

Desert and tropical ecosystems of the world harbour the most complex ant societies

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ABSTRACT

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Morphological diversity in the worker caste is present in ants, wasps, termites and thrips, but is particularly striking in ants, as they can produce distinct or continuous worker subcastes. This is referred to as worker caste polymorphism, which has enabled efficient division of labour and consequently, ecological dominance. Previous research shows that nutrition and colony demography during larval development are important determinants of worker polymorphism, which in turn can be mediated by the abiotic environment. However, little is known about the influence of environmental gradients on the geographic distribution of worker caste polymorphism. Here, I developed and tested three hypotheses explaining the global distribution of worker polymorphism: (1) The Tropical Polymorphism Hypothesis, (2) The Desert Polymorphism Hypothesis and (3) The Extreme Climate Hypothesis. I therefore investigated the influence of geographic variation in temperature and precipitation on the distribution of worker polymorphism worldwide using 680 000 ant occurrences and identifying each occurrence point as polymorphic or not. Previous estimates suggested that 13% of ant species are polymorphic whereas my results show this number to be as high as 29%. Moreover, I found that the occurrence of polymorphism was highest in the most arid and tropical ecosystems, suggesting that it may be an adaptation to regions with extremely scarce or diverse resources. Additionally, warm climate is a pre-requisite for the evolution of worker caste polymorphism. Taken together, my work sheds light on the factors promoting complex social lifestyle in insects, and reveals that it is more common in ants than previously believed.

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INTRODUCTION

Worker polymorphism is one of the most complex stages of social evolution in insect societies (Wheeler 1986; Wilson 2009). Insect societies typically display morphologically distinct reproductive and non-reproductive castes, but few display variation in the worker caste to the degree found in ants where workers of the same colony vary drastically in their head-to-body ratio (Wilson 1953; Wheeler 1986; Wolf & Seppa 2016). This leads to efficient division of labour within a colony and is associated with increases in colony size, which in turn, has led to the ecological success of ants in terrestrial ecosystems (Wilson 1953; Hölldobler & Wilson 1990; Bonner 1993; Wilson 2003; Wirth *et al.* 2013). Because ants are ecosystem engineers (Wilson 1953; Hölldobler & Wilson 1990; Wilson 2003; Wirth *et al.* 2013), ecologically successful polymorphic species often play a crucial role in the functioning of ecosystems. Though polymorphic ants are ecologically dominant, it is estimated that 13% of ant species exhibit complex worker castes (Hölldobler & Wilson 1990; Fjerdingstad & Crozier 2006; Suarez *et al.* 2018). However, this number has never been investigated. Recent studies identify determination of worker polymorphism is achieved primarily through nutrition and social regulation at the colony level (Wheeler & Nijhout 1981; Wheeler & Nijhout 1983, 1984; Passera *et al.* 1996; Rajakumar *et al.* 2012; Alvarado *et al.* 2015; Rajakumar *et al.* 2018). It is known that nutrition and the strength of biotic interactions along environmental gradients (Jeanne 1979; Schemske *et al.* 2009; Roslin *et al.* 2017), yet it is unclear what the effect of these environmental factors on the distribution of polymorphism is. In this study, I aim to investigate whether the abiotic environment influences the global distribution of worker polymorphism in ants, to bridge our

current knowledge of development and behavior to broader scale patterns to better understand the evolution of social complexity.

In ants, abiotic and biotic variation in the environment can influence caste determination. In queens, seasonal temperature cues signal a colony to feed larvae more and increase production of queens, as the mating flights take place at specific times of year (Passera & Suzzoni 1979; Hölldobler & Wilson 1990; Schwander *et al.* 2008; Favé *et al.* 2015; Amor *et al.* 2016). In workers, the relationship between nutrition and the developmental processes regulating polymorphism is well known. In *Pheidole* workers for example, if larvae receive sufficient protein during a critical window of development, juvenile hormone (JH) levels surpass a threshold and activate the development of soldiers (Wheeler 1991; Rajakumar *et al.* 2012; Rajakumar *et al.* 2018). Soldiers are a morphologically distinct and behaviourally defensive worker caste. These developmental changes are also regulated at the colony level where soldiers inhibit the production of more soldiers through contact pheromones (Gregg 1942; Wheeler & Nijhout 1984; Passera *et al.* 1996; Lillico-Ouachour & Abouheif 2017). As the supply of soldiers belonging to a given colony is depleted due to competition, predation or disease occurring outside the colony, the inhibition from the soldier pheromone no longer has an effect (Gregg 1942; Wheeler & Nijhout 1984; Passera *et al.* 1996; Lillico-Ouachour & Abouheif 2017). As a result, the production of new soldiers increases (Gregg 1942; Wheeler & Nijhout 1984; Passera *et al.* 1996; Lillico-Ouachour & Abouheif 2017). While there is a genetic influence on body size variation, nutrition and social interactions during development are recognized as the primary external determinants of adult size, which in turn may be affected by climate at broader scales (Gadagkar 1997; Hughes *et al.* 2003; Rheindt *et al.* 2005; Schwander *et al.* 2005; Bowsher *et al.* 2007; Rajakumar *et al.* 2012; Shbailat & Abouheif 2013; Alvarado *et al.* 2015; Lillico-Ouachour

& Abouheif 2017). To better understand the link between the abiotic factors and worker polymorphism, I will test three hypotheses (1) The Tropical Polymorphism Hypothesis, (2) The Desert Polymorphism Hypothesis and (3) The Extreme Climate Hypothesis, which make clear predictions regarding the relationship between the probability of worker polymorphism occurrence and climatic variables.

The Tropical Climate Polymorphism Hypothesis

I propose the tropical hypothesis, which posits that polymorphism will occur more frequently in warm and wet environments (Figure 1a and 1d). Though the only study to directly address the distribution polymorphism concludes that it is more frequent in the tropics, it lacks statistical tests and broad geographic coverage (Wilson 1968). Therefore, here, I will reformulate this hypothesis based on the importance of nutrition in determining worker caste polymorphism and provide empirical tests to accept or reject it. As such, I propose two key mechanisms that may promote polymorphism in tropical environments by directly or indirectly affecting colony nutrition: the need to defend space and resource exploitation. In polymorphic species with discrete subcastes, soldiers or major workers often take on defensive roles in the colony (Busher *et al.* 1985; Mertl & Traniello 2009; Kamhi *et al.* 2015), which can be facilitated through intensification of biotic interactions, where competition for space and resources is increased relative to temperate environments with less biotic interactions (Jeanne 1979; Schemske *et al.* 2009; Roslin *et al.* 2017). This may lead species to adapt and evolve morphological specializations to better defend the space they occupy (Wilson & Hölldobler 1985; Hölldobler & Wilson 1990; Blanchard & Moreau 2017). Additionally, resource selectivity and morphological adaptation due to worker caste polymorphism can lead to efficient exploitation resources and

minimize competition with other species (Wilson 1980; Rockwood & Hubbell 1987; Traniello 1989; Mueller *et al.* 2018). Finally, the sheer amount of resources available (Cramer *et al.* 1999; Davidson *et al.* 2003; Seabloom *et al.* 2017) can facilitate polymorphism as the developmental basis of polymorphism may rely on resource availability, making the exploitation of resources less difficult and consequently, facilitating the evolution of this trait (Rajakumar *et al.* 2012; Rajakumar *et al.* 2018). These two mechanisms act on both nutrition and the inhibition of soldiers, as the rate at which soldiers leave the nest ensures that a colony can continually produce soldiers and maintain worker polymorphism. Therefore, if polymorphism occurs more commonly in the tropics, I expect the distribution of polymorphism to favour high temperatures and high precipitation (Figure 1a and 1d).

The Desert Polymorphism Hypothesis

I also propose the arid hypothesis; which posits that warm and dry environments promote higher occurrence of polymorphism (Figure 1b and 1e). Though Wilson (1968) highlights the relationship between polymorphism and tropical environments, he also notes that it seems to be more prominent than expected in arid systems, which is also noted in recent studies (Wilson 1968; Boulay *et al.* 2017). Ant worker polymorphism can therefore be an adaptation to resource poor environments as higher competition intensity are expected with low food abundance (Davidson 1978; Brown *et al.* 1979; Davidson 1998). Therefore, the two mechanisms promoting worker caste polymorphism as an adaptation to arid climates are facilitating colony defense and enhancing resource exploitation, which can directly or indirectly affect a colony's nutrition. Worker polymorphism can therefore be an adaptation that can act against food scarcity for seed resources as having a polymorphic workforce may enable size matching between individuals and

seed resources (Davidson 1978; Retana *et al.* 1994; Davidson 1997, 1998; Willott *et al.* 2000; Arnan *et al.* 2011). It can also be an adaptation allowing foraging activities to take place during a longer period of time where worker size determines time of day the individuals can forage due to thermal tolerance, thereby facilitating resource exploitation (Davidson 1978, 1997; Boulay *et al.* 2017). Finally, it can be an adaptation to better defend the space that a species occupies as some predatory ants pose a threat to the survival of desert ants (Huang & Wheeler 2011). One behaviour that is of note in desert ants is territoriality, whereby defending individuals will display aggressive behaviour towards potential nest intruders, therefore, defending the space they occupy (Hölldobler 1976; Gordon 1992). Though worker caste polymorphism is costly to a colony in resource poor environments, it may enable their ecological dominance through efficient colony defence and resource exploitation (Wheeler & Nijhout 1984; Passera *et al.* 1996; Lillico-Ouachour & Abouheif 2017; Rajakumar *et al.* 2018). Therefore, if polymorphism occurs more frequently in arid environments, I expect the distribution of polymorphism to favour areas that experience high temperatures and low precipitation (Figure 1b and 1e).

The Extreme Climate Polymorphism Hypothesis

The third and final hypothesis I propose is a combination of both previous hypotheses, whereby I expect polymorphism in places that exhibit climatic extremes. Specifically, we expect polymorphism to occur in the warmest parts of the world that are either extremely “wet” or “dry”. Previous research suggests that the prevalence of polymorphism is elevated in both the tropics (wet) and in deserts (dry) (Wilson 1968; Boulay *et al.* 2017). These extreme precipitation regimes may promote higher occurrence of polymorphism due to the need to defend space or efficiently exploit resources, both of which affect nutritional and social context within a colony

(Wilson & Hölldobler 1985; Hölldobler & Wilson 1990; Blanchard & Moreau 2017; Lillico-Ouachour & Abouheif 2017). Conversely, moderate to low temperatures and moderate precipitation may produce less polymorphism as the need to defend space and acquire resources is not as great as in the tropics and in deserts. Therefore, I predict a U-shaped relationship between precipitation and polymorphism, with the relationship between temperature and polymorphism remaining linearly positive (Figure 1c and 1f).

In this study, I (1) quantify global frequency of worker polymorphism, (2) map the geographic distribution of polymorphism at a global scale, and (3) explore the environmental factors driving the distribution of polymorphism worldwide. To accomplish this, I use an occurrence database of over 682 066 points covering the globe, which includes over 15 152 species of ants, and a classification of each of these species into polymorphic or monomorphic species (Figure 2). I hypothesize that temperature and precipitation positively influence ant worker polymorphism if it occurs more frequently in the tropics because of resource specialization or the need to defend space (Wilson 1968). Alternatively, if arid conditions promote polymorphism, the probability of occurrence of polymorphism will show a negative relationship with mean annual precipitation and positively relate to mean annual temperature (Davidson 1978; Brown *et al.* 1979; Retana *et al.* 1994; Davidson 1998). To test if both tropical and arid environments are influencing the distribution of worker polymorphism (i.e. the Extreme Climate Hypothesis), I expect the relationship with temperature to remain positive and the relationship with precipitation to favour the extremes of this climatic factor, forming a U-shaped curve (see Figure 1c and 1f). Here, I aim to understand the influence of the abiotic environment on the distribution of worker polymorphism in ants across the globe to better understand the link between development and broad scale patterns.

MATERIALS & METHODS

Ant Worker Polymorphism Classification

Allometry or scaling is the relative growth of a body part in relation to overall body size (Wilson 1953; Huxley 1993). In ants, worker caste polymorphism is characterized by a disproportionate head to body size ratio within a colony, often leading to drastically different worker morphologies (Wilson 1953; Wheeler 1991). Wilson (1953) formally defined worker polymorphism as “allometry occurring over a sufficient range of size variation within a normal mature colony to produce individuals of detectably different form at the extremes of the size range”. Wilson (1953) categorized five different types of worker polymorphism observed in ants, which he based on the different allometric relationships observed between head size and overall body size (Wilson 1953). These five categories (Figure 2) are: monophasic, diphasic, triphasic, dimorphic, and in very rare cases, trimorphic allometry (Wilson 1953).

Wilson (1953) refers to all ant species lacking worker polymorphism as monomorphic. The allometric relationship between head and body size is a straight line with limited size variation (i.e. isometry) (Wilson 1953, 1954; Wilson 1968; Wilson 1971). Within a colony, individual workers have similar scaling between the head and body size, and therefore, it is difficult to discriminate any morphological differences between individuals. By contrast, a monophasic species exhibits worker caste polymorphism but are considered weakly polymorphic because there is a subtle allometry between head and body size (Wilson 1953, 1954, 1971). For example, the fire ants (*Solenopsis invicta*) are monophasic as their body size variation is large with subtle differences in the scaling of head to body ratios between the extreme individuals (Tschinkel 1988; Tschinkel 2006; Tschinkel 2013).

Diphasic species exhibit a more marked worker caste polymorphism than monophasic ones because head:body allometry increases in larger individuals relative to other individuals of the same colony and individuals at the extreme of the size distribution have larger heads and relatively smaller bodies (Wilson 1953, 1954; Wilson 1968; Wilson 1971). In species with a triphasic allometry, the head:body size scaling relationship is such that it starts to form two distinct curves of different slopes representing minors and majors, with a few intermediate individuals (i.e. media) joining both lines (Wilson 1953, 1954; Wilson 1968; Wilson 1971). Species falling in this category are considered to have two distinct worker subcastes, ‘minors’ and ‘majors’, with a few intermediate individuals. In the worker caste of *Camponotus floridanus*, the worker subcaste has larger head:body scaling than the other and participate in different roles within a colony (Alvarado *et al.* 2015).

Species with complete dimorphism have two distinct head:body allometric slopes forming two morphologically distinct worker subcastes, ‘minor workers’ and ‘majors’ (also called soldiers), with no intermediates. Species within the hyperdiverse ant genus *Pheidole*, also called ‘big-headed’ ants, are a classic example of dimorphic allometry (Wilson 1984; Wilson 2003). Finally, there are at least 8 trimorphic species within *Pheidole* that evolved an additional supersoldier or supermajor subcaste and form three distinct worker subcastes (Huang & Wheeler 2011; Rajakumar *et al.* 2012). Though rare, these trimorphic species form three distinct lines, varying in slope representing the minor, major and supermajor castes. For the purposes of this study, I classified 15 152 species as polymorphic (i.e. possessing allometry in the worker caste) and monomorphic (i.e. lacking allometry in the worker caste).

Classification of ant species into categories of polymorphism

AntWiki (Urbani & Andrade 2017) and AntWeb (Fisher & Ward 2002), two open access repositories curated by myrmecologists that collate information and list studies on each ant species, were used. These databases were chosen because resources are easily accessible and the taxonomic upkeep of the species pages is consistent (Fisher & Ward 2002; Urbani & Andrade 2017). Using the primary literature cited on these pages, explicit mention of the terms monomorphic, polymorphic, or any of the categories of polymorphism listed in Wilson (1953) and described above were searched for. The most recent articles on the species were preferred, but all articles were considered to ensure proper description of the trait in question. Species were considered to be polymorphic if the primary literature reported any type of head:body allometry from monophasic allometry (continuous morphological variation) to trimorphic allometry (discrete morphological variation). If the species or species specific references were not found in AntWiki or AntWeb, I used the scientific name of the species in Google Scholar to find more up to date papers. An important note of caution for most species-level descriptions that are based on the data available is that they often lack in allometric precision or it is altogether not mentioned.

If the type of polymorphism for a given species was not explicitly mentioned, the genus level description from Bolton (2003) was assigned. If more genus specific references were available, those were used as well. This was most common among certain Australian ant genera, as well as recent work on the subfamily *Dorylinae*, *Dolichoderinae* and *Ponerinae* (Shattuck 2000; LaPolla *et al.* 2010; Schmidt & Shattuck 2014; Borowiec 2016; Shattuck & Cover 2016). Most authors describing monomorphic genera did not explicitly mention if the species in question was monomorphic. Therefore, most monomorphic species were identified using genus level descriptions available through Bolton (2003) or otherwise specified sources. Two types of worker polymorphism – monomorphic and polymorphic – species were recorded in the database

as ‘0’ or ‘1’ respectively. If a more specific type of polymorphism was given (e.g. monophasic), then I would write this as a note for future reference. References for all these classifications can be found in the database. This protocol was followed for more than 15 000 species for which occurrence data was also available through the Global Ant Biodiversity Informatics (GABI) database (Guenard *et al.* 2017). Summary statistics of the database, showing the breakdown of occurrence data for each subfamily is provided (Table A1).

Blanchard and Moreau (2017) focused on genus-level characterizations of ant worker polymorphism. Most of the discrepancies between our study and Blanchard and Moreau (2017) stems from the taxonomic-level and definition of ant worker polymorphism used. I include and analyze species with monophasic allometry, whereas other studies have focused only on highly polymorphic (diphasic, triphasic, dimorphic, trimorphic) species. Second, our analysis is at the species-level, whereas previous studies focused on the genus-level. *Paraponera clavata* is an example of the type of discrepancies that can arise: it is considered monomorphic in Bolton (2003) and in Blanchard and Moreau (2017). However, I found articles showing this species is monophasic, indicating that although it may not have an explicit defensive caste, it can be considered weakly polymorphic (Breed & Harrison 1988). Members of the subfamily *Amblyoponinae* are also believed to be for the most part monomorphic as they are an older subfamily, but some members of the genus *Mystrium* were characterized as polymorphic (Yoshimura & Fisher 2014). Although this differs from previous classifications, several sources indicate that the species of this small genus are polymorphic, with some workers even exceeding the size of the queen (Moffett 1986; Yoshimura & Fisher 2014). The genus *Monomorium* and *Crematogaster* were not considered polymorphic in my analysis as polymorphic species represent a small fraction of this genus, but were considered polymorphic by Blanchard and

Moreau (2017). The final discrepancy was found to be with the genus *Plagiolepis*, where they were classified as polymorphic in Blanchard and Moreau (2017) because of an article published by Arnold in the 1920s, but I consider all species of this genus to be monomorphic, unless otherwise specified. These discrepancies arose because polymorphism was not explicitly stated in any of the articles describing species I researched, so I chose to use Bolton (2003) classification.

In the absence of more accurate species-level information, especially in the case of poorly studied genera, the number of polymorphic species reported here is believed to be conservative as more continuous allometries (i.e. monophasic) are inconsistently reported in the literature. This leads to underestimation of the number of truly polymorphic species, because in nature, monophasic species are hard to distinguish from monomorphic species. Moreover, dimorphic and triphasic allometries were almost always explicitly mentioned in the articles describing the species.

Compilation of Occurrence Data

I used the species occurrence data from the GABI database (N=682 066) and matched this to the polymorphism database, which lists species trait values. The occurrence database used here is the Global Ants Bioinformatic database (GABI) (Guenard *et al.* 2017). The database is a collection of published literary records, prioritizing community ecology journal articles, with careful consideration for taxonomic records (Guenard *et al.* 2017), and recent papers are continuously being added to the GABI database (Guenard *et al.* 2017). It also includes records extracted from 25 online, open source databases, such as Antweb, as well as Museum records. In total, the GABI database comprises 1.7 million data points around the world (Guenard *et al.* 2017). I

extracted all spatially validated occurrence points from the database up until May 2018, from this, over 682 066 occurrence points could be used in the analysis. From this data set, I chose to exclude occurrences on small oceanic islands because I wanted to look at the latitudinal gradient in relation to abiotic environment. Small oceanic islands tend to have more homogenous environmental factors and be colonized by organisms with appropriate dispersal abilities (Simberloff & Wilson 1969; Diamond & May 1976; MacArthur 1996).

Modelling the Distribution of Polymorphism at the Global Scale

To assess the influence of temperature and precipitation on the distribution of polymorphism, I performed a series of generalized linear mixed models (hereafter referred to as GLMM) assuming a binomial distribution. The response variable was the presence or absence of polymorphism. Mean annual temperature (hereafter referred to as “Temperature”) and mean annual precipitation (hereafter referred to as “Precipitation”) were used as explanatory variables.

To avoid the bias produced from pseudo-replication and difference in sampling efforts between different parts of the world, I divided the world into grid cells and within each grid cell, reduced multiple entries for one species to a single occurrence point (N=105 758). Specifically, I divided the world into 1 latitude and 1 longitude grid cells. And for each grid cell, species could only have one entry for either their classification as polymorphic or not, and for climatic association.

Mean annual temperature and mean annual precipitation for each occurrence data point were extracted from WorldClim (Fick & Hijmans 2017) using the *raster* package in R (Hijmans & van Etten 2014). I then took the average for the climatic values for a single species with multiple entries and these average values for temperature and precipitation were used in the analysis. Temperature and Precipitation were chosen as the primary climatic factors as they relate

most directly to our hypotheses and they were the best predictors selected in a preliminary round of model selection using all available WorldClim variables (Fick & Hijmans 2017).

Due to the number of data points analyzed, I was unable to spatially weight our analysis due to computational issues. I opted to account for potential spatial autocorrelation by using the “Site ID” (assigned based on the one latitude by one longitude grid cell) as a random effect in all models. These models were run using the *lme4* package in R (Bates *et al.* 2014).

To ensure that the explanatory variables were not collinear meaning that explanatory variables were correlated and likely explain the same variation, a variance inflation factor between temperature and precipitation was calculated. To do this, I used the *usdm* package in R and found that the variance inflation factor is 1.57, indicating little collinearity, thus, both variables could be included in our models (Naimi 2015). I also verified if they were overdispersed. I found that overdispersion in my models to be less than 1, indicating very little overdispersion and proceeded with the model selection procedure. I then selected models based on the Akaike Information Criterion (hereafter referred to as AIC), choosing the model with the lowest AIC as the best model (Akaike 1992; Bolker *et al.* 2009). For a model to be selected and be considered a significantly better model, it needed to be at least 2 units lower than the second lowest AIC (Akaike 1992). AIC was chosen as the metric of model selection because it selects the most parsimonious model and minimizes the information lost by a model (Akaike 1992). All statistical analyses were carried out using the R statistical software [*R Core Team version 3.5.0*].

RESULTS

In contrast to earlier estimates that polymorphic ants accounted for 13% of all ant species (Fjerdingstad & Crozier 2006; Suarez *et al.* 2018), I found that approximately 29% of the 15 152 species in the polymorphism database are polymorphic (i.e. showing monophasic to trimorphic allometry; Table A2). Using a defined threshold of >50% of species within the genus being polymorphic, I found that roughly 16% of the 306 genera of ants are polymorphic, while 29% of genera have at least one polymorphic species (Table A2). I used maps to visualize the global distribution of worker polymorphic species relative to all known occurrences (Figure 3a) and to investigate the relationship between global distribution of worker polymorphism and the abiotic conditions favoured by polymorphic ants. I also estimated the influence of evolutionary history and biogeography using phylogenetic analysis and continental spatial models.

To assess the influence of temperature and precipitation on the global distribution of polymorphism, I created GLMMs and performed AIC model selection. I found that the best model relating polymorphism to abiotic factors is one which has a second-degree polynomial for Precipitation and a linear term for Temperature as fixed effects (Table 1 and Table A3). The second-degree polynomial for Precipitation was used to test if both the tropical and arid hypothesis could be reconciled under the ‘Extreme Climate’ hypothesis, which predicts a positive coefficient for the second-degree polynomial of precipitation and a positive linear coefficient for temperature (Figure 1). The only random effects in the best model is Site ID, to correct for spatial autocorrelation.

I found that temperature was positively related to polymorphism occurrence (slope= 0.285; $p = <2.000e^{-16}$; Table 2 and Figure 3b). The second-degree polynomial of Precipitation was negatively related to polymorphism, producing a hump shaped curve (slope =-0.097; $p =$

$<2.000e^{-16}$; Table 2 and Figure 3c). This upward facing U shape matches our predictions under the Extreme Climate Hypothesis, where dry and wet environments favour higher occurrence of polymorphic species (Figure 1f and Figure 3c). The linear term for precipitation was negatively related to polymorphic occurrence (slope= -0.327; $p=<2.000e^{-16}$; Table 2a). In sum, temperature shows a positive linear trend with polymorphism, while precipitation shows a non-linear U shaped trend supporting the Extreme Climate Hypothesis.

DISCUSSION

Developmental and behavioural mechanisms determining morphological variation in the worker caste show that nutrition is a key factor, which in turn can help bridge the developmental mechanisms and external factors mitigating this trait (Smith 1942; Wheeler & Nijhout 1981; Wheeler & Nijhout 1983; Rajakumar *et al.* 2012; Alvarado *et al.* 2015; Metzl *et al.* 2018; Rajakumar *et al.* 2018). Though nutrition is highly contingent on climatic conditions, little is known of the relationship between the abiotic environment and polymorphism. In the present study, I use a combination of the largest occurrence database for ants, as well as the largest compiled polymorphism database to explore the relationship between polymorphism and the abiotic environment. I predicted that polymorphism would be favoured in either tropical, arid or a combination of tropical and arid habitats (see Figure 1). Here, I show that worker polymorphism is concentrated in the warmest parts of the world, and (2) in both dry and wet habitats. Taken together, I find support for the Extreme Climate Hypothesis, which predicts that worker caste polymorphism is more likely to occur in tropical and arid climates.

Polymorphism more prevalent than previous estimates

From the trait database I constructed, I find that 29% of all ant species are worker polymorphic, whereas previous estimates suggest only 13% of species are polymorphic (Hölldobler & Wilson 1990; Fjerdingstad & Crozier 2006; Suarez *et al.* 2018). However, at the genus level, we find 16% of genera are polymorphic, which is almost identical to the proposed estimates ranging between 13-16% (Hölldobler & Wilson 1990; Blanchard & Moreau 2017). This suggests that polymorphism is much more prevalent across species than previously believed, but similar in estimation across genera. This is the first study, to my knowledge, to formally document polymorphism across a large proportion of ant species, from 306 ant genera.

Temperature influences the distribution of polymorphism

At the global scale, temperature has a positive relationship with polymorphic occurrence. . Warmer temperatures could directly affect developmental time undergone by workers, where warmer temperatures speed up developmental time (Ratte 1984; Oms *et al.* 2017). Therefore, higher temperatures might buffer the costs of larger, more nutritionally expensive individuals by reducing the time it takes to reach metamorphosis, thereby inducing polymorphism in warmer temperatures and restricting it to warmer environments (Ratte 1984; Oms *et al.* 2017). However, it is important to note that the relationship between temperature and size is not consistent in all ant taxa and can be altered by other colony level properties, such as colony size (Porter & Tschinkel 1985; Cassill & Tschinkel 2000). Warmer temperatures may also speed up the queen-worker switch and lead to earlier worker caste determination, in this case, temperature can induce higher occurrences of polymorphism, where temperatures are warm (Wheeler 1986; Fjerdingstad & Crozier 2006). Higher temperatures may also increase nutrient availability or

diversity and lead to higher production of soldiers or major workers, facilitating the evolution of polymorphism in warmer environments. Therefore, temperature is an important influence on the distribution of polymorphism that can have potential effects on larval development, acting to either promote or restrict the evolution of polymorphism geographically.

Precipitation influences the distribution of polymorphism

I expected polymorphism to occur predominantly in either the tropics, in deserts or in a combination of both these extreme environments. I find that worker caste polymorphism occurrence is high in wet and dry areas, as predicted under the Extreme Climate Hypothesis. Precipitation in conjunction with warm temperatures in these models is a proxy for energy availability. Therefore, worker caste polymorphic occurrence may be driven by the extremes of energy availability, where in the tropics there is an abundance of energy and deserts experience a lack of energy available. The two main mechanisms proposed to act in these two different environments to promote polymorphism are resource exploitation and colony defense both directly or indirectly affecting energy acquisition by a colony. In tropical environments, resources are abundant, but there are higher biotic interactions (Jeanne 1979; Schemske *et al.* 2009; Roslin *et al.* 2017) which may make resource acquisition more difficult. Therefore, evolving polymorphism as an adaptation to better defend space or more efficiently acquire resources may ensure a species' ability to persist (Wilson 1983; Wetterer 1995; Powell 2009; Camarota *et al.* 2016). Conversely, deserts are energy limited and traits that enable efficient resource acquisition are important to sustain a colony. Therefore, worker caste polymorphism may be an adaptation to be able to better exploit the environment or to defend the space these species occupy to improve access to resources (Davidson 1978; Retana *et al.* 1994; Davidson

1997; Cerda & Retana 2000; Boulay *et al.* 2017). Both these environments experience extremes of competition and resource availability, which is not experienced in environments that have moderate precipitation and annual temperatures, which may be why there are less polymorphic species. In sum, tropical and arid climates both have a higher occurrence of polymorphic species.

Conclusion and Future Directions

To conclude, my results demonstrate the importance of temperature and precipitation on shaping the distribution of polymorphism. I find that the overall pattern of where ant worker polymorphism occurs geographically widespread than previously believed, occurring more frequently in both tropical and arid environments (Wilson 1968; Boulay *et al.* 2017; Suarez *et al.* 2018). This pattern is likely driven by temperature and precipitation, which can affect resource availability and likely influences development directly or indirectly through nutrition. Temperature may create a boundary which prevents the evolution or dispersal of polymorphism to cold environments as it can become too costly for a colony to produce a diverse worker caste. A combination of both temperature and precipitation influence resource availability and the biotic interactions of a system, which can influence polymorphic occurrence. Future studies should aim to better understand the effect local and regional scales on the distribution of polymorphism as there are no studies that study worker caste polymorphism at this scale. Additionally, as there is no species level phylogeny for ants, I was unable to penalize for evolutionary history, which is an important to consideration for future studies. This study represents an important step in furthering our understanding of what induces and what restricts the distribution of polymorphism and bridge developmental processes to large scale patterns of polymorphism.

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TABLES

Table 1: Results of model selection for the generalized linear mixed models for the global distribution of worker caste polymorphism. The bolded AICs represent the lowest AIC (i.e. best model) for the global distribution of worker polymorphism.

Model	AIC
<i>I</i>	125450.0
<i>I + Site ID</i>	123075.8
<i>Temperature + Site ID</i>	122768.9
<i>Precipitation + Site ID</i>	122951.2
<i>Temperature2 + Site ID</i>	122710.4
<i>Precipitation2 + Site ID</i>	122872.4
<i>Precipitation + Temperature + Site ID</i>	122406.2
<i>Precipitation2 + Precipitation + Temperature + Site ID</i>	122316.0
<i>Precipitation*Temperature + Site ID</i>	122397.8

Table 2: Summary of coefficients, standard error, Z value and p value of best spatial global model. The AIC of this model is 122316.0. The random effect was site ID, which had a variance of 0.220. This model has 105 753 degrees of freedom.

Variable	Estimate	Standard Error	Z Value	P value
Intercept	-1.193	0.017	-70.522	$<2e^{-16}$
Precipitation	-0.327	0.016	-21.015	$<2e^{-16}$
Precipitation ²	0.097	0.010	9.836	$<2e^{-16}$
Temperature	0.285	0.012	23.932	$<2e^{-16}$

Figures

Figure 1: Predictive framework for predictive probability of polymorphism. A-C are the predicted curves for temperature under the tropical, desert and extreme climate hypotheses respectively. D-F are the predicted curves for precipitation under the tropical, desert and extreme climate hypotheses respectively.

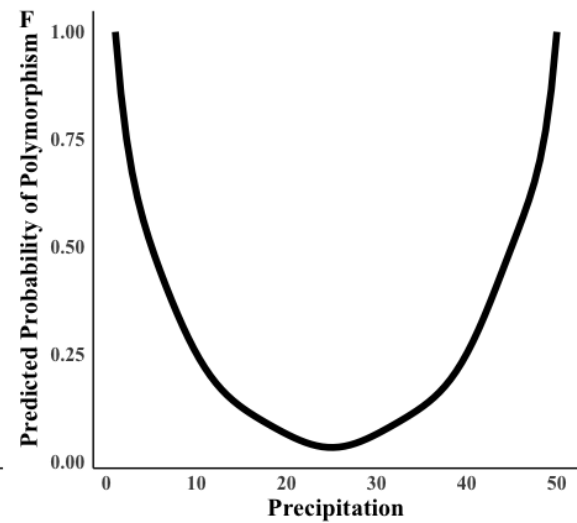
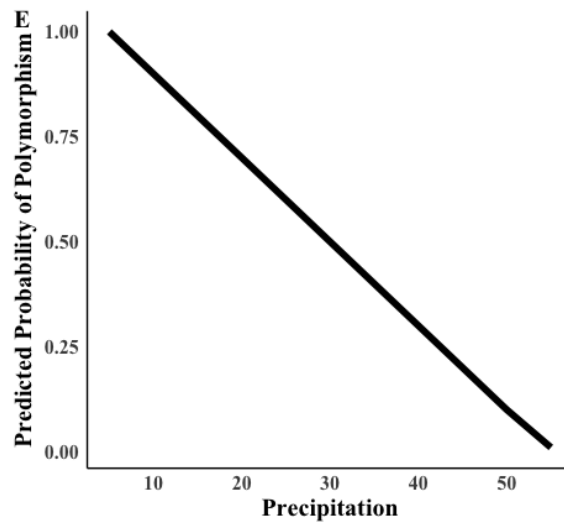
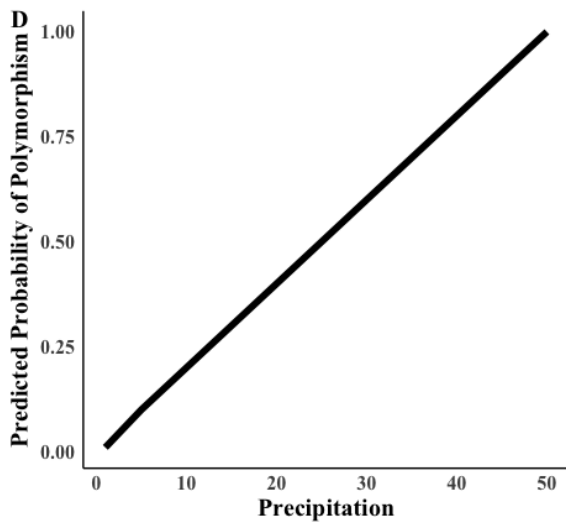
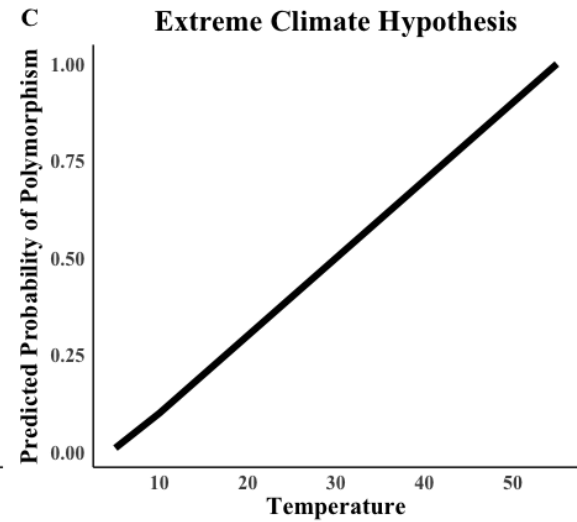
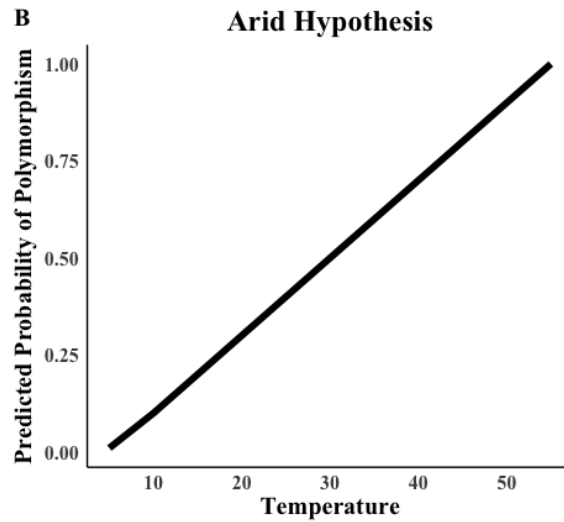
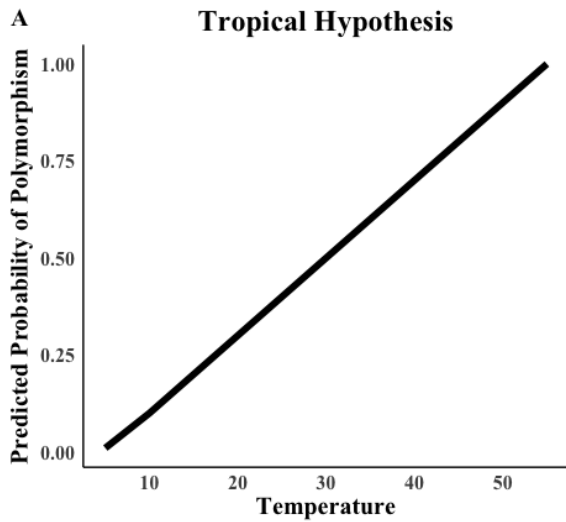


Figure 2: Diagram of allometries for the different categories of worker polymorphism. The graphs represent the allometric scaling of head width and total body size and the bottom is a diagram of how this would translate in the natural world. The x axis represents total body length or a proxy for total body length (logged) and the y axis represents head width (logged). A) An example of monomorphic ants. B) A monophasic allometry. C) A diphasic allometry. D) A triphasic allometry. E) A dimorphic allometry.

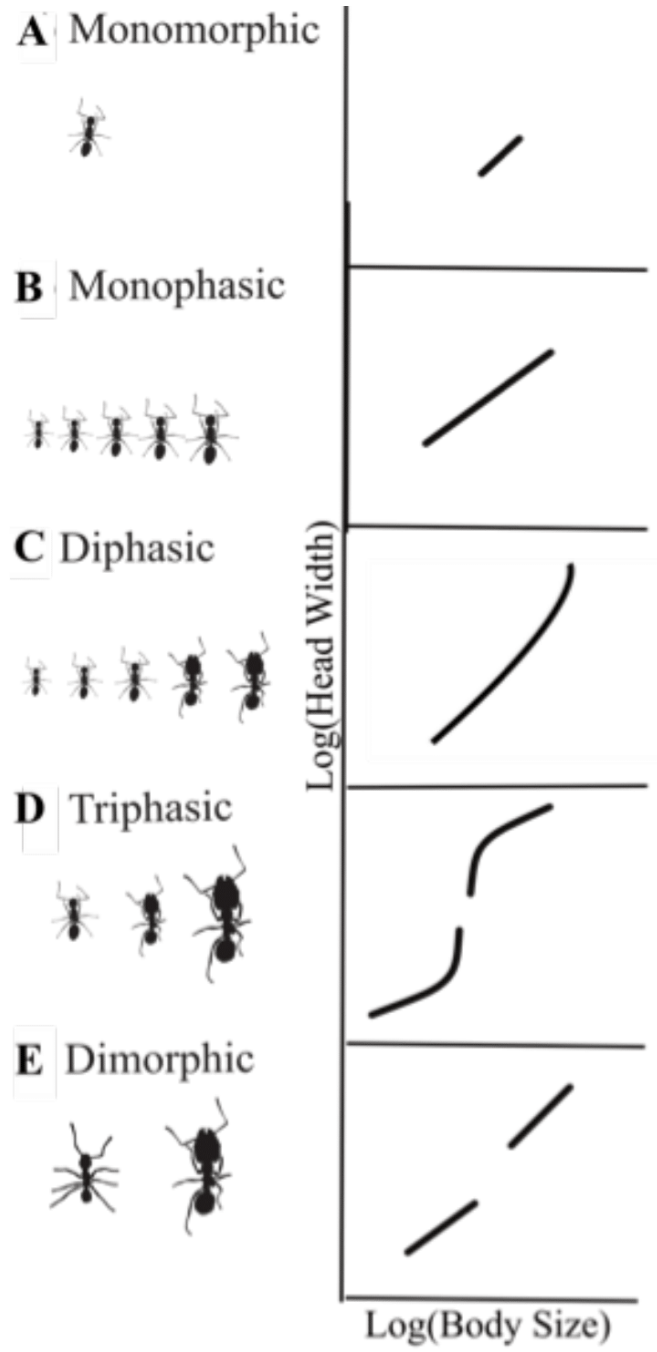
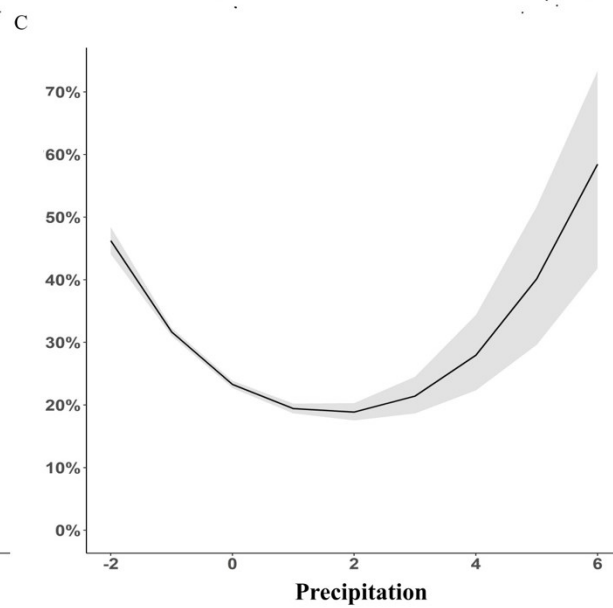
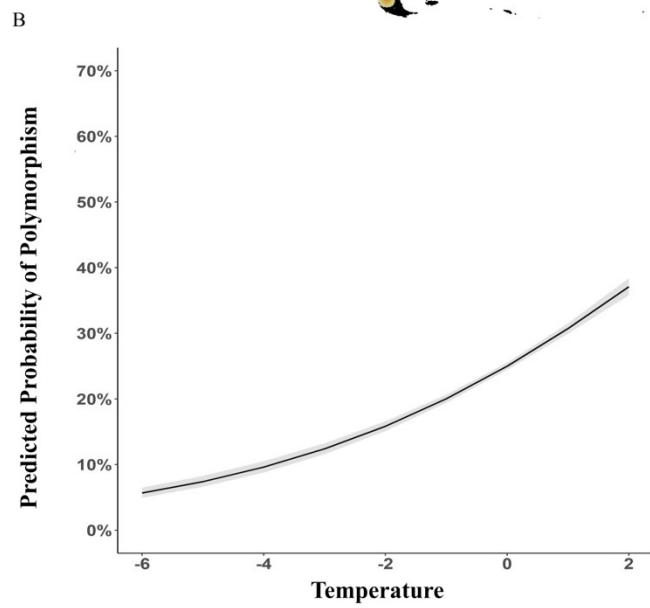
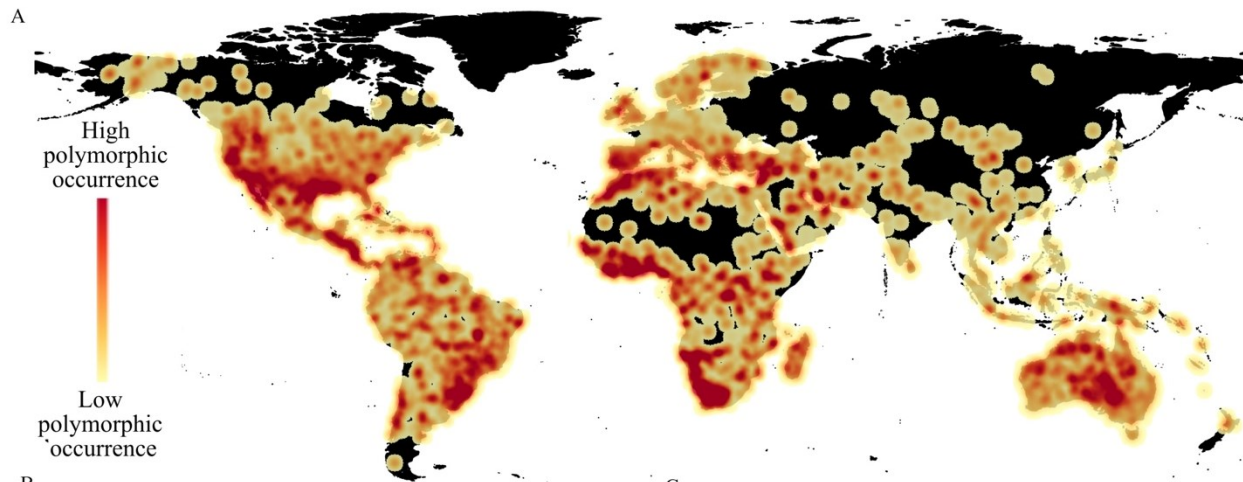


Figure 3: Map of the global distribution of ant worker polymorphism where A) represents a map of polymorphism penalized by sampling density. Red indicates areas of high occurrence density, whereas yellow indicates areas of low point density. I chose to penalize the occurrence data by sampling density because I encountered sampling bias in our data. B) Graph of the relationship between temperature and polymorphism of the best model, where temperature is scaled. C) Graph of the relationship between temperature and polymorphism of the best model, where precipitation is scaled.



APPENDIX

Table A1: Database breakdown of the number of polymorphic and monomorphic species and subspecies by subfamily.

SUBFAMILY	MONOMORPHIC	MONOPHASIC	DIPHASIC	TRIPHASIC	DIMORPHIC	POLYMORPHIC
<i>Agroecomyrmecinae</i>	1					
<i>Amblyoponinae</i>	129				1	7
<i>Aneuretinae</i>						1
<i>Apomyrminae</i>						1
<i>Dolichoderinae</i>	676					150
<i>Dorylinae</i>	498					301
<i>Ectatomminae</i>	264					
<i>Formicinae</i>	1768	1		7	16	1993
<i>Heteroponerinae</i>	32					
<i>Leptanillinae</i>	61					
<i>Martialinae</i>	1					
<i>Myrmeciinae</i>	90					3
<i>Myrmicinae</i>	5518	11			1149	667
<i>Paraponerinae</i>		1				
<i>Ponerinae</i>	1284					14
<i>Proceratiinae</i>	138					
<i>Pseudomyrmecinae</i>	257					1

Table A2: Percentage of polymorphic species and genera in the database.

Classification	Absolute percentage of polymorphism	Percent polymorphic genera	Percent of genera with at least 1 polymorphic species
Percent Polymorphic	29%	16%	29%
Percent Monomorphic	71%	84%	71%
Total Number of Species/Genera	15132	306	306

Table A3: Summary of spatial model formulas. The + represents covariables added to the models and * represents interaction terms added to the models.

Model	Response Variable	Fixed Effects	Random Effects
Model 1	Polymorphism (0 or 1)	1	NA
Model 2	Polymorphism (0 or 1)	1	Site ID
Model 3	Polymorphism (0 or 1)	Precipitation + Temperature	Site ID
Model 4	Polymorphism (0 or 1)	Precipitation ² +Precipitation+ Temperature	Site ID
Model 5	Polymorphism (0 or 1)	Precipitation* Temperature	Site ID

Table A4: Model selection using different genus level worker caste polymorphism classifications from Blanchard & Moreau (2018). In bold is the best model selected.

Model	AIC
<i>I</i>	124457.0
<i>I + Site ID</i>	122516.9
<i>Temperature + Site ID</i>	122279.5
<i>Precipitation + Site ID</i>	122337.2
<i>Temperature2 + Site ID</i>	122205.9
<i>Precipitation2 + Site ID</i>	122224.5
<i>Precipitation + Temperature + Site ID</i>	121876.4
<i>Precipitation2 + Precipitation + Temperature + Site ID</i>	121753.3
<i>Precipitation*Temperature + Site ID</i>	121858.9

Table A5: Summary of best model using Blanchard &Moreau (2017) classifications.

Variable	Estimate	Standard Error	Z Value	P value
Intercept	-1.251	0.017	-73.120	$<2e^{-16}$
Precipitation	-0.334	0.014	-23.120	$<2e^{-16}$
Precipitation ²	0.105	0.009	11.500	$<2e^{-16}$
Temperature	0.252	0.011	22.100	$<2e^{-16}$

Figure A1: Map of polymorphism and monomorphism occurrence around the globe. Note that these values were not weighted by sampling density as in Figure 3.

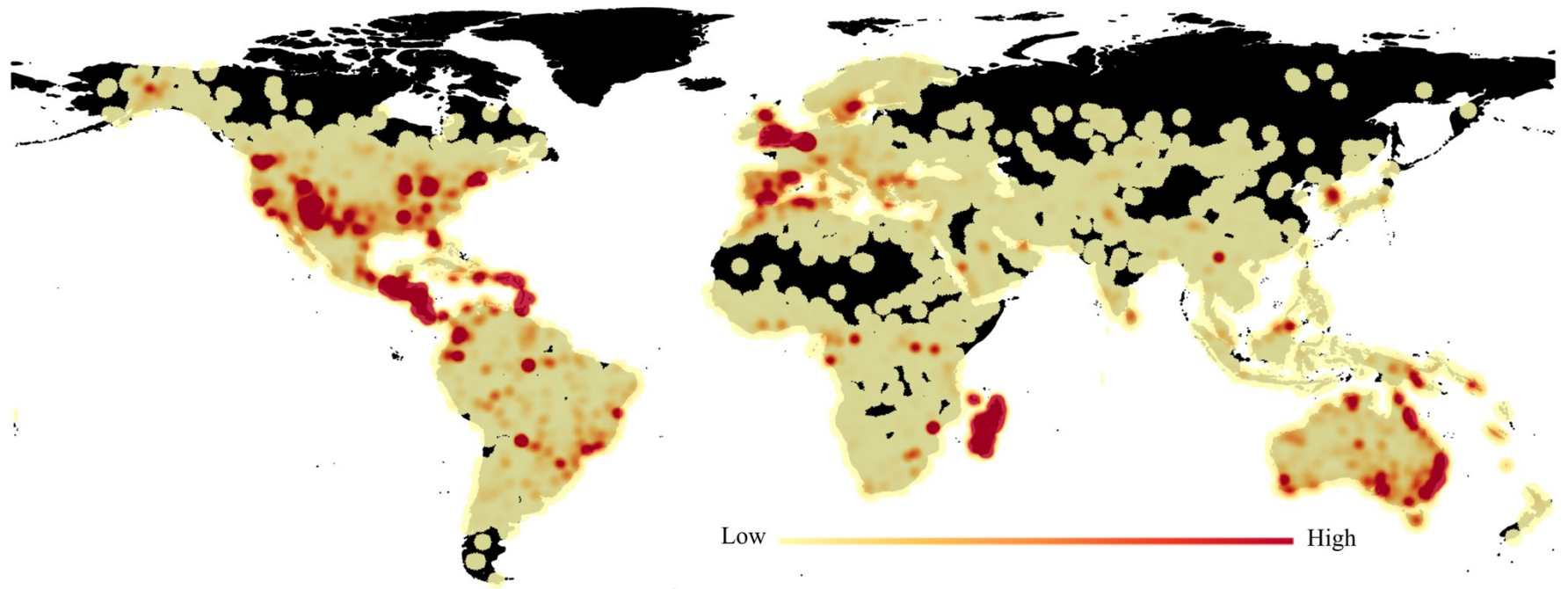
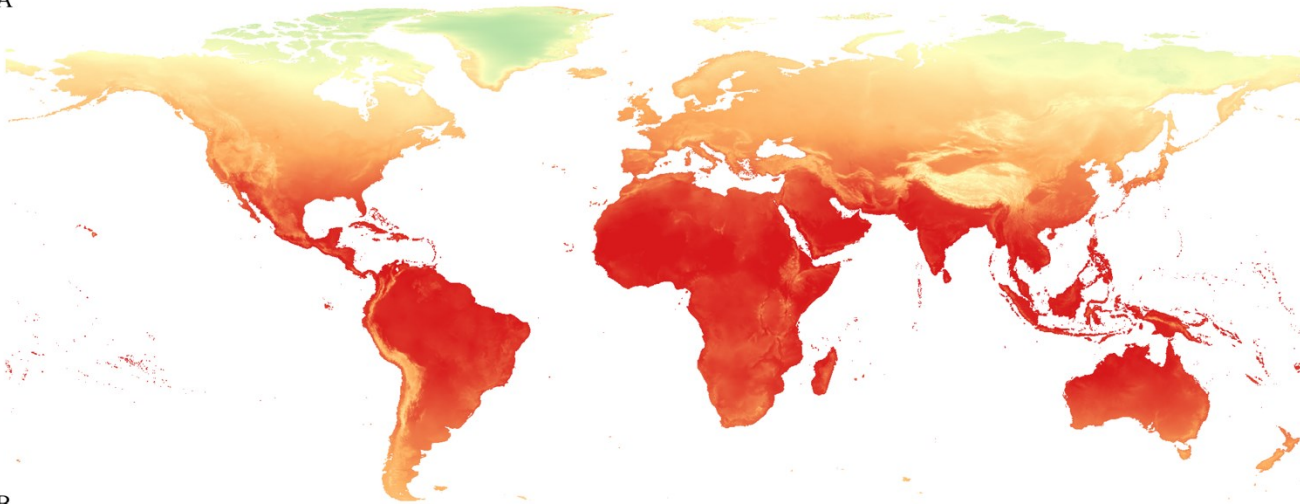


Figure A2: Climate maps where A) is temperature and B) is precipitation.

A



B

