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THESIS ABSTRACT

Taxonomic and functional ecology of montane ants

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Abstract. Why is biological diversity distributed in the way that it is? This question has been central to ecology and biogeography for centuries and is of great importance for pure and applied reasons. I use a functional trait view of ecology to complement standard sampling protocols to better understand the distribution and structure of ant (Hymenoptera: Formicidae) diversity across mountains. I use a long-term dataset of ant diversity and abundance, combined with a recently collected morphological trait dataset to examine how the alpha and beta diversity of ants responds to changes in temperature along an extensive elevational gradient in southern Africa. In addition, I link morphological thermoregulatory traits to each other and to the environment with a new database of ant elevational abundances from across the globe. Finally, I analyse how physiological thermal tolerances vary and constrain foraging patterns in montane ants. I find that temperature is a strong driver of both alpha and beta diversity patterns. In addition, morphological traits such as colour and body size are found to have a significant relationship to ambient temperatures. This relationship also implies that the relative abundances of different ant species change depending on their thermoregulatory traits (colour and body size) and the surrounding thermal environment. Furthermore, the critical thermal minimum (CT_{min}) of the ant species investigated and the lowest environmental temperatures are found to be key in constraining foraging activity patterns. The data presented here strengthen and link existing ideas about how thermoregulation can influence ecological communities and also suggests important ways in which diversity patterns may change in the future.

Key words. Ants, functional diversity, macroecology, mountains, thermal physiology, thermoregulation.

Introduction

The diversity of life on Earth is vast and not evenly distributed. This fact has fascinated biogeographers for centuries. An understanding of these patterns of diversity, and the processes that generate and maintain them, is important for two reasons. First, the distributions of organisms are a fundamental component of their biology and are inherently interesting. The patterns of biodiversity through space and time simultaneously tell us

about the evolutionary past, ecological present and potential future of species and ecological communities. Second, the rapid rate of global change due to climate warming and habitat loss is placing an unprecedented pressure on the global ecosystem (Cardinale et al. 2012). In order to manage and protect species, and the crucial ecosystem functions that they provide, we need to understand their current distributions, how these combine to generate patterns of diversity (Ricklefs

2008) and learn how they will change in the face of anthropogenic threats.

I bring together principles and techniques from biogeography (Brown and Lomolino 1998), macroecology (Brown 1995), macrophysiology (Chown et al. 2004) and functional biogeography (Violle et al. 2014) to address a number of unresolved issues in our understanding of the distribution of biodiversity through space and time. Ants (Hymenoptera: Formicidae) in mountain environments are used as a model system. Ants are charismatic, globally abundant (Hölldobler and Wilson 1990) and functionally important (Evans et al. 2011, Zelikova et al. 2011). They also have a strong foundation of taxonomic and methodological literature (Alonso and Agosti 2000). Mountains house much of the Earth's biodiversity and are useful natural experiments – they provide a huge range of abiotic environments over a relatively small geographic space (Körner 2007, Sundqvist et al. 2013). Consequently, biological sampling in mountains represents a wide variety of abiotic conditions whilst minimising the likelihood of encountering patterns that may be the result of evolutionary processes operating over larger spatio-temporal scales.

The broad question of interest is: how does temperature correlate with the assemblage structure and diversity of montane ant communities? In my Thesis (Bishop 2016) I explore this question through three research themes that are each united by key variables and address major gaps in the literature.

In the first theme I analyse patterns of species richness and how they correlate with spatial, temporal and environmental variables. Across elevational gradients, a range of different species richness patterns have been observed (Szewczyk and McCain 2016). The most common are mid-elevational peaks or linear declines in species richness with increasing elevation (Rahbek 1995, Rahbek 2005). Many different mechanisms have been proposed to explain these patterns (e.g. Colwell and Lees 2000). What is often ignored, however, is how species richness may vary through time. Temporal variation is important as it allows us to tease apart the factors that generate the

patterns we observe (White et al. 2010). For example, variation in species richness through time cannot be explained by area or geometric hypotheses (assuming the sampling occurs in the same place) but may be explained by changes in an environmental variable.

In the second theme the compositional differences, or beta diversity, between assemblages are considered in relation to changes in elevation. The approach to beta diversity taken here distinguishes between both turnover and nestedness patterns, and species and functional views of assemblages. Turnover and nestedness imply very different ecological contexts and consequences but are rarely separated. Turnover can be caused by factors that promote endemism (Bond et al. 2001) whilst nestedness appears as the ordered extinction (or colonisation) of species along a gradient (Ulrich et al. 2009). Ecological mechanisms that could be acting to increase the differences in species assemblage composition are likely to operate on the functional traits of species, rather than on their identities per se (McGill et al. 2006). For example, only species with a high thermal tolerance can survive in a hot environment, whilst the narrow interstices and complexity of the leaf litter environment may select for animals with relatively short legs.

The third theme investigates morphological and physiological thermoregulatory traits and links them to temperature and UV-B variables. If temperature is able to strongly regulate assemblage structure then its signature should be seen in the thermoregulatory traits of organisms. Both theory and data suggest that ectothermic organisms in cold places should have a combination of: large body sizes, dark colouration and physiological tolerance to low temperatures (Janzen 1967, Gates 1980, Willmer and Unwin 1981, Stevenson 1985). The relationships between these traits and the thermal environment have been tested for single species and in restricted geographic locations (e.g. Moreno Azócar et al. 2015). What isn't known, however, is whether these thermoregulatory traits can influence the entire makeup of ecological assemblages at a biogeographic scale. Furthermore, in a narrower sense, it is unknown how

the thermal physiology of montane ants varies, how it relates to ambient temperatures and whether it is capable of constraining activity and diversity.

Whilst ants are eusocial, colonial organisms, the abilities of individual workers to forage outside the nest are under the same thermoregulatory constraints as solitary organisms. As a consequence, it is the assemblage patterns of these foraging workers that are of interest here. Colonies themselves, however, do have a suite of thermoregulatory mechanisms available to them (Kadochová and Frouz 2013). Unfortunately, colony-level community or demographic data are notoriously difficult, if not impossible, to obtain (but see Ingram et al. 2013).

My work addresses the outstanding issues highlighted above relating to species richness, beta diversity, and thermoregulatory traits in order to improve our understanding of how temperature regulates montane ant assemblages. In sum, the main questions are: (1) how does ant species richness vary across elevation, and through time, and what factors best explain this? (2) How does ant beta diversity change across elevation and do species and functional patterns differ? (3) Do thermoregulatory traits explain variation in montane ant assemblage structure and distribution?

Methods

The main field site for my research was the Sani Pass in the Maloti-Drakensberg Mountains of southern Africa (Fig. 1). This is part of the grassland biome of southern Africa (Cowling et al. 1997) and the entire elevational transect ran from 900 m a.s.l. to 3000 m a.s.l.. As well as spanning a large elevational range this site is particularly useful as it has a road traversing the entire gradient, making the extraction of live specimens for physiological testing and repeated sampling easier to achieve.

In addition to this main site, I collaborated with ant ecologists throughout South Africa, Argentina and Australia (Fig. 2) to generate a large ant-elevational dataset, which was used to address my questions concerning the thermoregulatory traits of colouration and body size. All of these 13 additional elevational transects used a similar, and often identical, method of pitfall trap sampling as the Maloti-Drakensberg transect (Bishop et al. 2016). These additional sites were partly chosen based on existing collaborations and networks but were also selected to maximise the latitudinal range of the elevational gradients and the diversity of the biogeographical contexts that were included in the analyses.

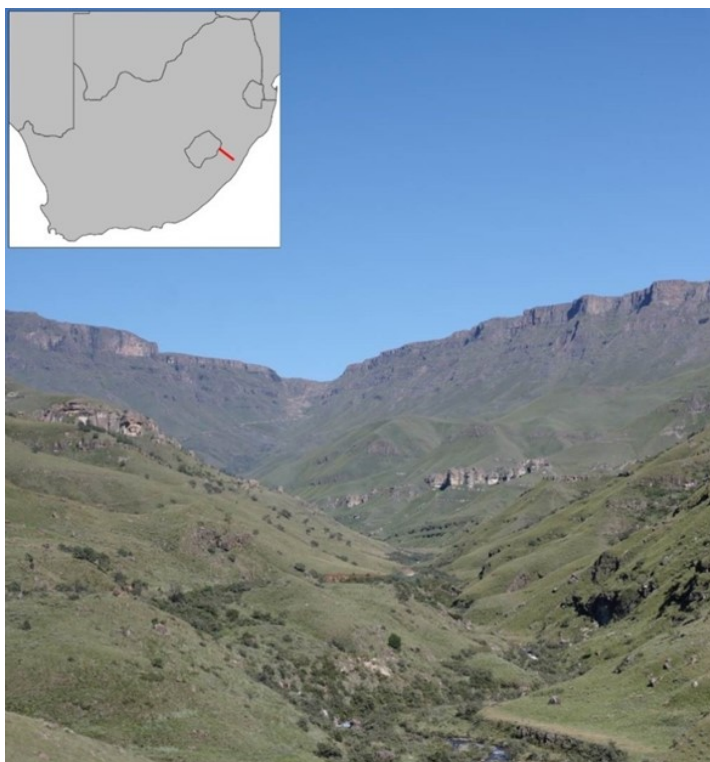


Figure 1. Photo of the Sani Pass, Maloti-Drakensberg, taken from 1500 m a.s.l. looking up in a north westerly direction to the top of the southern African escarpment at 3000 m a.s.l.. Inset map shows location of the main transect used in this study (red line) within southern Africa. The highest and westernmost points are located in the enclave of Lesotho. Photo by Jesse Kalwij.

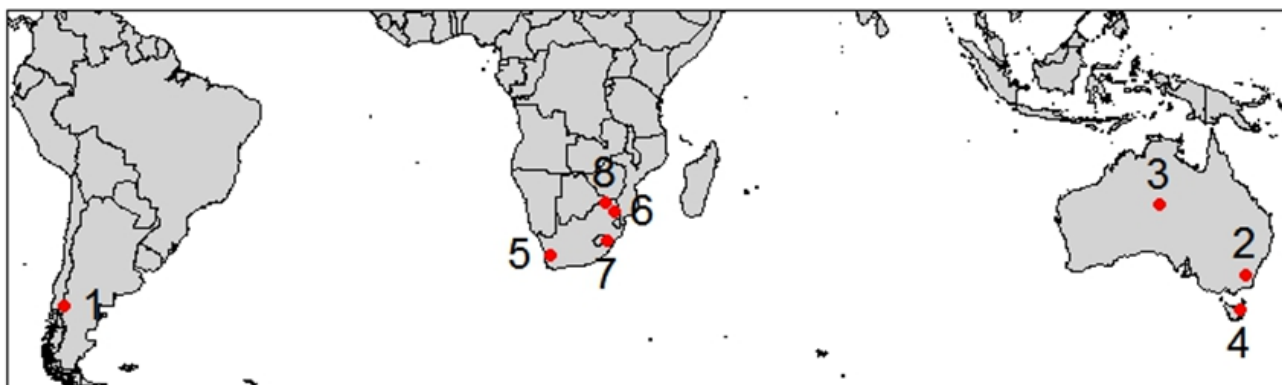


Figure 2. Map of the southern hemisphere showing locations of sampled regions as red circles for the chapter on thermoregulatory trait variation. The number of elevational gradients at each site and the elevational range is given in parentheses. 1: Patagonia ($n = 5$, 800–2000 m a.s.l.), 2: Snowy Mountains ($n = 1$, 400–2000 m a.s.l.), 3: MacDonnell Ranges ($n = 1$, 600–1400 m a.s.l.), 4: Ben Lomond Plateau ($n = 1$, 400–1400 m a.s.l.), 5: Cederberg ($n = 2$, 250–1900 m a.s.l.), 6: Mariepskop ($n = 1$, 700–1900 m a.s.l.), 7: Maloti-Drakensberg ($n = 1$, 900–3000 m a.s.l.), 8: Soutpansberg ($n = 2$, 800–1700 m a.s.l.). These transects were used in Bishop et al. (2016).

Results

Species richness was highest at mid-elevations in the Maloti-Drakensberg (Bishop et al. 2014). Ant species richness peaked at ~ 1500 m a.s.l. in the wet season and at ~ 1800 m a.s.l. in the dry season (Fig. 3a). These findings were consistent across the 7 year time series. The linear mixed models showed that these patterns were largely driven by differences in temperature, with only a very small effect of available elevational area. Both temperature and available area correlated positively with ant species richness. As a result of the temporal changes in diversity that were explained by temperature, hypotheses relating to geometric constraints were ruled out.

Both species and functional beta diversity increased with increasing elevational distance but in strikingly different ways (Bishop et al. 2015). Species compositional change was dominated by species turnover, but functional compositional change was a result of functional nestedness (Fig. 3b-c). In other words, different species were found at different elevations but these represented an increasingly nested subset of functional types. Ants at the highest elevations tended to look like habitat and dietary generalists, whilst at lower elevations there was a much greater diversity of ant morphological forms (Bishop et al. 2015). The species beta diversity patterns could not be recreated by null models, whilst the functional

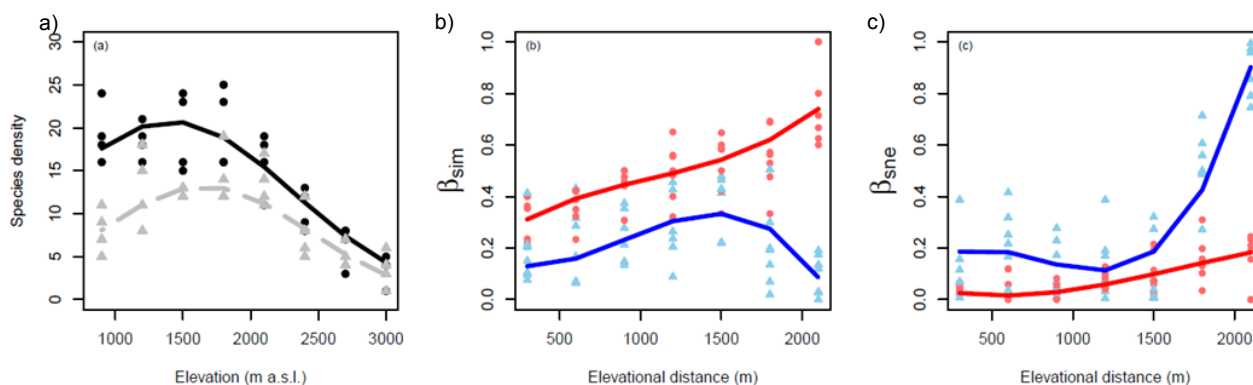


Figure 3. Plots showing changes in alpha (a) and beta diversity (b-c) in the Sani Pass, Maloti-Drakensberg. In (a), black line and circles are predictions and data for the wet season whilst the grey dashed line and triangles are for the dry season. For (b) and (c) red lines and data points indicate species beta diversity and blue lines and points represent functional beta diversity. (b) shows turnover (β_{sim}) and (c) shows nestedness (β_{sne}). Plot (a) modified from Bishop et al. (2014), plots (b-c) modified from Bishop et al. (2015).

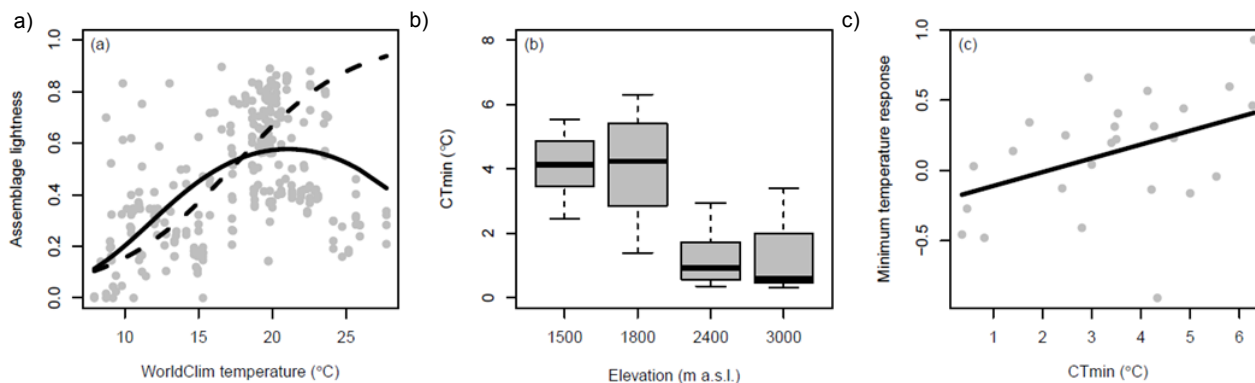


Figure 4. Plot (a) shows the relationship between average assemblage lightness (colour) and ambient temperature. Solid line indicates relationship in the presence of high UV-B irradiation, dashed line is under low UV-B conditions. Plot (b) shows the critical thermal minimum changing with increasing elevation. Plot (c) illustrates how the “minimum temperature response” is related to CT_{min} . The temperature response is the correlation between a species’ abundance and the ambient temperature over a 7 year time series. Data points are assemblages in (a) and are species in (b-c). Plot (a) modified from Bishop et al. (2016), plots (b-c) modified from Bishop et al. (2017).

beta diversity patterns could. This implies that the functional beta diversity patterns are no different from random change.

Assemblage-level morphological thermoregulatory traits had a strong correlation with temperature across the elevational gradients of the southern hemisphere (Fig. 2). In colder places (e.g., high elevations or closer to the South pole) or in colder years the most common ants were darker in colour (Fig. 4a) and had larger body sizes (Bishop et al. 2016). Furthermore, this was influenced by UV-B. In the Australian desert, for example, where one might have expected the ants to be pale in colour to combat the high temperatures, the ants were dark. This pattern correlated with an increased UV-B load at this location relative to the other elevational gradients – I hypothesise that the dark colouration is a protective mechanism against high UV-B. Consequently, changes in ant assemblage structure over space and time appear to be strongly linked to the need to thermoregulate effectively (Bishop et al. 2016).

Finally, ants at higher elevations, and consequently occupying colder environments, tended to have lower physiological thermal limits. The average critical thermal minimum (CT_{min}), was lower at higher elevations (Fig. 4b, Bishop et al. 2017). Furthermore, the CT_{min} of the different ant species was related to activity patterns (Fig. 4c). Ants with lower CT_{mins} tended to be active over a large range of temperatures but those with a high

CT_{min} , and therefore unable to tolerate the cold, were only active at higher temperatures (Fig. 4c, Bishop et al. 2017).

Discussion

I have used a combination of macroecological tools and detailed field observations and experiments to test some unresolved ideas in ecology and biogeography. These all relate to the broad question of how temperature may regulate the structure and diversity of assemblages. I have used different kinds of data and approaches that combine to show that it is the ability of different species to respond to temperature that influences assemblage structure and diversity patterns.

Bishop et al. (2014) shows that species richness is highest at mid-elevations. Its overall spatial and temporal distribution is most closely linked to temperature, however. Bishop et al. (2015) describes how ant assemblages become more and more dissimilar with increasing elevation, or decreasing temperature. This effect is present when viewing assemblages as a collection of species, or as a distribution of functional trait values. Bishop et al. (2016) highlights how colour and body size relate to assemblage structure through space and time. In cool places the ants tend to be darker in colour with larger bodies. Bishop et al. (2017) illustrates how minimum temperatures and tolerances constrain foraging

activities. There are a number of questions left unanswered by these individual research projects that link to the wider literature, or to each other.

Bishop et al. (2015) questions what factors may be driving the turnover of ant species with elevation. The functional morphological traits investigated here appear to change at random with respect to elevation and the underlying species turnover. This is in contrast to a prominent study on the elevational beta diversity of tropical trees (Swenson et al. 2011) which found a number of traits (e.g., tree height, leaf area, leaf nitrogen) that appeared to change non-randomly. This implies that there may be unmeasured traits that are linked to the observed ant species turnover in Bishop et al. (2015). I suggest that physiological traits may be responsible for the changing species composition across elevation. Indirectly, the data from Bishop et al. (2017) support this idea. I show that species moderate their activity based on their ability to tolerate low temperatures. It is conceivable that as minimum temperatures get lower with increasing elevation, only ants with adequate thermal physiology will be able to exist at these sites—driving the observed species turnover.

My research on ant colouration (Bishop et al. 2016) shows that the relative abundances or identities of species in a local assemblage can change depending on their colour, body size and the ambient temperature. My physiological thermal tolerance work discusses how species' thermal physiology can constrain when (and, by extension, where) they are actively foraging (Bishop et al. 2017). Together, these results suggest that there may be a coupled evolution of thermoregulatory traits that ultimately have an effect on the success of a species in a given context. This idea is not new (Bogert 1949), but the data presented in these two papers provides solid insights into the mechanisms behind thermal preferences in ants at both large and small scales – cuticle colour and body size, and physiological thermal tolerance.

A major take home message from the work presented here is the role of low temperatures in driving ant ecology. In mountain ecosystems,

such as those focussed on here, my data suggests that minimum temperatures are the most limiting—a fact not often explicitly recognised in the literature. For example, there is a strong focus on maximum temperatures and maximum thermal tolerances (Cerdá et al. 1998, Kaspari et al. 2015). Many of these studies are based in extremely warm environments which justifies their emphasis on upper thermal limits. My work (Bishop et al. 2017) and those of others (Warren and Chick 2013), however, are beginning to suggest that low temperatures and lower thermal limits have an important and underappreciated role in shaping ant biology and diversity.

In sum, my work highlights the importance of thermoregulatory traits in structuring ant diversity patterns. It also generated a variety of ideas for future research programs which would expand our knowledge in the fields of ant ecology, functional traits, biogeography, macroecology and macrophysiology significantly. Based on this work, three major avenues on ant ecology and the link to functional traits are suggested for future research, these are: Under what conditions are abiotic or biotic factors more important for structuring ant diversity? How do ant functional traits vary intraspecifically and how plastic are they? How do functional traits map onto the performance and success of colonies?

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