>r</i>	<i>R²</i>	<i>Adjusted R²</i>	<i>Residual SE</i>	Contribution of variable to model			
	<i>t</i>	<i>P</i>	<i>SE</i>	<i>GLS</i>	<i>PGLS</i>	<i>R²</i>	<i>Adjusted R²</i>	<i>Contribution</i>
<i>Pearson's r</i>	0.608	0.370	0.3491	0.209				
<i>(Constant)</i>	-5.649	0.000	0.874	0.000	0.000			
<i>T_{env}</i>	-2.116	0.035	0.288	0.081	0.002	0.309	0.293	0.062
<i>Temperature Seasonality</i>	-1.616	0.107	0.018	0.050	0.170	0.361	0.344	0.009
<i>Precipitation</i>	2.954	0.003	0.013	0.003	0.000	0.299	0.282	0.071
<i>PET</i>	4.708	0.000	0.000	0.000	0.375	0.331	0.313	0.039
<i>LAI</i>	3.913	0.000	0.007	0.000	0.377	0.254	0.240	0.116
<i>LST</i>	3.904	0.000	0.000	0.000	0.000	0.342	0.324	0.028
<i>T_{env} x Precipitation</i>	3.372	0.001	0.004	0.002	0.155	0.350	0.331	0.020
<i>T_{env} x LAI</i>	2.039	0.042	0.001	0.055	0.844	0.363	0.343	0.007
<i>T_{env} x LST</i>	2.093	0.037	0.000	0.086	0.002	0.362	0.343	0.008
<i>Temperature Seasonality x LAI</i>	2.212	0.028	0.001	0.021	0.220	0.361	0.342	0.009
<i>Precipitation x LAI</i>	-5.592	0.000	0.000	0.000	0.000	0.316	0.295	0.055
<i>PET x LAI</i>	-3.940	0.000	0.000	0.000	0.367	0.3429	0.323	0.027

OLS AIC: -96.22, GLS AIC: -94.02, PGLS AIC: -176.45

Table I10) Ground-dwelling

<i>Dependent variable: -Log(k-T_b)</i>	<i>r</i>	<i>R²</i>	<i>Adjusted R²</i>	<i>Residual SE</i>	Contribution of variable to model		
					<i>R²</i>	<i>Adjusted R²</i>	<i>Contribution</i>
Pearson's r	0.725	0.526	0.495	0.205			
	t	P	SE				
(Constant)	-5.183	0.000	1.074				
T_{env}	-3.708	0.000	0.347		0.355	0.3271	0.171
Temperature Seasonality	2.757	0.006	0.020		0.484	0.458	0.042
Precipitation	2.646	0.009	0.018		0.383	0.357	0.143
Precipitation Seasonality	0.177	0.860	0.014		0.478	0.452	0.048
LAI	1.751	0.082	0.002		0.461	0.431	0.066
LST	4.364	0.000	0.000		0.456	0.426	0.070
T_{env} x Precipitation	5.655	0.000	0.004		0.442	0.408	0.084
T_{env} x Precipitation Seasonality	-2.694	0.008	0.005		0.507	0.477	0.019
T_{env} x LST	3.879	0.000	0.000		0.487	0.455	0.040
Temperature Seasonality x Precipitation	3.065	0.003	0.009		0.502	0.471	0.025
Temperature Seasonality x Precipitation Seasonality	-2.741	0.000	0.011		0.506	0.476	0.020
Precipitation x LAI	-4.986	0.007	0.001		0.4608	0.428	0.065

Table I11) Arboreal

<i>Dependent variable: -Log(k-T_b)</i>	<i>r</i>	<i>R²</i>	<i>Adjusted R²</i>	<i>Residual SE</i>	Contribution of variable to model		
	<i>t</i>	<i>P</i>	<i>SE</i>		<i>R²</i>	<i>Adjusted R²</i>	<i>Contribution</i>
<i>Pearson's r</i>	0.844	0.712	0.6393	0.120			
<i>(Constant)</i>	-4.721	0.000	1.826				
<i>T_{env}</i>	-2.105	0.039	0.015		0.676	0.606	0.036
<i>Temperature Seasonality</i>	-2.992	0.004	0.747		0.568	0.509	0.145
<i>Precipitation</i>	-3.361	0.001	0.103		0.601	0.521	0.111
<i>Precipitation Seasonality</i>	3.023	0.004	0.126		0.598	0.524	0.114
<i>PET</i>	3.254	0.002	0.000		0.574	0.504	0.138
<i>LAI</i>	3.669	0.000	0.015		0.641	0.579	0.071
<i>LST</i>	3.717	0.000	0.000		0.646	0.569	0.066
<i>T_{env} x Temperature Seasonality</i>	-2.642	0.010	0.016		0.682	0.608	0.030
<i>Temperature Seasonality x Precipitation</i>	2.187	0.032	0.015		0.692	0.619	0.021
<i>Temperature Seasonality x Precipitation Seasonality</i>	3.767	0.000	0.027		0.651	0.569	0.061
<i>Temperature Seasonality x PET</i>	3.309	0.002	0.000		0.665	0.587	0.047
<i>Temperature Seasonality x LAI</i>	2.039	0.045	0.002		0.695	0.623	0.018
<i>Temperature Seasonality x LST</i>	2.331	0.023	0.000		0.689	0.616	0.023
<i>Precipitation x PET</i>	3.851	0.000	0.000		0.649	0.566	0.064
<i>Precipitation Seasonality x PET</i>	-3.108	0.003	0.000		0.671	0.593	0.042
<i>Precipitation Seasonality x LAI</i>	2.432	0.018	0.002		0.687	0.613	0.025
<i>PET x LAI</i>	-3.711	0.000	0.000		0.6532	0.5716	0.059

Table I12) Saxicolous

<i>Dependent variable: -Log(k-T_b)</i>	<i>r</i>	<i>R²</i>	<i>Adjusted R²</i>	<i>Residual SE</i>	Contribution of variable to model		
	<i>t</i>	<i>P</i>	<i>SE</i>	<i>PGLS</i>	<i>R²</i>	<i>Adjusted R²</i>	<i>Contribution</i>
<i>Pearson's r</i>	0.504	0.254	0.2049	0.182			
<i>(Constant)</i>	2.689	0.009	6.900	0.798			
<i>T_{env}</i>	3.228	0.002	0.735	0.610	0.137	0.104	0.117
<i>PET</i>	-2.622	0.011	0.005	0.839	0.061	0.025	0.193
<i>LST</i>	-2.893	0.005	0.000	0.876	0.146	0.124	0.108
<i>T_{env} x LST</i>	-3.247	0.002	0.000	0.603	0.150	0.106	0.104
<i>PET x LST</i>	2.702	0.009	0.000	0.836	0.182	0.140	0.072

Insularity

Table I13) Island

<i>Dependent variable: -Log(k-T_b)</i>	<i>r</i>	<i>R²</i>	<i>Adjusted R²</i>	<i>Residual SE</i>	Contribution of variable to model		
	<i>t</i>	<i>P</i>	<i>SE</i>	<i>R²</i>	<i>Adjusted R²</i>	<i>Contribution</i>	
Pearson's r	0.913	0.834	0.768	0.1088			
(Constant)	0.327	0.745	4.589				
<i>T_{env}</i>	-1.283	0.205	0.072	0.407	0.222	0.426	
Temperature Seasonality	4.824	0.000	3.659	0.530	0.417	0.304	
Precipitation	-5.117	0.000	1.622	0.601	0.495	0.233	
Precipitation Seasonality	-5.588	0.000	4.116	0.661	0.571	0.173	
PET	1.262	0.213	0.000	0.361	0.192	0.473	
LAI	4.833	0.000	0.266	0.653	0.561	0.181	
LST	-0.615	0.541	0.000	0.686	0.603	0.148	
T_{env} x Temperature Seasonality	-5.261	0.000	0.266	0.738	0.642	0.096	
T_{env} x Precipitation Seasonality	3.102	0.003	0.000	0.801	0.727	0.033	
Temperature Seasonality x Precipitation	-6.693	0.000	0.558	0.679	0.561	0.155	
Temperature Seasonality x Precipitation Seasonality	-4.685	0.000	0.210	0.758	0.669	0.076	
Temperature Seasonality x PET	5.174	0.000	0.243	0.741	0.646	0.093	
Temperature Seasonality x LST	-4.855	0.000	0.070	0.752	0.661	0.082	
Precipitation x Precipitation Seasonality	-2.955	0.005	0.000	0.804	0.731	0.030	
Precipitation x LAI	-2.048	0.046	0.000	0.819	0.753	0.015	
Precipitation x LST	5.070	0.000	0.017	0.745	0.651	0.089	
Precipitation Seasonality x LAI	2.645	0.011	0.001	0.810	0.740	0.024	
Precipitation Seasonality x LST	5.558	0.000	0.000	0.705	0.605	0.129	
LAI x LST	-4.765	0.000	0.003	0.755	0.665	0.079	

Table I14) Mainland

<i>Dependent variable: -Log(k-T_b)</i>	<i>r</i>	<i>R²</i>	<i>Adjusted R²</i>	<i>Residual SE</i>				
<i>Pearson's r</i>	0.570	0.325	0.301	0.204				
					Contribution of variable to model			
						<i>Adjusted R²</i>		
						<i>R²</i>	<i>R²</i>	<i>Contribution</i>
(Constant)	t	P	SE	GLS	PGLS			
<i>T_{env}</i>	-5.652	0.000	0.849	0.000	0.000			
<i>Temperature Seasonality</i>	-0.586	0.558	0.013	0.507	0.432	0.255	0.236	0.070
<i>Precipitation</i>	-2.382	0.018	0.017	0.020	0.912	0.311	0.291	0.014
<i>PET</i>	2.729	0.007	0.013	0.004	0.051	0.264	0.246	0.061
<i>LAI</i>	5.225	0.000	0.000	0.000	0.008	0.260	0.239	0.065
<i>LST</i>	5.182	0.000	0.007	0.000	0.827	0.215	0.200	0.110
<i>T_{env} x Precipitation</i>	3.847	0.000	0.000	0.000	0.002	0.293	0.271	0.032
<i>T_{env} x LAI</i>	3.220	0.001	0.004	0.005	0.625	0.303	0.281	0.022
<i>Temperature Seasonality x LAI</i>	2.221	0.027	0.001	0.052	0.739	0.314	0.293	0.011
<i>Precipitation x LAI</i>	2.186	0.030	0.001	0.013	0.369	0.315	0.293	0.010
<i>PET x LAI</i>	-3.821	0.000	0.000	0.000	0.044	0.294	0.271	0.031
	-5.040	0.000	0.000	0.000	0.773	0.270	0.247	0.055

OLS AIC: -116.23, GLS AIC: -98.15, PGLS AIC: -97.38

Appendix J

Table J1: Moran's I correlations for the OLS multiple regression models. P < 0.05 indicates significant spatial autocorrelation.

<i>Model</i>		<i>Moran's I</i>	<i>Distance Class</i>						
			<i>0</i>	<i>1</i>	<i>2</i>	<i>3</i>	<i>4</i>	<i>5</i>	
Global	<i>Global</i>	Moran's I Correlation	0.218	0.000	0.070	0.035	0.060	-0.002	
		P	0.010	0.455	0.059	0.178	0.079	0.426	
Land Cover	<i>Closed Vegetation</i>	Moran's I Correlation	-0.013	-0.082	-0.068	-0.104	0.112		
		P	0.426	0.208	0.248	0.248	0.198		
	<i>Semi-Open Vegetation</i>	Moran's I Correlation	-0.104	0.054	0.017	0.007	0.123	-0.002	
		P	0.139	0.149	0.426	0.446	0.059	0.436	
	<i>Open Vegetation</i>	Moran's I Correlation	-0.177	0.034	0.350	0.239	0.000	0.023	
		P	0.158	0.317	0.020	0.059	0.495	0.337	
	<i>Urban</i>	Moran's I Correlation	0.122	-0.307	1.315		0.164		
		P	0.248	0.140	0.020		0.188		
	<i>Barren</i>	Moran's I Correlation	-0.010	-0.255	0.193		-0.028		
		P	0.426	0.069	0.267		0.426		
	Activity Time	<i>Diurnal</i>	Moran's I Correlation	0.132	0.075	0.039	0.127	-0.045	-0.024
			P	0.059	0.050	0.139	0.010	0.128	0.079
<i>Nocturnal</i>		Moran's I Correlation	-0.289	-0.404	0.417	0.091	0.586		
		P	0.188	0.158	0.228	0.208	0.109		
Substrate	<i>Terrestrial</i>	Moran's I Correlation	0.129	0.055	0.043	-0.009	0.022	0.066	
		P	0.010	0.040	0.139	0.426	0.218	0.050	
	<i>Ground</i>	Moran's I Correlation	-0.116	0.019	0.037	0.019	0.041	0.055	
		P	0.099	0.347	0.297	0.376	0.327	0.287	
	<i>Arboreal</i>	Moran's I Correlation	-0.006	-0.040	0.016	0.030	-0.054	0.011	
		P	0.426	0.465	0.426	0.416	0.416	0.426	
	<i>Saxicolous</i>	Moran's I Correlation	0.197	0.237	0.433	0.207	-0.060	-0.069	
		P	0.149	0.050	0.020	0.168	0.436	0.327	
	Insularity	<i>Island</i>	Moran's I Correlation	-0.551	-0.093	0.012	0.043	0.111	
			P	0.040	0.158	0.416	0.317	0.307	
		<i>Mainland</i>	Moran's I Correlation	0.179	0.065	0.003	-0.019	-0.018	0.099
			P	0.030	0.069	0.396	0.327	0.347	0.010

Table J2: Blomberg's K and Pagel's Lambda values for the OLS multiple regression models. Variables are significant at $P < 0.05$.

Significance of both Blomberg's K and Pagel's Lambda for a model indicates significant phylogenetic signal amongst the model residuals.

Model		Blomberg's K		Pagel's Lambda	
		K	P	L	P
Global		0.177	0.001	0.622	0.000
Land Cover	Closed Vegetation	0.451	0.065	0.707	0.279
	Semi-Open Vegetation	0.135	0.087	0.067	0.011
	Open Vegetation	0.362	0.014	0.246	0.212
	Urban	0.635	0.083	0.000	1.000
	Barren	0.177	0.125	0.000	1.000
Activity Time	Diurnal	0.186	0.001	0.609	0.000
	Nocturnal	0.674	0.645	0.000	1.000
Substrate	Terrestrial	0.167	0.001	0.561	0.000
	Ground	0.098	0.662	0.343	0.001
	Arboreal	0.237	0.247	0.401	0.045
	Saxicolous	0.478	0.001	0.803	0.000
Insularity	Island	0.325	0.318	0.431	1.000
	Mainland	0.178	0.001	0.679	0.000

Appendix K

OLS multiple regression models globally and per land cover ran without including leaf area index (LAI), land surface temperature (LST) and their pairwise interactions.

Table K1) Global; Land Cover - Table K2) Closed Vegetation, Table K3) Semi-Open Vegetation, Table K4) Open Vegetation, Table K5) Urban, Table K6) Barren.

Table K1) Global

<i>Dependent variable: -Log(k-T_b)</i>	<i>r</i>	<i>R</i> ²	<i>Adjusted R</i> ²	<i>Residual SE</i>
<i>Pearson's r</i>	0.509	0.260	0.243	0.221
	<i>t</i>	<i>P</i>	<i>SE</i>	
<i>(Constant)</i>	-8.748	0.000	0.112	
<i>T_{env}</i>	3.590	0.000	0.008	
<i>Temperature Seasonality</i>	2.350	0.019	0.014	
<i>Precipitation</i>	4.837	0.000	0.049	
<i>Precipitation Seasonality</i>	0.979	0.328	0.012	
<i>PET</i>	0.421	0.674	0.000	
<i>T_{env} x Precipitation</i>	5.762	0.000	0.004	
<i>Temperature Seasonality x Precipitation</i>	3.066	0.002	0.006	
<i>Precipitation x Precipitation Seasonality</i>	2.372	0.018	0.004	
<i>Precipitation x PET</i>	-5.368	0.000	0.000	

Land Cover

Table K2) Closed Vegetation

<i>Dependent variable: -Log(k-T_b)</i>	<i>r</i>	<i>R²</i>	<i>Adjusted R²</i>	<i>Residual SE</i>
<i>Pearson's r</i>	0.810	0.656	0.606	0.147
	t	P	SE	
<i>(Constant)</i>	0.122	0.904	0.267	
<i>T_{env}</i>	3.586	0.001	0.078	
<i>Temperature Seasonality</i>	4.368	0.000	0.036	
<i>Precipitation</i>	-4.861	0.000	0.028	
<i>Precipitation Seasonality</i>	3.474	0.001	0.017	
<i>PET</i>	-3.681	0.001	0.000	
<i>T_{env} x Precipitation</i>	6.288	0.000	0.007	
<i>T_{env} x PET</i>	-2.573	0.013	0.000	
<i>Temperature Seasonality x Precipitation</i>	-2.675	0.010	0.015	

Table K3) Semi-Open Vegetation

<i>Dependent variable: -Log(k-T_b)</i>	<i>r</i>	<i>R²</i>	<i>Adjusted R²</i>	<i>Residual SE</i>
<i>Pearson's r</i>	0.608	0.370	0.339	0.193
	t	P	SE	
<i>(Constant)</i>	-8.580	0.000	0.143	
<i>T_{env}</i>	-2.898	0.004	0.041	
<i>Temperature Seasonality</i>	4.116	0.000	0.064	
<i>Precipitation</i>	2.584	0.011	0.049	
<i>PET</i>	2.613	0.010	0.000	
<i>T_{env} x PET</i>	2.919	0.004	0.000	
<i>Temperature Seasonality x PET</i>	-3.653	0.000	0.000	
<i>Precipitation x PET</i>	-2.816	0.006	0.000	

Table K4) Open Vegetation

<i>Dependent variable: -Log(k-T_b)</i>	<i>r</i>	<i>R²</i>	<i>Adjusted R²</i>	<i>Residual SE</i>
<i>Pearson's r</i>	0.601	0.361	0.324	0.235
	<i>t</i>	<i>P</i>	<i>SE</i>	
<i>(Constant)</i>	-3.678	0.000	0.194	
<i>T_{env}</i>	-1.714	0.089	0.053	
<i>Temperature Seasonality</i>	2.613	0.010	0.028	
<i>Precipitation Seasonality</i>	1.919	0.058	0.024	
<i>PET</i>	-1.557	0.123	0.000	
<i>T_{env} x Precipitation Seasonality</i>	-2.543	0.012	0.011	
<i>T_{env} x PET</i>	3.102	0.002	0.000	

Table K6) Urban

<i>Dependent variable: -Log(k-T_b)</i>	<i>r</i>	<i>R²</i>	<i>Adjusted R²</i>	<i>Residual SE</i>
<i>Pearson's r</i>	0.794	0.630	0.573	0.154
	<i>t</i>	<i>P</i>	<i>SE</i>	
<i>(Constant)</i>	-23.703	0.000	-0.929	
<i>T_{env}</i>	4.000	0.000	0.060	
<i>Temperature Seasonality</i>	-2.375	0.025	-0.076	
<i>Precipitation Seasonality</i>	-3.232	0.003	-0.068	
<i>T_{env} x Precipitation Seasonality</i>	-4.601	0.000	-0.127	

Table K7) Barren

<i>Dependent variable: -Log(k-T_b)</i>	<i>r</i>	<i>R²</i>	<i>Adjusted R²</i>	<i>Residual SE</i>
<i>Pearson's r</i>	0.843	0.711	0.624	0.115
	t	P	SE	
(Constant)	2.431	0.023	2.194	
<i>T_{env}</i>	2.359	0.025	0.102	
Temperature Seasonality	4.632	0.000	0.202	
Precipitation	2.831	0.008	0.805	
Precipitation Seasonality	2.181	0.037	0.040	
PET	-2.59	0.015	0.002	
T_{env} x Temperature Seasonality	2.331	0.027	0.005	
T_{env} x Precipitation	2.433	0.021	0.037	
Temperature Seasonality x Precipitation	4.597	0.000	0.073	
Precipitation x PET	-2.538	0.017	0.001	

Appendix L

OLS multiple regression models at a global scale. The table reports P values of all variables remaining in the final models. Variables are significant at $P < 0.05$.

'Global All Data' – Indicates the final OLS global multiple regression model ran using all global data.

'Global Reduced Data' – Indicates 3 repetitions of global models run using 100 data points from South America; reduced from 212 South America data points.

	Global All Data	Global Reduced Data		
		1	2	3
Dependent variable: -Log(k-T_b)				
<i>R</i> ²	0.337	0.346	0.360	0.341
<i>Adjusted R</i> ²	0.317	0.322	0.336	0.317
<i>df</i>	382	273	271	271
<i>Residual SE</i>	0.215	0.211	0.211	0.220
P values of environmental variables and their interactions				
<i>T_{env}</i>	0.066	0.264	0.097	0.030
<i>Temperature Seasonality</i>	0.027	0.176	0.016	0.009
<i>Precipitation</i>	0.000	0.000	0.000	0.000
<i>Precipitation Seasonality</i>				
<i>PET</i>	0.029	0.000	0.000	0.000
<i>LAI</i>	0.460	0.005	0.007	0.002
<i>LST</i>	0.354	0.003	0.000	0.000
<i>T_{env} x Temperature Seasonality</i>				
<i>T_{env} x Precipitation</i>	0.000			
<i>T_{env} x Precipitation Seasonality</i>				
<i>T_{env} x PET</i>				
<i>T_{env} x LAI</i>		0.030	0.007	0.010
<i>T_{env} x LST</i>				
<i>Temperature Seasonality x Precipitation</i>				
<i>Temperature Seasonality x Precipitation Seasonality</i>				
<i>Temperature Seasonality x PET</i>				
<i>Temperature Seasonality x LAI</i>	0.030	0.044	0.017	0.007

Temperature Seasonality x LST

Precipitation x Precipitation Seasonality

Precipitation x PET

0.005

Precipitation x LAI

0.000

0.000

0.000

0.000

Precipitation x LST

Precipitation Seasonality x PET

Precipitation Seasonality x LAI

Precipitation Seasonality x LST

PET x LAI

0.002

0.004

0.001

PET x LST

0.022

LAI x LST
