Does Environmental Predictability Affect Risk-Mitigation Behaviours in Ants?

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MSc by Research
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Biology

January 2023

Abstract

Social animals develop in environmental conditions which are always in flux. These changes can be either predictable or unpredictable, and social insects must be prepared to adjust to both. Resource distribution, and in particular, food availability is important in determining many aspects of a social insect's life history and behaviour. Multiple strategies have evolved within humans and/or the wider animal kingdom to minimise the risks of acquiring food in an unpredictable environment. These include diversification/generalism, food storage, nomadism/migration/relocation, and food exchange/polydomy. Due to the difficulty of collecting direct information on food predictability and the strong influence of the environment on food distribution we used environmental predictability as a proxy for food predictability. By carrying out a meta-analysis of the model clade Formicidae, which displays all four of these behaviours, we attempted to answer two questions:

1. When during the evolution of the ant taxa, have different risk-mitigation strategies evolved?
2. Which of these behaviours are used under different levels of environmental predictability?

In order to answer the first question we carried out an ancestral state reconstruction. We found that the ancestral state for the Formicidae is a combination of both nomadism and generalism strategies. We also found that the same combination was the most common state throughout the evolutionary history of the Formicidae. Generalism and nomadism behaviours are both found widespread throughout the phylogeny, while storage and polydomy have evolved multiple times in more distinct groups. For answering the second question we used temperature and precipitation to model environmental predictability using Cowell's indices. We then carried out a Bayesian categorical logistic regression on this weather data. Our analysis informed us that as temperature constancy increases, nomadism becomes more common with respect to a generalism. Conversely as precipitation constancy and contingency increases, nomadism becomes less common with respect to generalism.

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Acknowledgements

I would like to thank my supervisors Prof. Elva Robinson and Dr. Katie Davis for their guidance throughout my project. They have been ever supportive, not only in answering my academic queries and furthering my understanding of both behavioural and evolutionary biology respectively, but also pastorally through the many unfortunate events that took place for me throughout the past year.

I would also like to thank Jessamy Ahmed for allowing me access to her project data and methodology, of which some was adapted for use in this project, and the wider Ant Lab at York University for their friendship, feedback, and support on a day-to-day basis throughout the year. I thank Dr. Corrie Moreau for providing access to the ant phylogeny which I used and for providing feedback on my work, my Thesis Advisory Panel member, Prof. Calvin Dytham for his help during my TAP meetings, along with the many members of the IUSSI and ASAB societies who I had the pleasure of discussing my project with at their corresponding conferences.

Finally, I would like to thank all my friends and loved ones for their support and advice, in particular Lili Vizer, who has been there for me from the first day until the last, truly I could not have done it without you.

Declaration

I declare that this thesis is a presentation of original work, and I am the sole author. This work has not previously been presented for an award at this, or any other, University. All sources are acknowledged as References.

1. Introduction

1.1: Background

The environment around us is constantly changing. In response, animals evolve behaviours which limit the impact of these changes and maximise their fitness. Our environments are formed by a complex network of interacting biotic and abiotic factors which combine to create the world we live, interact, and survive in and ultimately alter our fitness (Figure 1). These factors can vary in how predictable they are, and this degree of predictability may have a differing effect on our ability to adjust to our environment. Thus, depending on their degree of predictability, the behaviours we develop may differ.

The day-night cycle is a regular, highly predictable cycle that creates circadian rhythms. These rhythms determine the times animals will sleep and forage (Gerhart-Hines & Lazar, 2015). In turn, these animals may be prey species themselves whose daily and annual cycles influence the hunting times of their predators. Seasonal changes determine annual weather cycles and plant life cycles, which in turn affect the fluctuations of animal populations. For example, winter moth caterpillars emerge to feed on new oak leaves that grow each Spring. In turn, great tits time their egg laying so that the hatching period is synchronised with caterpillar appearance (Cole et al., 2021). Within these annual changes there is variation in the consistency of these patterns. For example, there is variation in developmental plasticity which means some organisms are better able to track and respond to cues (Blackman, 2017). Therefore, some populations may be able to remain relatively uniform annually, whereas others may vary more unpredictably.

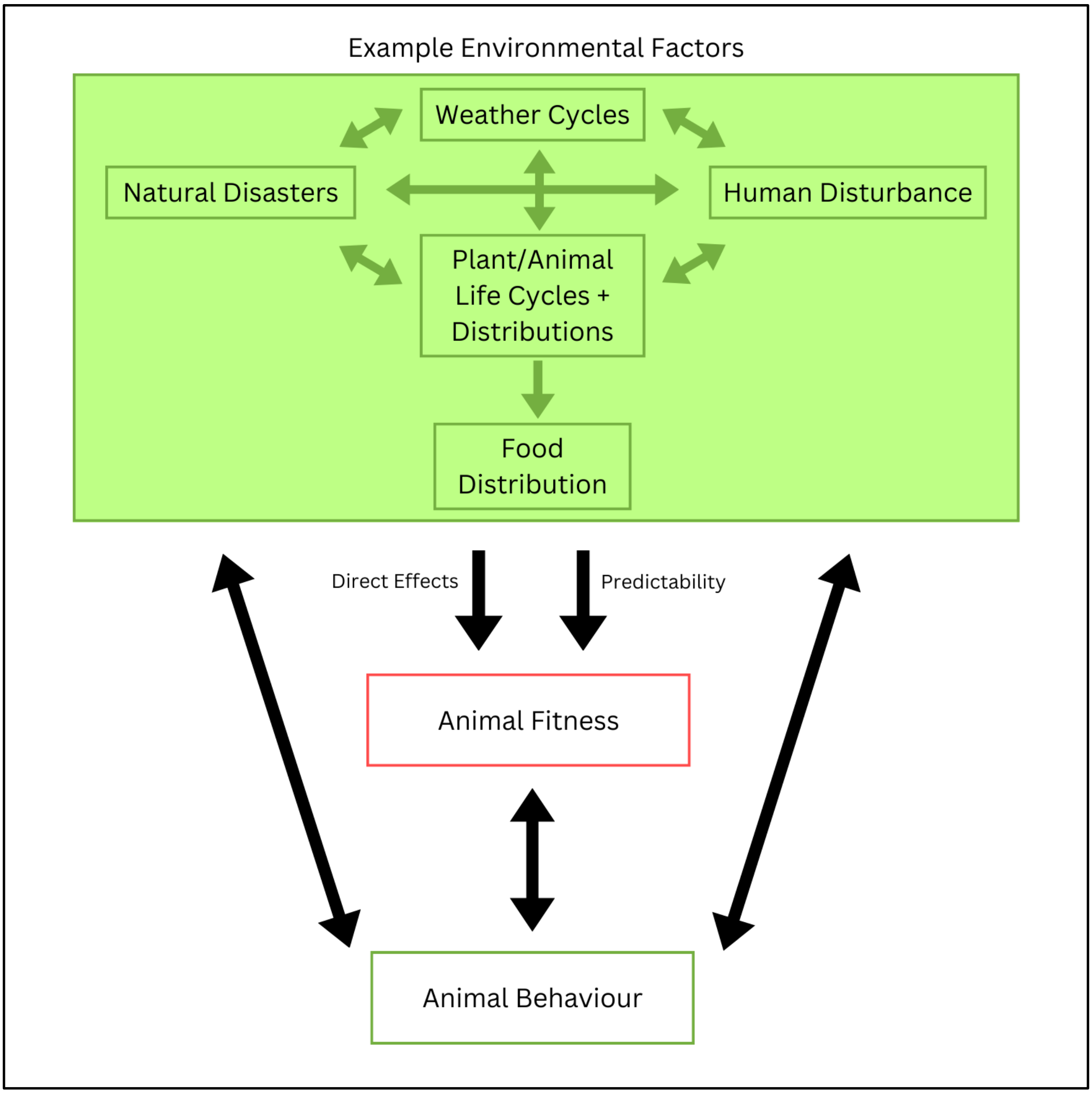


Figure 1.1: Different biotic and abiotic factors interact with one another to create our environment. This environment affects our fitness and over evolutionary time scales, our behaviours evolve, and we adapt to the environment. Arrows denote a direction of effect.

Additional factors may further change the predictability of an environment. Tropical storms cause sudden alterations in weather patterns, while other natural disasters, such as earthquakes and floods, may completely change the landscape. Human disturbance can also alter the predictability of an environment. Urbanisation causes light pollution which interferes with natural circadian cycles (Wyse et al., 2014), while deforestation removes nesting spaces and food resources (Sekercioglu et al., 2002). Continuing with our great tit example, increasing climate temperatures mean that Spring arrives earlier each year and the oak leaves sprout sooner. In turn caterpillar populations reach their peak earlier and so great tit hatching times are becoming increasingly unsynchronised (Cole et al., 2021). This will lead to a lowered fitness of the hatched offspring who are unable to exploit their caterpillar food sources to the fullest. Areas affected by oak dieback, a disease which causes development of sparse canopies, results in a further asynchrony, hypothesised by the authors to be due to interference with the normal cues used to initiate breeding or a reduction in resource availability to begin breeding (Cole et al., 2021). Poor canopies also create a sparsity in high quality resources and changes in the spread of the disease create spatial unpredictability. Due to the effects these environmental factors have on fitness, they will have an impact on the evolution of an animal's behaviour. Over generations the great tits have begun to adjust their hatching times to earlier in the year. Furthermore, the spatial variation in the environment caused by dieback will mean the great tits should develop behaviours to select better breeding sites.

1.2: Food Resources

Whether it is the prey distribution of a predator, the locations of appropriate nesting sites, or any number of resources an organism needs, the distribution of it is one environmental factor especially important in altering our fitness. Food as a resource is of particular importance, as acquiring food is essential for all aspects of an animal's life history (Siems & Sikes, 1998), from growth, to courtship, to reproduction and raising offspring. Indeed, roe deer select their habitats based on food availability (Dupke et al., 2017). Meanwhile, when food resources are unpredictable, zenaida doves are more aggressive between one-another (Goldberg, 2001) and in artificial environments unpredictable food resources result in lower testosterone levels and reproductive rates in scrub-jays (Bridge et al., 2009). The distribution and consistency of food resources is therefore highly influential in determining animal fitness.

Resource distribution can be measured using five factors (Goldberg, 2001). These are: resource abundance (the average quantity of a resource in an area over time), spatial and temporal predictability (the ability to predict intervals between the occurrence a resource in space and time, respectively) and spatial and temporal clumping (the variation in abundance of a resource over space and time, respectively). Within this study we are interested in considering the effects of temporal predictability. Here we define temporal predictability as the degree to which one can predict the intervals between the occurrence of a resource in a particular location over time. Predictability can be measured using Colwell's Indices.

1.3: Predictability

Predictability is primarily made up of two aspects (Colwell, 1974). The first is constancy, the continuous state of a variable across a time period. For example, a tree may produce fruit at a constant rate throughout the year, across multiple years, with very little variation. The second aspect is contingency, the repeated pattern of occurrence of a variable across multiple consecutive time periods, regardless of whether there is constancy within each individual time period. For example, if the tree did not produce fruit at a constant rate, but instead produced fruit on a seasonal basis, every Spring, then while the tree may have a low degree of constancy within a year, it has a high degree of contingency, which would make the resource predictable annually. The sum of these two measures provides us with the overall degree of predictability:

Predictability = Constancy + Contingency

Food distribution is part of the network of interacting factors that make up our environment. It can be heavily influenced by seasonality (Puig et al., 1996) as well as the weather and climate change (T. Wheeler & von Braun, 2013). Variations in weather patterns and other abiotic factors such as temperature, precipitation and humidity will create an environment that has low constancy. If these fluctuations are regular over seasons, this low constancy will be mitigated by higher contingency. Human interference may reduce or improve predictability. Deforestation and changes of land use may restrict the amount of a food resource available or limit the access to it (Manchego et al., 2017). Alternatively, interference may increase constancy if human presence creates a food source itself. For example, spotted hyenas aggregate at human waste sites in prey-depleted regions of Ethiopia (Yirga et al., 2015). Climate change is becoming an increasingly greater issue for many species around the world (Gregory et al., 2005; Maurer et al., 2019; Nerem et al., 2018). Climate change creates a much more unpredictable environment for animals, as it more rapidly changes the state of the environment they have adapted to. At the extreme, regions which are prone to regular natural disasters - such as droughts, tropical storms, and wildfires - will have both low constancy and contingency, as such changes may not be as easy or even possible for animals to anticipate and mitigate.

Based on foraging theory, a food resource would be predictable if an animal can determine the location, quality, or quantity of the resource via the environmental factors that may affect it, for example season, time of day and temperature (Stephens and Krebs 1986). To adapt to and adjust to different degrees of predictability, animals must evolve to be able to either directly remember changes to their environments and adjust within their lifetimes or evolve to match or detect changes over many generations. Many corvid species are able to remember the locations of food caches stored in an area (Bednekoff et al., 1997; Bennett, 1993) and rats are able to remember the locations of food within a maze (Roberts, 2006). These are both examples of memory development. Alternatively, the great tits in our earlier examples (Cole et al., 2021) synchronise their egg hatching to food resources that are adjusted to over multiple generations. Through plasticity within the population, those individuals with the greatest synchrony to caterpillar peak abundance will be selected through their higher fitness. Indeed, within the model organisms for our own study – the ants - there are some species which are able to remember their environments based on visual cues (Wehner & Räber, 1979), retain memories over extended periods of time (Errard, 1994; Josens et al., 2009) and make use of their memory for foraging purposes (Johnson, 1991). They also develop behaviours such as storage (Gross et al., 1991; Went et al., 1972) which can be selected on over evolutionary time scales to follow trends in resource peaks and scarcities.

1.4: Ants - A Model Taxon

Ants (Formicidae) are a vast family of social insects, made up of over 14,000 extant species and 800 fossil-record species (Bolton, 2021). They have a combined geographical range spanning every continent except Antarctica (Guénard et al., 2017). The size and spread of this family mean that it includes species living under a range of different environmental conditions and presenting a diverse array of behaviours. Ants therefore make an ideal group of organisms to carry out both studies on behaviour and environmental effects. Their wide ranging behaviours are often comparable to those of other social organisms, and so ants are commonly used in experiments to model and simulate human behaviours ranging from disease mitigation (Curtis, 2014), to resource management (Ahrndt et al., 2015), to crowding (Haghani & Sarvi, 2018). In addition, ants themselves are an important group to study because of their own impact on the environment. They are both essential bioindicators (King et al., 1998) and keystone species (Uhey & Hofstetter, 2021), as well as major pests (Della Lucia et al., 2014) and invasive species (Holway, 1999), making understanding their behavioural ecology important in ecosystem and climate sciences, pest control and conservation.

1.5: Risk Mitigation Strategies

In order to survive in environments of varying predictability, it is logical that animals would develop behaviours which reduce the impact the uncertainty has on their fitness - by mitigating low constancy and contingency scenarios. Here we describe these behaviours as risk-mitigation strategies, and we attempt to answer the following two questions:

1. When during the evolution of the ant taxa, have different risk-mitigation strategies evolved?
2. Which of these behaviours are used under different levels of environmental predictability?

Historically, humans have used four different methods of risk-mitigation: storage, nomadism, exchange and diversification/generalism (Halstead et al., 1989; O'Dwyer, 2020). These four strategies are also commonly seen in various species throughout the animal kingdom, and all four behaviours have been observed in ants (see below).

1.5.1: Storage

We define storage as the accumulation of nutrients which are not consumed immediately, but instead stored for consumption at a later point in time. These nutrients can be stored internally, for example fat-tailed dwarf lemurs increase body fat stores in preparation for hibernation, doubling their body mass (Fietz & Dausmann, 2007). Alternatively, they can be stored externally, for example many Parid species create food caches throughout the year and in periods of less predictable supplies of food (Pravosudov, 2006; Pravosudov & Grubb, 1997). Indeed, food storage of fruits, seeds and nuts is commonly seen throughout a range of bird and mammal species (C. C. Smith & Reichman, 1984).

Although use of storage often occurs over periods of higher uncertainty, food stored externally will typically be perishable or at risk of theft and kleptoparasitism, creating a time limit to the strategy use. Therefore, we would expect storage to be more common when there is a low level of constancy, but higher contingency to the predictability of the food source - the animal may have sparse resources for a limited period of time but will regain access after waiting out the unstable period.

Within the ants many forms of storage behaviour are seen, which fall under two main categories. Internal storage consists of food resources that are stored within the bodies of the adult ants or larvae within a colony. These may take the form of specialist replete workers, who are fed the resources by other workers for storage, and then regurgitate it when required for feeding through the process of trophallaxis. Honeypot ants have a class of workers who act exclusively as living food larders which store nectar within their gasters (Conway, 1986). Cannibalism is an interesting strategy to consider as storage. In some cases, the behaviours may be destructive acts to sustain the colony during starvation or stress (Sorensen et al., 1983). We would not consider self-destructive cannibalism as a storage strategy. Alternatively, larvae may intentionally be produced in excess to feed the colony (Nonacs, 1991), or be fed on partially as both a living food store and a future worker via larval hemolymph feeding (LHF). LHF is a behaviour in which adult ants feed off of the hemolymph of their own colony larvae, without apparent long-term consequences to the larvae and never to the point of larval death (K. Masuko, 1989).

External storage, where food is stored outside of the colony members and may be either dead or living. Harvester ants are primarily granivores which collect and store various types of plant seeds (Mackay, 1984; C. R. Smith, 2007). Alternatively, Leaf-cutter ants cultivate edible fungi gardens (Shik et al., 2014), while *Lioponera turneri* collects larvae of *Pheidole* ants, which they then place into a state of paralysis. These larvae remain alive for weeks within the *L. turneri* nest until they are consumed by workers (Hölldobler, 1982). While other behaviours could arguably be described as external storage - some ant species protect and manage aphid symbionts as producers of honeydew (Giannetti et al., 2021; Yamamoto & Del-Claro, 2008) - we do not consider these storage behaviours here, as the ants must immediately collect the output. Instead, these behaviours are more akin to food conversion rather than storage and if stored, the produced honeydew is usually stored within repletes. Likewise, we would also not consider the temporary construction of booty caches that is seen in *Neivamyrmex* as storage. While food is stockpiled in locations after raids, this is purely for collection efficiency purposes and colonies will proceed to migrate to the most abundant caches and consume the supply until depletion (Mirenda et al., 1982).

1.5.2: Exchange/Polydomy

Food exchange is defined as the transfer of food resources between groups, and which is not given under duress or being stolen. Typically, this would be where receiving individuals or groups have an otherwise lower availability of food resources than the donors. For ants, peer-to-peer food exchange between individuals of a colony via trophallaxis is near ubiquitous across ant species and an integral aspect of their ecology (Meurville & LeBoeuf, 2021). The transfer of resources between distinct nests is less common and is termed polydomy. This is seen in many different ant species, such as some colonies of red wood ants *Formica lugubris* in which different nests exchange food, workers and other resources as one interlinked colony (Ellis et al., 2014), as well as Japanese queenless ants *Diacamma indicum (*Tsuji, 1988*)* and *Dinomyrmex gigas* (Pfeiffer & Linsenmair, 1998). Many other perceived examples of food exchange between animals may not necessarily be classified as true exchange. For example, food tributes given to invasive fire ants by native ant species (Bhatkar, 1979) would better be described as theft, as one party within these interactions is being coerced into the interaction. Although some exchange occurrences appear to be true exchange (G. C. Wheeler & Wheeler, 1970), such interspecific exchange lies out of the scope of focus for our intraspecific risk-mitigation behaviour.

Within historical human societies, exchange has been the common practice when food resources have been temporally unpredictable and one social group has excess food relative to another (Dillian & White, 2010). Other papers suggest exchange is less common at either extreme of predictability than at moderate conditions (Spikins et al., 2021). Even more contrary is research which finds exchange most common under predictable conditions (Ringen et al., 2019); however, the authors question the accuracy of their proxies for predictability. Therefore, it is unclear under what level of predictability food exchange is more likely to occur.

While food exchange within a group is certainly common, particularly within the social insects (Meurville & LeBoeuf, 2021), outside of humans and ants, true food exchange between spatially distinct groups is uncommon. This practice is primarily only otherwise observed in bonobos, which when given the choice will not only preferentially share food with another individual rather than eat alone (Hare & Kwetuenda, 2010), but will even share food with members of other troops (Fruth & Hohmann, 2018). This is a behaviour that has not been found within even our other close relatives such as chimpanzees (Gilby, 2006; Silk et al., 2005).

1.5.3: Nomadism/Migration

Nomadism, also described as vagility, relocation, migration, or, within ants, nest movement, in this context refers to the capability of an animal/animals to move from an area of low food resource availability or quality to a higher one. Some desert bird species determine their flight paths by following irregularly emerging feeding opportunities (Dean, 2004) and examples of food-associated nomadic behaviours have been observed in mammals, reptiles, birds, fish and crustaceans (Teitelbaum & Mueller, 2019).In mammals, nomadism becomes more common in more temporally unpredictable environments (Mueller & Fagan, 2008; Singh et al., 2012). As both constancy and contingency become low, the recurrence of a resource within an area should reach a point at which the cost of relocation to new food sources is lower than the cost of locating limited food resources in the current area.

Nomadism is a common behaviour within many ant species. While in some cases relocation is in direct response to other factors, such as nest humidity or predation (McGlynn et al., 2004), many species are nomadic specifically in order to locate new food sources. Army ants are the prime example of such behaviour, whose predatory colonies form swarming raids which can relocate every few days to new hunting patches (Song et al., 2018; Topoff, 1984). Many nomadic ant species establish bivouacs - low cost, temporary nests constructed from the bodies of the ants themselves - or preformed cavities - rather than digging energy costly subterranean nest networks themselves (Maschwitz & Hänel, 1985). These bivouac style nesting strategies are therefore a good indicator as to whether a species performs nomadic behaviours or not, when direct observations of relocation are rare.

We would expect that nomadism is most common under conditions of both low constancy and contingency. This is because migratory behaviour would allow ants to follow food gradients and relocate to new sites when a resource is depleted in an area. This behaviour is suited to highly unpredictable environments as there is no reliance on a resource being seasonal or recurring in a location.

1.5.4: Diversification/Generalism

Generalism is the ability to use multiple distinct sources to acquire a type of nutrient (e.g. carbohydrate or protein) by a single population of a species during the same year/season. One breakdown of generalist - specialist definitions (Table 1) described by (Loxdale & Harvey, 2016) is given below:

Table 1.1: Definitions of generalism and specialism adapted from (Loxdale & Harvey, 2016).

Degree of Generalism	Definition
Broad Generalist (True generalist)	The consumption of distinctly different prey or plant species at a population level
Composite Generalist (Species Generalist)	The consumption of distinctly different prey or plant species at a species level but many closely related species (same family) at a population level
Broad Specialist	The consumption of many closely related prey/plant species at a species level
Narrow Specialist (True Specialist)	The consumption of one or a very small number of prey/plant species at a species level

A generalist diet is expected to occur in conditions where there is less predictable food availability, whereas specialists are found when the occurrence of a food source can be relied upon (Overington & Lefebvre, 2011). Simulations of the evolution of specialism-generalism under different levels of predictability show that instances of generalism increase by 40% under completely unpredictable conditions compared to completely predictable ones (Overington et al., 2008).

Within ants, generalism is widespread. Many of the most common ants are general scavengers (Hölldobler & Wilson, 1990). *Carebara perpusilla* has a diet consisting of various invertebrate families (Khalife & Peeters, 2020), and *Dinomyrmrex gigas* consumes protein sources varying from carcasses and carion to faecal matter and urine (Pfeiffer & Linsenmair, 1998). Even within the typically specialist Army ants, some species will capture whatever protein sources they find on their nomadic raids (Schneirla & Reyes, 1966). Argentine ants adjust their diet in order to change their trophic niche, depending on whether they are native or invasive within a region, as well as dependent on the stage of the invasion they are in (Tillberg et al., 2007). Invasive ant species typically exist in an unpredictable environment as they are moving into new locations with unfamiliar conditions they do not have specific adaptations for - akin to a changing climate for non-invasive populations.

1.5.5: Other behaviours - Hibernation

In many temperate ant species, seasonal hibernation is a common strategy to shelter over winter periods (Heinze et al., 1996; Shiroto et al., 2011). There is even evidence that early hominins practised hibernation to survive the colder months (Bartsiokas & Arsuaga, 2020). Hibernation is also often associated with storage behaviours, as mammals typically increase their food stores as part of their overwintering strategy (Fietz & Dausmann, 2007) and ants have been observed to go into an overwintering/hibernation state (Heinze et al., 1996; Shiroto et al., 2011). However, we have not considered hibernation as a strategy for food-risk mitigation in this study, as these behaviours typically occur in response to low temperatures in which the ants are physically unable to move or survive, rather than due to a limitation of food resources.

1.6: Hypotheses

We propose that across ant species the temporal environmental predictability, as a proxy of food predictability, influences their choice of risk-mitigation strategy. We predict that all strategies will be more common under lower constancy, as a high level of constancy would mean an abundance of food that does not require risk-mitigation strategies to develop.

Within environments with high contingency, food storage behaviours will be more prevalent, while in environments with low contingency and thus complete unpredictability, nomadism and generalism will be more common. Food exchange behaviour is less often observed than our other focal strategies, and, even within humans, it is less clear whether we would expect the behaviour in predictable or unpredictable environments. Instead, we suggest that polydomy becomes more common under medium levels of contingency than at either high or low levels of contingency.

Table 1.2: Degrees of constancy and contingency for which we expect the highest prevalence of each strategy.

Strategy	Constancy	Contingency
Generalism	Low	Low
Nomadism	Low	Low
Polydomy/Exchange	Low	Medium
Storage	Low	High

We also expect some interactions between the evolution of certain strategies, specifically, we predict that storage and nomadic behaviours will preclude one another as found in previous studies from the lab (Ahmed & Robinson, Unpublished). This is likely to be because the cost of nomadism is likely to increase with higher transport costs. If an ant colony has a large food reserve, migrating will require more energy expenditure when relocating and involve the additional risks of loss of reserves.

2. Methodology

To test our hypotheses, we collected published data on the risk-mitigation strategies used by ant species to carry out an ancestral state reconstruction of changes in strategy use over evolutionary time within the Formicidae. Using the geographical data available in the papers, we also collected data on the environment in which the strategies were observed which we incorporated into a model to identify relationships between predictability and strategy used.

2.1: Literature Search

To identify papers containing suitable data, we conducted a search of the Web of Science (WoS) database, due to its comprehensive coverage of scientific journals (Cavacini, 2015; Norris & Oppenheim, 2007). The Scopus database was also considered; however, after an initial test with our first search term, the high redundancy between the results of the two databases made searching both an ineffective use of time. Our search protocol was adapted from a similar study by Ahmed & Robinson (Unpublished), as follows. An initial keyword list (Appendix A) was compiled by taking common keywords from papers on the first page of WoS results, sorted by relevance, when searching the terms “Ants + [Strategy]” for each of our strategies of interest. These were then combined with the keywords used in Ahmed & Robinson (Unpublished) for Storage and Nomadism behaviours. These keywords were used as the input terms to conduct WoS searches of the levels of title and abstract across all WoS databases. We limited the search to just these two levels in order to obtain a balance between maximising the discovery of papers and reducing the number of irrelevant papers that would need to be filtered through. All searches were carried out in the Google Chrome (version 96.0.4664.45) Incognito Browser. Incognito was chosen to limit the effects of search profiling and tracking cookies from biassing our search results (Pozsgai et al., 2021); however, we were logged into the WoS database as this enabled us to save lists of previous search results and therefore more quickly identify duplicate results across different search terms. A breakdown of our search and subsequent filtering process can be found in Figure 2.1.

The initial literature search proved to have a limited coverage of the breadth of ant genera with many papers focusing on a few well-researched species and a high degree of irrelevance in search results. We therefore took a second approach to our list of papers through a systematic search of the AntWiki (*AntWiki*, n.d.). AntWiki is a detailed online information repository of the ant family which acts as an aggregation of multiple databases and references to scientific literature, edited by experts within the field of myrmecology.

While the site itself is not formally peer reviewed, the editors are vetted experts and the website acts as a good starting point for quickly identifying relevant literature. We systematically inspected the page of each genus recorded on the website and noted down any reference cited regarding one of our four strategies. Where this information was not present on the genus page, we searched the type species page and the pages of any extant species within the genus that were linked directly from the genus page. Where there were no such links and the genus had under 10 extant species, we searched each species page separately. In total, we acquired 162 additional sources (Fig 2.1).

Finally, we also collected 42 papers on polydomy after combing through the sources referenced in the review of polydomy conducted by (Debout et al., 2007) and two papers from the dataset in Ahmed & Robinson (Unpublished) which filled in gaps for the genera for which we had no data gathered after completing the previously mentioned searches.

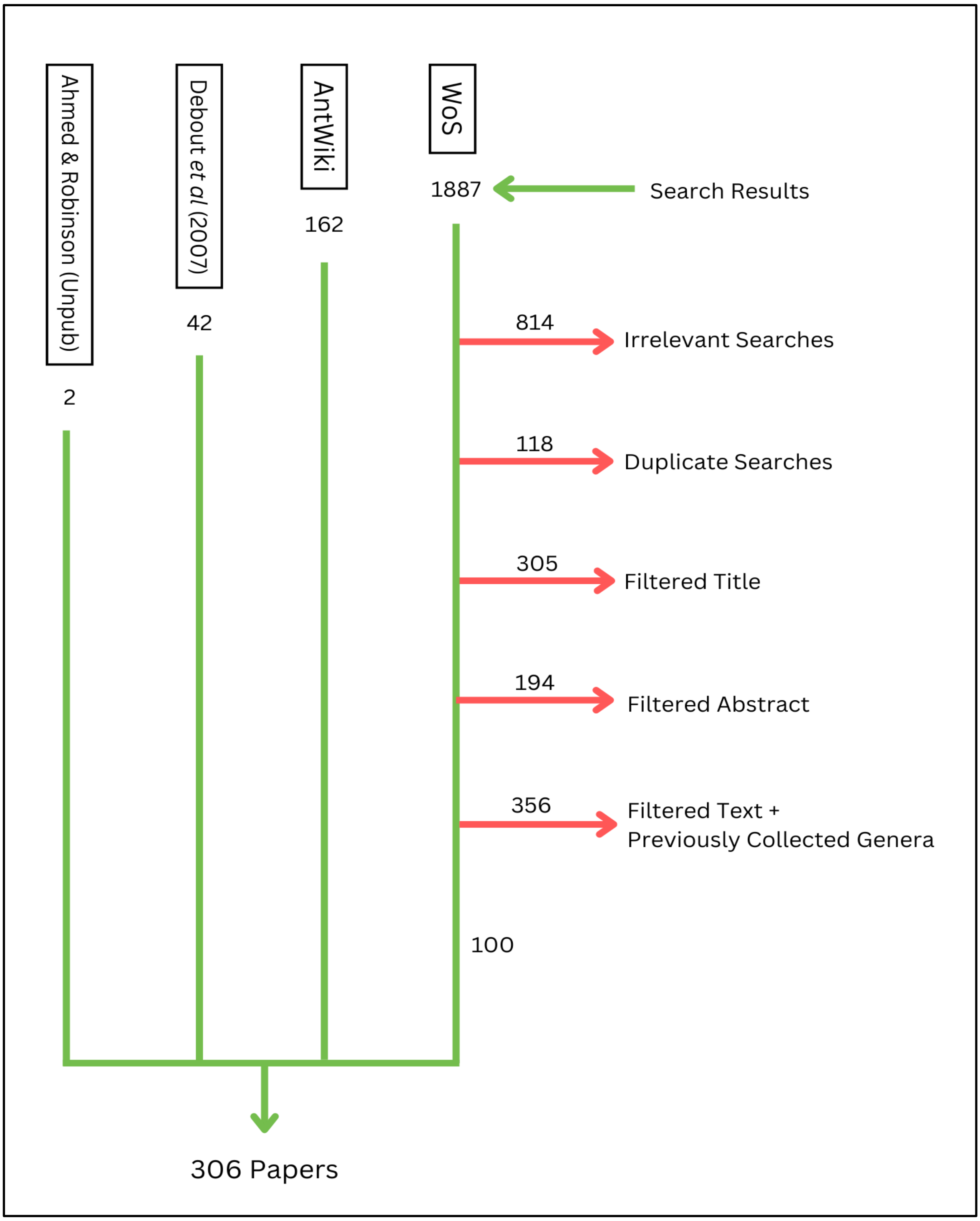


Figure 2.1: Breakdown of paper sources and search result filtering steps. After 20 consecutive irrelevant paper titles in the results of a WoS search query, the remaining results were discarded as "Irrelevant searches". Duplicate papers were discarded and then papers were filtered for relevance by title, abstract and text. After positive data for a species*strategy combination had been successfully collected once or a genus*strategy combination three times, additional papers were not reviewed.

2.2: Data Extraction

For each paper, a datapoint was recorded for each species+strategy+location combination referenced in each paper, or where only genus was identified, genus+strategy+location. For each datapoint as much of the following data were collected as possible (key information in bold):

Taxonomic data: genus and species names were recorded directly from the publications. The subfamily was found through AntWiki (*AntWiki*, 2022), and **updated genus and species names** were recorded where publications used outdated nomenclature. Where a common name exists for the species, this was also recorded.

Food resource data: any food resources used, and if available the proportion of the diet each made up; whether the food sources were a carbohydrate or protein source; or both.

Strategy data: which category of **risk-mitigation strategy** was associated with the food resource collected and any **specific details of the behaviour**. For a breakdown of which observations we considered to fall into each category, see Appendix B.

Habitat/environmental data: the **location of the sample site; geographical coordinates**; elevation above sea level; **human disturbance at location based on mention of disturbance or site located in urban or agricultural habitat (Y/N)**; whether the region had seasonal variation, and if so, in what season/environmental conditions samples were collected; the type of habitat; and the details of intra-specific competition (density of colonies/distance to nearest colony).

Additional information: the year, and where available the date or season of the study was also recorded; whether the species was invasive at the study site; whether the study was carried out in a lab or field setting; and whether the data were observational or experimental.

2.3: Estimating predictability

The diets of different ant genera can vary substantially, with food types including fungi, various forms of liquid sugars such as honeydew, nectar and plant secretions, many different life stages of dead and alive invertebrates, grains and excrement (Torres, 1984). Gathering complete data on availability of each food resource directly from the papers proved to be difficult, as the quality and availability of such data varied wildly and the process of finding such information for each of our genera would become a nearly impossible task. Weather conditions are closely linked to the abundance and predictability of these food resources (Alibegovic-Grbic et al., 2004; Ewald et al., 2015; Leahy et al., 2020; Pszczółkowska et al., 2019; Scott, 1970; Talley et al., 2002), particularly temperature and precipitation. We therefore used the predictability of these two weather measures to act as overarching proxies for food predictability.

For the location of each study site, geographical coordinates in decimal degree format were obtained. Where coordinates were not already provided, the location name was found on Google Maps and coordinates were extracted based on the location at the base of the pin drop marker. Coordinates were taken to two decimal places, which represented an accuracy of 1.11km. We did not go any more specific than that as neither the environmental parameters or the species occurrence records are likely to vary substantially at a finer scale. Additionally, for many of our sample papers the study sites rather than specific nest locations were stated. Any general location names which described a region larger than one decimal degree were excluded from our predictability analyses as these broad descriptions typically encompassed a wide range of climatic/environmental conditions.

Using the coordinates, daily weather data (e.g. average, minimum and maximum temperature; total precipitation; average humidity) between 1st January 2012 - 31st December 2021 were collected from the nearest weather station or combination of stations using the Visual Crossing database (visualcrossing.com). Average temperature and total precipitation were used to calculate Colwell's indices (Colwell, 1974) to provide separate measures of constancy and contingency for each. For this, we used the Colwells() function of the Hydrostats package (Bond, 2022). Ideally, at least 40 years of data would provide the most accurate representation of the long-term values of Colwell's indices, as short time frames of data generate higher index values. However, we were unable to obtain over ten years of data for all locations and in such cases it is then best to use as similar a time range as possible across each location so any effect of time frame is uniform across all sites (Weis & Schwartz, 1988).

2.4: Data Analysis

We carried out all our data analysis using R (v4.2.2) (R Core Team, 2022). We used the R package ggplot2 (v3.3.6) (Wickham, 2016) to generate visualisations of our data to observe any biases in our dataset (Figures 3.1-3.3).

2.4.1: Phylogenetic Comparative Methods

We modified the latest species-level ant phylogeny available in Nelsen et al. (2018) for use in all our analyses. This phylogeny comprised 1731 species representing all extant subfamilies. We did not have enough data to run analyses at a species level, so we trimmed the tree down to genus level. Based on the methodology of (Greer & Moreau, 2021), using the drop.tip function of the ape package (Paradis and Schliep, 2019) and with the aid of the R package MonoPhy (v1.3) (Schwery & O’Meara, 2016) we removed tips from the 13 paraphyletic genera, leaving each genus represented by one species tip. The resulting phylogeny contained 285 genera. We also dropped tips for genera which we did not have any strategy data at all, or those where only negative data was available (i.e. data representing the absence of a strategy, which for the purposes of the ancestral state reconstruction (ASR) analyses were equivalent to no data). This left us with a final total of 172 genera (Fig. 3.3). It should also be noted that we did not include genera that were primarily obligate parasites of other ant species as it was difficult to interpret whether they displayed our behaviours of interest or were just parasitising genera which did.

Our resulting phylogeny was then used to carry out our ASR using the Phytools (v1.0.3) (Revell, 2012) package, to estimate the ancestral state and the transition rates for both individual and polymorphic states (i.e. states where a genus makes use of more than one risk-mitigation strategy) using stochastic character mapping with a maximum likelihood approach. Our methodology is adapted from similar published analyses (Nelsen et al., 2018).

To carry out our ASR we first generated a discrete character evolutionary model which accounted for the occurrence of polymorphic states using the fitpolyMk() function. The use of a model which accounted for polymorphic states was necessary as, both at a genus and species level, it was a common occurrence that a single tip would make use of more than one of our strategies of interest. We produced models using a combination of common transition models and priors to determine the best fitting model for use with our data (Table 2.1). The transient model assumes that the rate of transition to any given state is different to the rate of transition from any given state. Conversely, the EQ model assumes that all transition rates to and from any state are equal. The SYM model assumes that each state has a different transition rate but this rate is equal for both transition to and from said state. Finally, the ARD model assumes that every transition rate is different for every state and the rate of transition to each state is different to the rate of transition away from the state. The equal prior (pi) assumes an equal probability distribution of all states prior to running the model, meanwhile, the estimated prior finds the stationary distribution of state frequencies and sets this ratio as the prior. Finally the fitzjohn prior sets the distribution as per Fitzjohn et al. (2009). Although the ARD model with a fitzjohn prior had the most positive log-likelihood value, which can be used to determine the best fitting model, comparison of Akaike information criterion (AIC) values is generally a better approach as it takes into account both the log-likelihood and degrees of freedom within the model. When considering this metric, the transient-fitzjohn combination had the lowest AIC and AICc (AIC values corrected for small sample sizes) values and highest weighted AIC. We therefore took this model and used it for the remainder of our analysis:

```
fit.unordered ← fitpolyMk(tree, v, ordered = FALSE, max.states = NA, pi = "fitzjohn", model = "transient")
```

We used stochastic character mapping over 500 simulations with the functions make.simmap() which use joint reconstruction methods to give us the likelihoods of ancestral state at each node of our tree. The summarised results of these simulations are found in Figures 3.5.

```
simtrees ← make.simmap(tree, fit.unordered$data, model = fit.unordered$index.matrix, nsim=500)
```

The describe.simmap() function provided us with average posterior probabilities of all of our nodes, the average number of transitions between each state and the average total number of changes between states. To simplify our analyses, we also subdivided the many polymorphic state combinations (e.g. Nomadism + Generalism, Polydomy+Generalism+Nomadism, etc.) into two categories dependent on the presence or absence of a given strategy in each polymorphic combination. This allowed us to analyse each of our four risk-mitigation strategies both in the context of the other strategies and their co-evolution, as well as independently.

Table 2.1: Comparison of PolyMk Model log likelihood, AIC, AICc and weighted AIC values

Transition Model	pi	logLik	df	AIC	AICc	AICw
transient	fitzjohn	-378.57	2	761.1401	761.217	0.721976
transient	estimated	-380.2253	2	764.4506	764.5275	0.1379278
transient	equal	-380.2942	2	764.5884	764.6653	0.1287427
ER	fitzjohn	-384.1145	1	770.2289	770.2544	0.0076719
ER	estimated	-385.869	1	773.738	773.7635	0.001327118
ER	equal	-385.869	1	773.738	773.7635	0.001327118
SYM	fitzjohn	-358.7446	28	773.4893	786.83	0.000983298
SYM	estimated	-361.2835	28	778.5669	794.4248	2.2055E-05
SYM	equal	-361.2835	28	778.5669	794.4248	2.2055E-05
ARD	equal	-344.9499	56	801.8997	864.6197	9.52936E-10
ARD	fitzjohn	-342.8659	56	797.7319	866.3268	4.0585E-10
ARD	estimated	-344.4058	56	800.8115	868.4815	1.38195E-10

2.4.2: Environmental Predictability Analysis

In order to test the relationship between strategies and environmental predictability while accounting for phylogeny we used a phylogenetic general linear mixed model (PGLMM). When testing the relationship between environmental predictability and risk-mitigation strategies we needed to also account for phylogenetic relatedness of our genera. We therefore used the brms package (Bürkner, 2021) to carry out a categorical Bayesian logistic regression. The brms package is a powerful tool that makes use of the Stan probabilistic programming language to fit Bayesian generalised linear and non-linear multivariate, multilevel models. Importantly, it accepts models which have both a categorical dependent variable and phylogenetic relatedness as a random effect, which other packages lack the flexibility to do.

We ran the model as follows:

Strategy ~ C.Temp + M.Temp + C.Prec + M.Prec + (1 | gr(Genus, cov = antphy)) + (1 | Genus) + (1 | Location)

Here we have taken constancy (C) and contingency (M) of temperature and precipitation as fixed effects on the presence of strategy as a categorical variable. We have also considered phylogenetic relatedness of samples as a random effect, as well as genus without the relatedness aspect and sample location. Our model took in data from 206 different locations for 153 different genera.

Additionally, we used the function *plot_model(type = "pred")* to generate marginal effects predicting the probabilities of strategies occurring at each degree of temperature and precipitation contingency and contingency. Probabilities were generated from sampled posterior probability distributions.

3. Results

3.1: Data Distribution

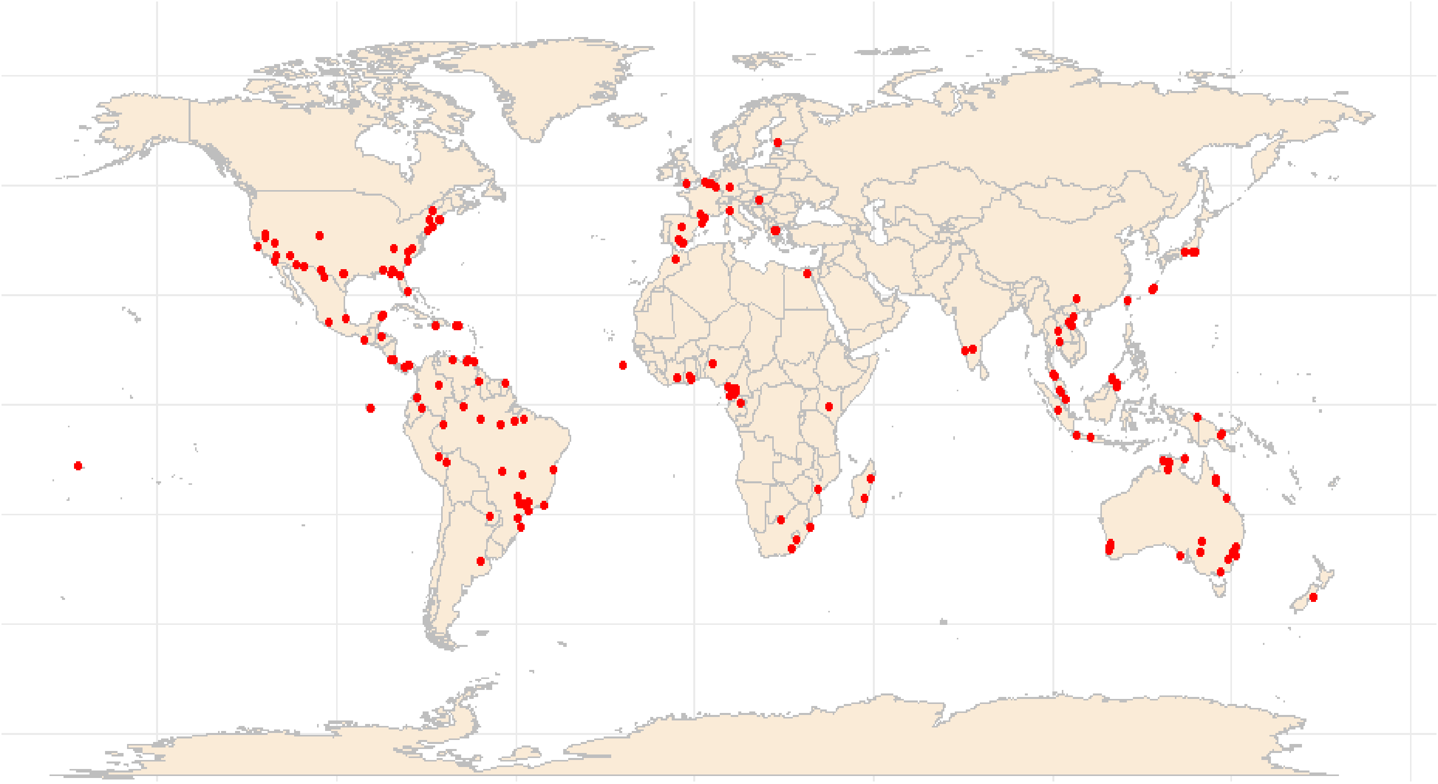


***Figure 3.1: The geographical distribution of positive* data samples (red dots) based on coordinates or country information provided in papers.**

The locations at which our data were taken from are well spread latitudinally between +50 degrees and - 50 degrees. There is good coverage across North and South America, Southeast Asia and Europe, however Central and Northeast Asia, as well as Northeast Africa are particularly lacking in data.

To assess how representative our dataset is of the breadth of ant genera, we compared the representation of the subfamilies in our dataset (by proportion of our sampled genera that are in each subfamily) with the actual proportion of ant genera that belong to that subfamily. We found a statistically significant association between the two groups (Fisher's exact test, two-sided $p < 0.0001$). Most genera were sampled from the Myrmicinae (41.7%), Formicinae (18.2%) and Ponerinae (14.6%). The most underrepresented subfamilies are the Leptanilla and Dolichoderinae. We were able to collect data on at least one genus for all subfamilies. See Figure 3.2 and Table 3.1 for a full breakdown of subfamily representation.

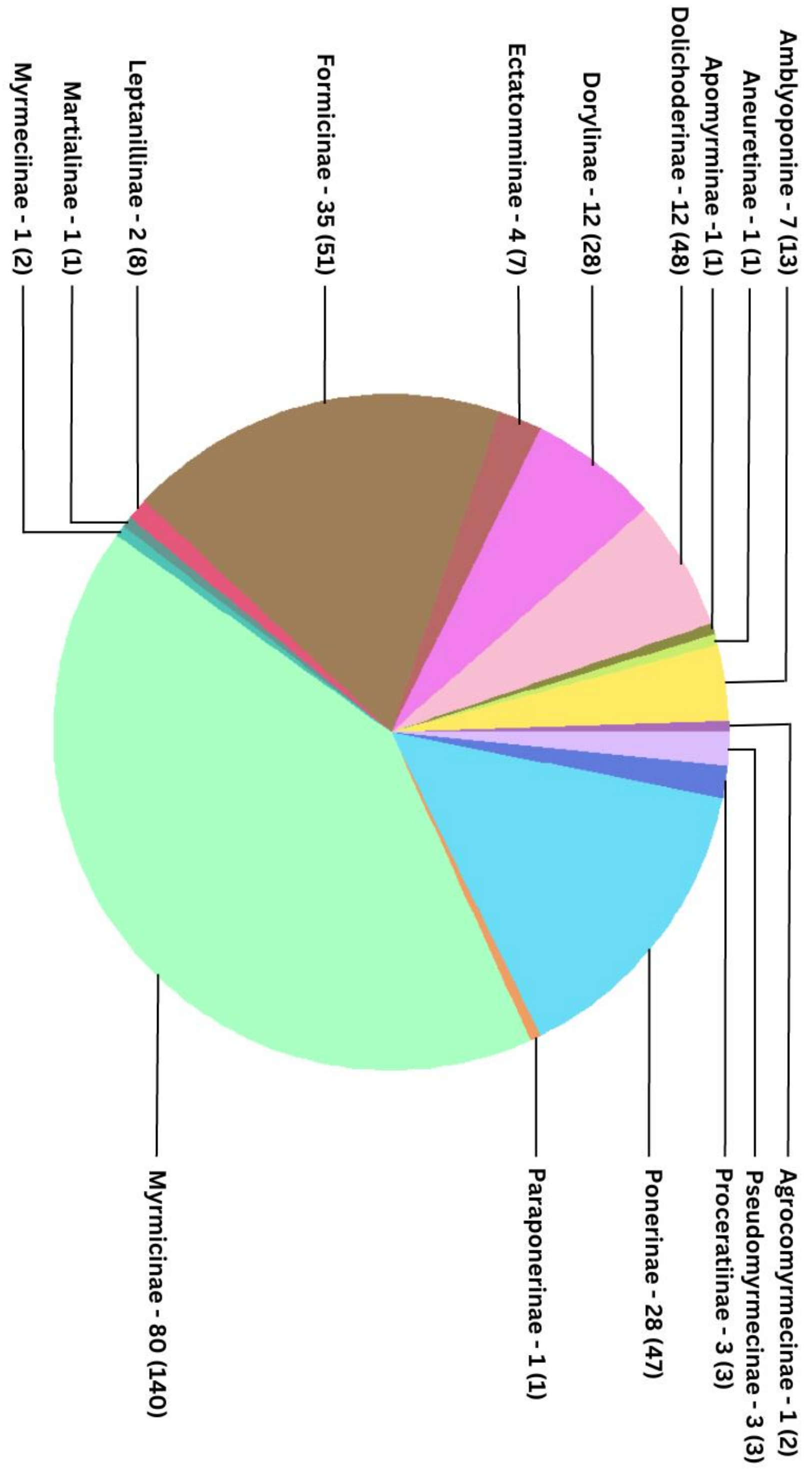


Figure 3.2: The distribution of sampled genera by subfamily. Labels follow the following structure: Subfamily name, number indicate the number of genera with available information on one or more strategies. Numbers in brackets indicate the total number of known extant genera.

Table 3.1: Breakdown of actual percentage proportion, sampled percentage proportion and the relative representation (RR) of each subfamily within the Formicidae. RR > 1 = over-representation, RR < 1 = under=representation.

Subfamilies	Actual Proportion (%)	Sampled Proportion (%)	Relative Representation
Agroecomyrmecinae	0.58	0.52	0.90
Amblyoponinae	3.76	3.65	0.97
Aneuretinae	0.29	0.52	1.80
Apomyrminae	0.29	0.52	1.80
Dolichoderinae	13.87	6.25	0.45
Dorylinae	5.20	6.25	1.20
Ectatomminae	2.02	2.08	1.03
Formicinae	14.74	18.23	1.24
Leptanillinae	2.31	1.04	0.45
Martialinae	0.29	0.52	1.80
Myrmeciinae	0.58	0.52	0.90
Myrmicinae	40.46	41.67	1.03
Paraponerinae	0.29	0.52	1.80
Ponerinae	13.58	14.58	1.07
Proceratiinae	0.87	1.56	1.80
Pseudomyrmecinae	0.87	1.56	1.80

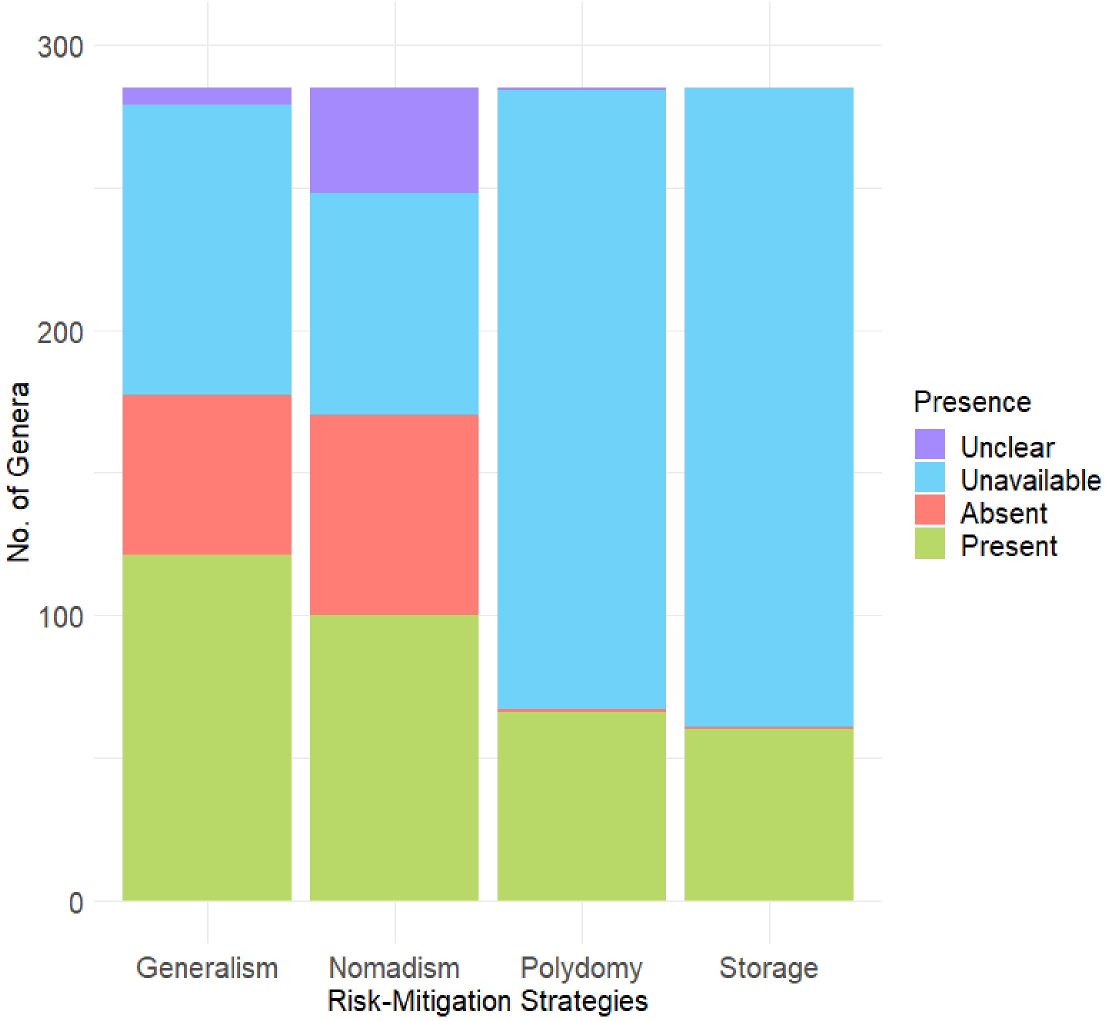


Figure 3.3: Summary of data availability for each risk-mitigation strategy (Generalism, Nomadism, Polydomy, Storage). Present (data indicating the strategy is used); Absent (data indicating the strategy is not used) Unclear (literature information was ambiguous/contradictory); Unavailable (no data on that strategy for the genus) (n=285).

The greatest amount of data (i.e. data where strategy was recorded to be present) was for generalism (n=121) compared to nomadism (n=100), polydomy (n=66) and storage (n=60). For nomadism and generalism, data were also available from which we could infer the absence of the strategy. This form of ‘absence’ data was not available for storage or polydomy, except for a single genus in each case. Our nomadism data also included 37 genera for which data were unclear. In these cases, either the data were contradictory between samples, or it was difficult for us to determine presence or absence of the strategy based on the information available, for example if a species nested under a log, it was unclear the degree of modification that occurred and thus the likelihood of the species being nomadic or not.

3.2: Ancestral State Reconstruction

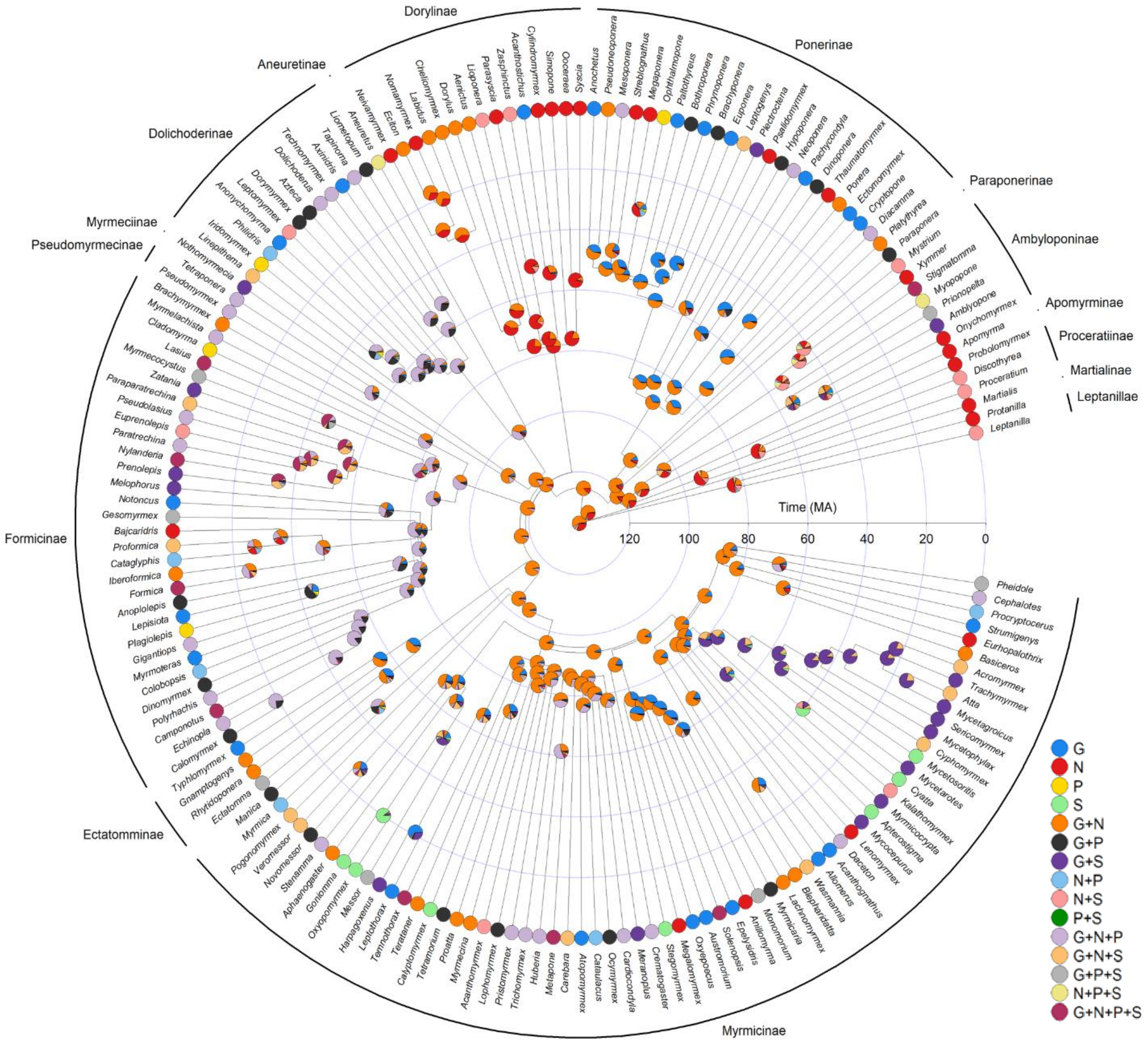


Figure 3.4: Ancestral and current states of risk-mitigation strategies in the Formicidae. Each tip indicates the current strategy or strategies used by each extant genus. The interior nodes display probability pie charts indicating the likelihood of each of the combinations of strategies at that node - the largest segment is the most likely combination. The outer ring labels indicate subfamily. G = Generalism, N = Nomadism, P = Polydomy, S = Storage. Nsim = 500.

Our ancestral state reconstruction found 324.2 changes between states on average over 500 simulations (Fig.3.4). We found that a combination of generalism and nomadism was the most likely ancestral origin (60.8% likelihood). This combination was also the most common state, making up 23.4% of the total time spent in each state, followed up by a combination of generalism, nomadism and polydomy (14.5%). Generalism was common in combination with all other states (7.07% with polydomy and 6.36% with storage). Generalism was the third most common, as well as the most common individual state at 13.7% of the total time. Nomadism followed this at 11.8%. Polydomy and storage as individual states were much less common at 1.18% and 2.17%, respectively. A polymorphic state of polydomy and storage was the least common state (0.242%), a full order of magnitude less common than any other individual or polymorphic state.

We found that over 500 simulations there were an average of 50.48 transitions away from generalism and 22.04 transitions towards generalism (Fig 3.5a). Generalism was present (individually or polymorphically) 76.8% of the time. Generalism is almost ubiquitous across the phylogeny, except in a few instances. There are two main transitions away from generalism in the Dorylinae around 80MA, at the same time period as Leptanillae, and just before the Ambyloponinae at 60MA. After the initial loss in the Dorylinae it appears that it is regained before the branch off from *Cheliomyrmex*. The earliest transition away from generalism is around 95MA in the Proceratiinae. There are at least three more recent transitions between 20-40MA in the Attine Myrmicinae, Formicinae and Ponerinae.

We found there was an average of 60.36 transitions away from nomadism and 30.92 transitions towards nomadism (Fig 3.5b). Nomadism was present (individually or polymorphically) 66.3% of the time. At around 55-60MA there is at least one major transition in the Ponerinae away from nomadism. Within the Formicidae there appear to be two main transitions away from nomadism around 70MA and 50MA. Finally, in the Myrmicinae we can see at least three transitions away, in the Attines at around 80MA, Crematogastrini around 70MA and a third in the Stenammini around 50MA.

Polydomy had the greatest number of transitions in the state of any risk-mitigation strategy. We found there was an average of 32.17 transitions away from polydomy and 53.39 transitions towards polydomy (Fig 3.5c). Polydomy was present (individually or polymorphically) 32.8% of the time. The primary transition to polydomy occurs in the Formicidae around 90MA, while in the Dolichoderinae it occurs at around 50MA. The Ambyloponinae also transition to polydomy at 55MA. Within the Myrmiciane, *Manica* and *Myrmica* lineages transitioned to polydomy at around 45MA while *Cephalotes* and *Procryptocerus* lineages transitioned around 70MA.

We found there was an average of 22.6 transitions away from storage and 52.5 transitions towards storage (Fig 3.5d). Storage was present (individually or polymorphically)

25.4% of the time. There is a major transition to storage among the fungus-cultivating Myrmicinae around 80MA. There is also a major transition towards storage around 55MA in the Ambyloponinae, which coincides with storage becoming a more likely behaviour in other areas of the tree such as repleteism in Formicidae and granivorous Myrmicinae.

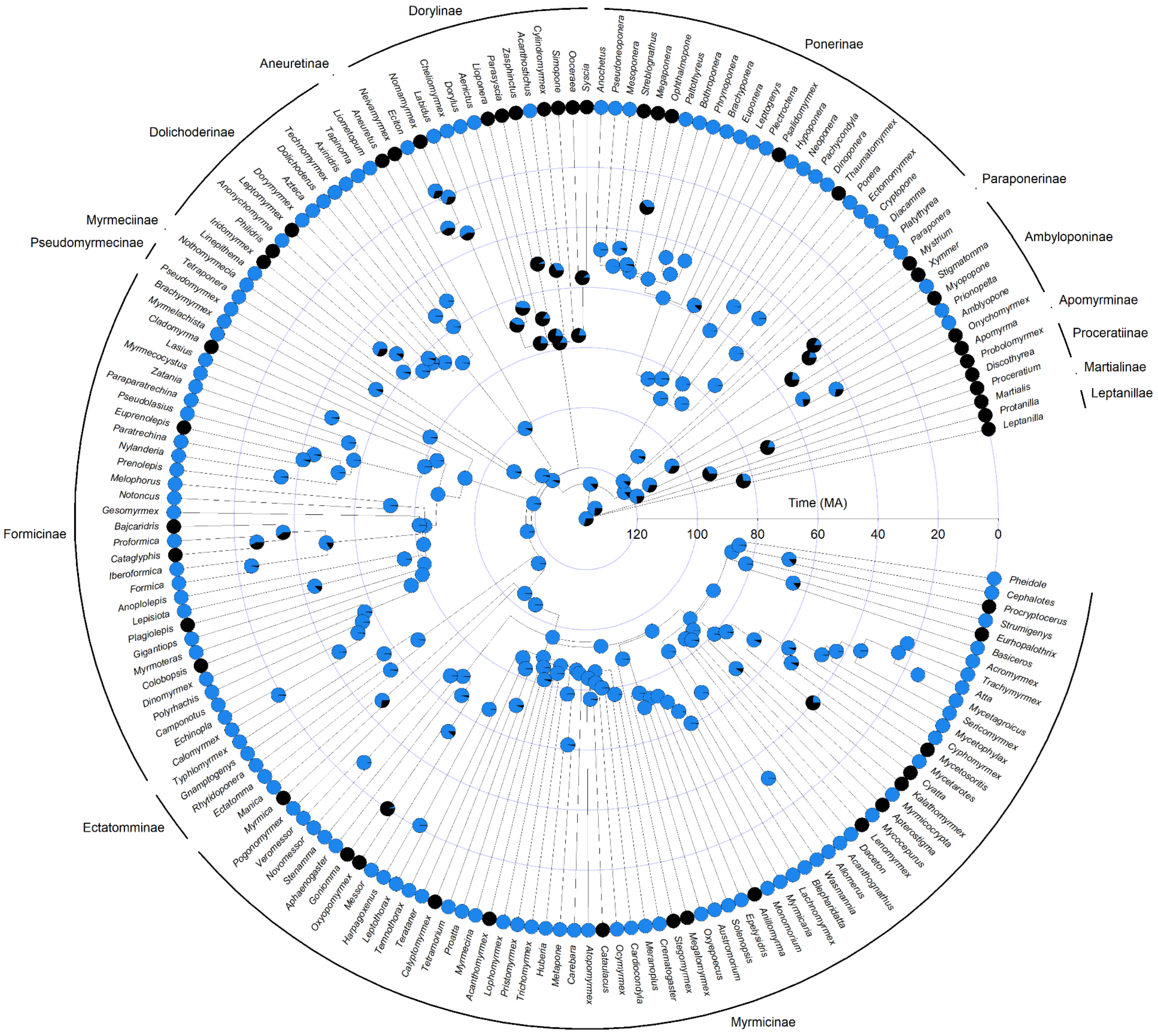


Figure 3.5a: Ancestral probability of generalism in the Formicidae (as an individual state or as part of a polymorphic state) at each node and the presence or absence of the trait for each extant genus at each tip. Presence (blue) or absence (black). The outer ring indicates subfamily. Nsim = 500.

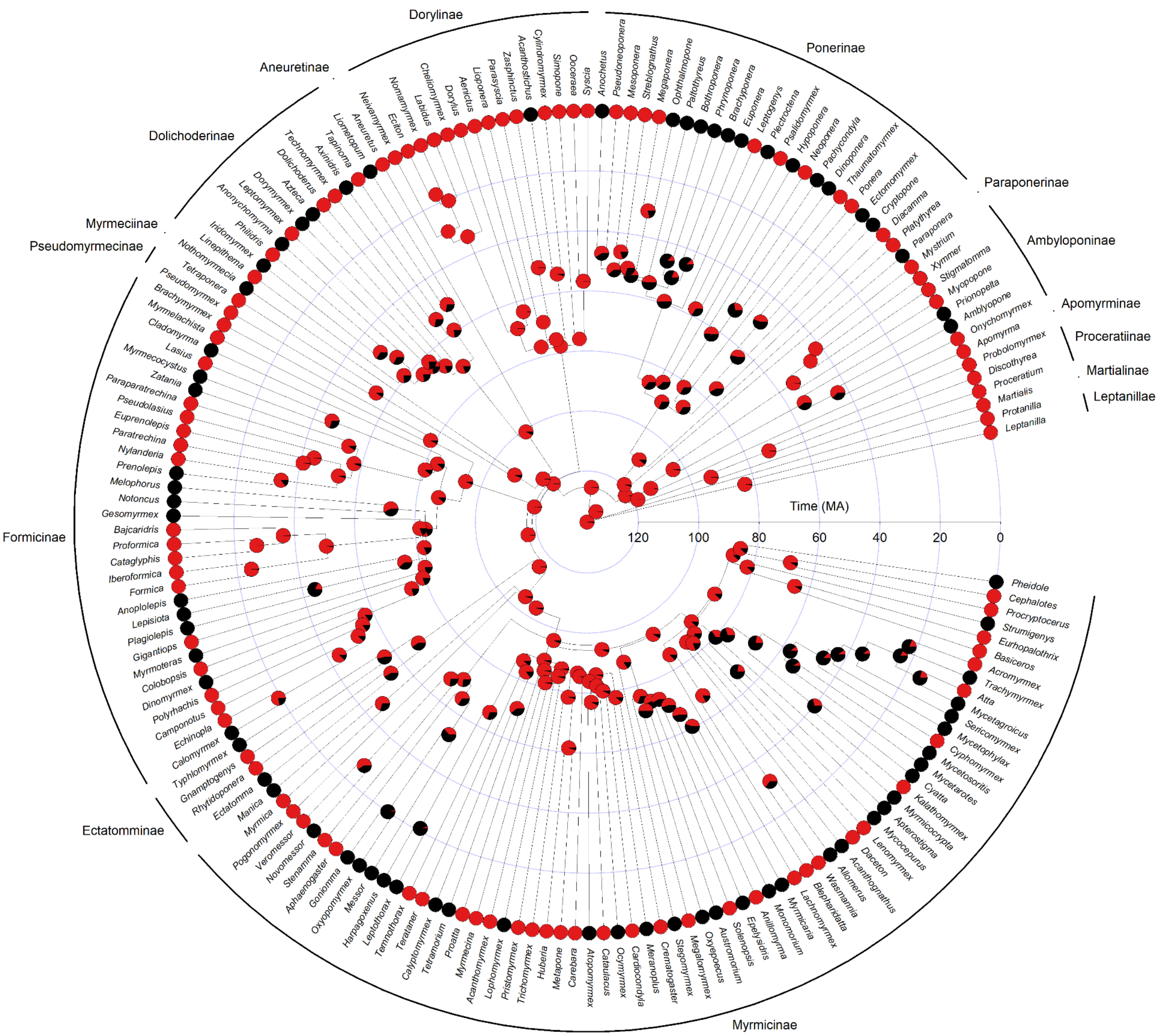


Figure 3.5b: Ancestral probability of nomadism in the Formicidae (as an individual state or as part of a polymorphic state) at each node and the presence or absence of the trait for each extant genus at each tip. Presence (red) or absence (black). The outer ring indicates subfamily. Nsim = 500.

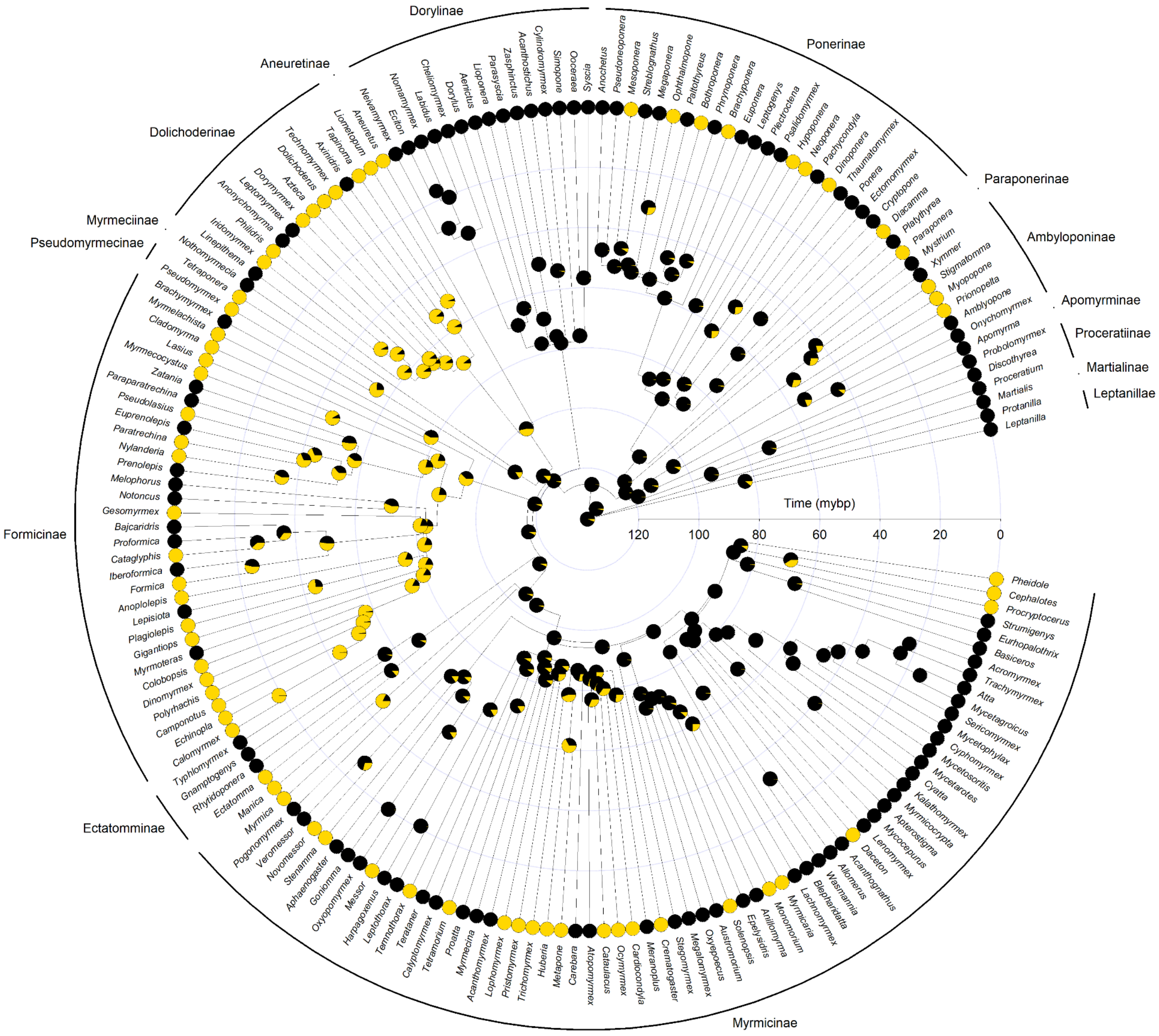


Figure 3.5c: Ancestral probability of polydomy in the Formicidae (as an individual state or as part of a polymorphic state) at each node and the presence or absence of the trait for each extant genus at each tip. Presence (yellow) or absence (black). The outer ring indicates subfamily. Nsim = 500.

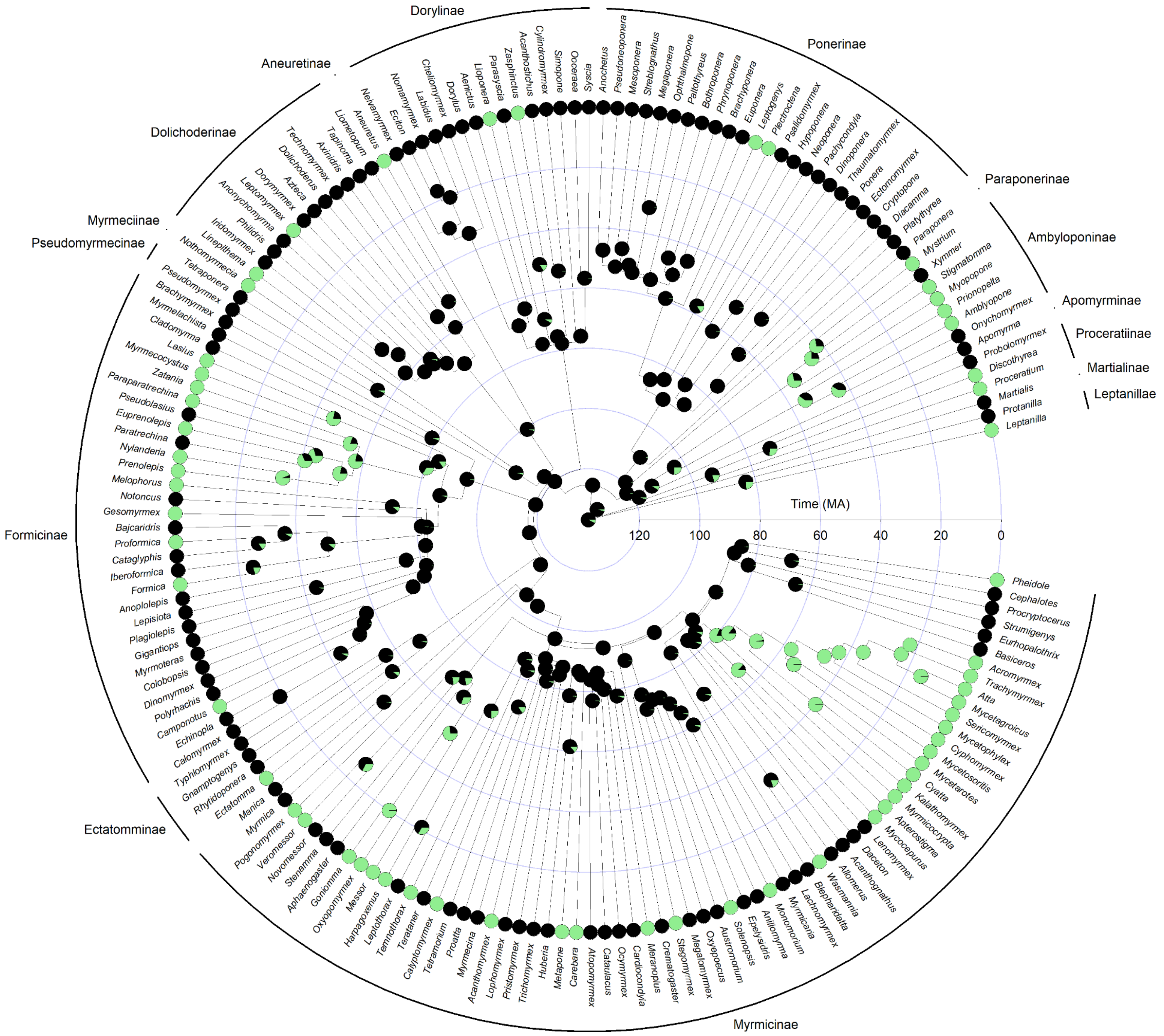


Figure 3.5d: Ancestral probability of storage in the Formicidae (as an individual state or as part of a polymorphic state) at each node and the presence or absence of the trait for each extant genus at each tip. Presence (green) or absence (black). The outer ring indicates subfamily. Nsim = 500.

3.3: Environmental Predictability

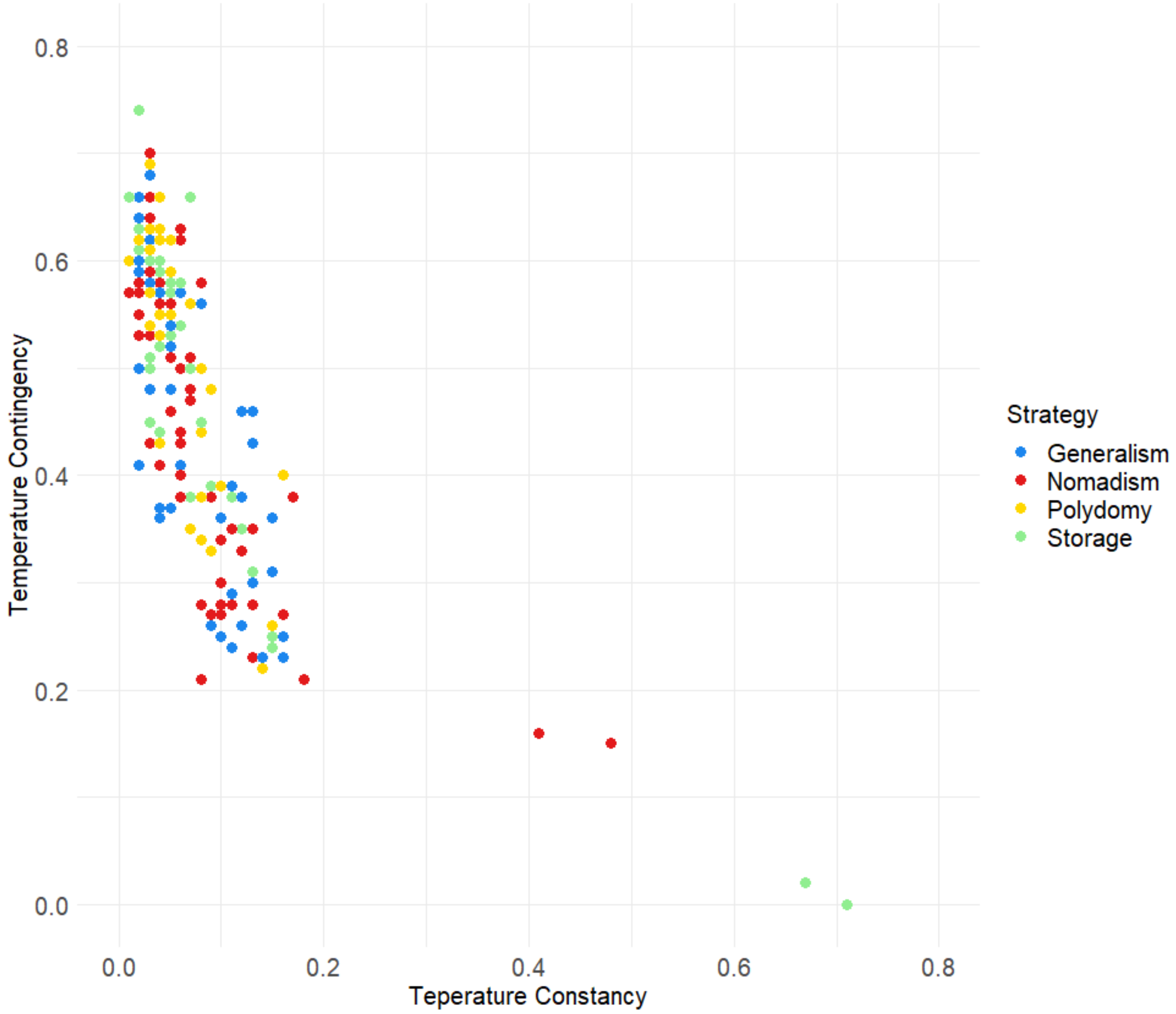


Figure 3.6b: Values of temperature predictability at each location data point and the associated strategy. Constancy is displayed on the x-axis and contingency is displayed on the y-axis. Colours indicate strategy.

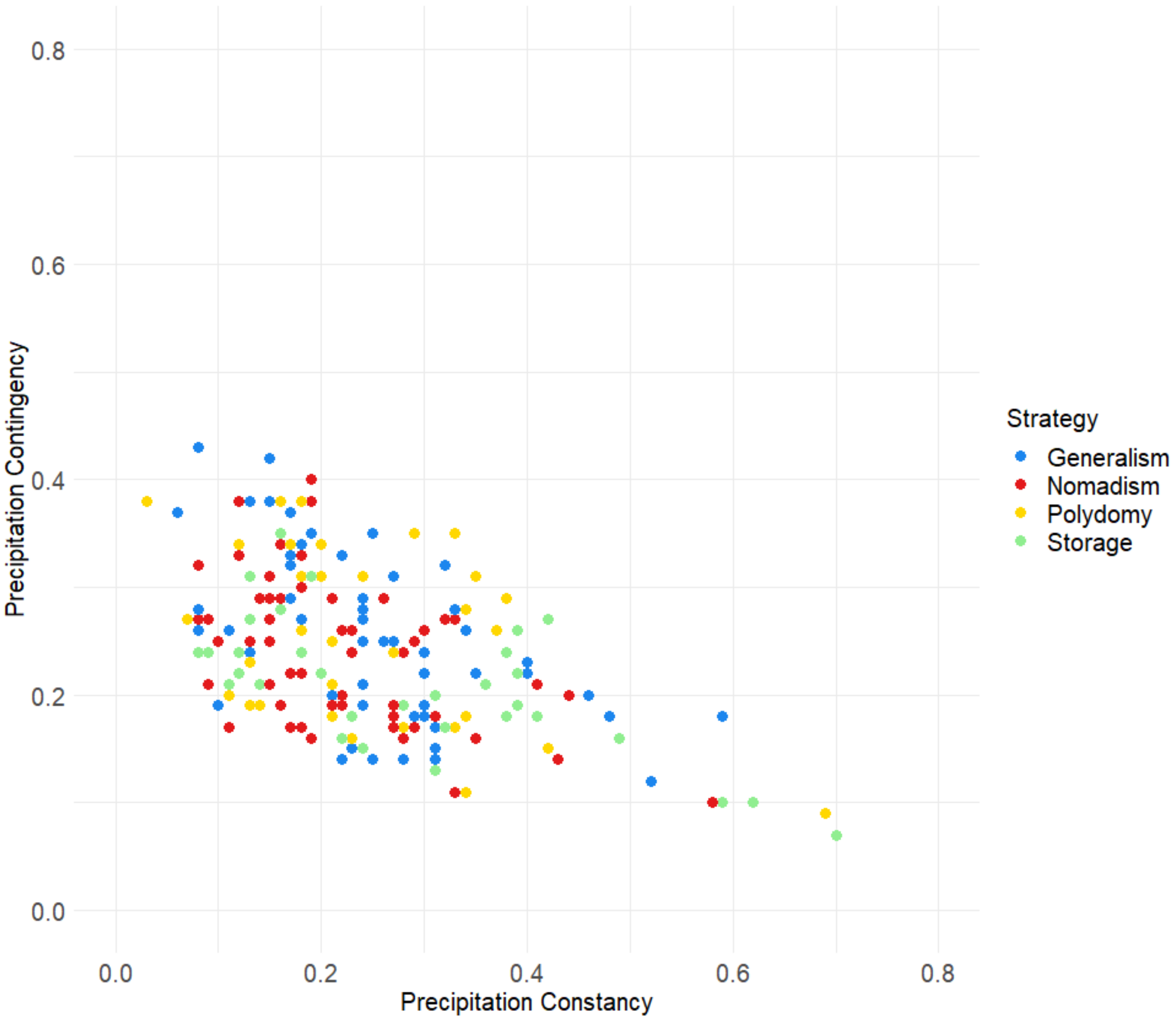


Figure 3.6b: Values of precipitation predictability at each location data point and the associated strategy. Constancy is displayed on the x-axis and contingency is displayed on the y-axis. Colours indicate strategy.

We can see that for temperature most instances of all four strategies occur at a low constancy between a narrow range of 0.0 - 0.2 (Fig 3.6a), with nomadism and storage having two instances of higher constancy each. All four strategies occur at a wider range of temperature contingency, between 0.2 - 0.7. Conversely, all four strategies occur at a narrower band of contingency (0.1 - 0.45) and a wider band of constancy (0.0 - 0.7) for precipitation. From these figures there is no clear indication that any strategies appear to be favoured at any particular degrees of constancy or contingency.

Categorical Bayesian logistic regression was used in our model to analyse the relationships between each of the following: temperature constancy, temperature contingency, precipitation constancy, precipitation contingency, with regards to the risk-mitigation strategy. Generalism was taken as the reference strategy our remaining strategies were compared to. Error was represented by an 89% HDI (Highest Density Interval) calculated from the posterior distribution, as is the standard for Bayesian regression (Kruschke, 2014).

For Bayesian statistics, a probability of direction (pd) can be equated to the p-value, with a >97% probability equating $p<0.05$. The ROPE percentage is an index of significance, allowing us to determine whether a change is non-negligible. ROPE<1% is significant and allows us to reject the null hypothesis.

It was found that temperature constancy has a probability of 99.33% of having a positive effect on nomadism, relative to the effect on generalism (Median = 5.85, 89% CI[1.94, 9.75]) and this can be considered as significant effect [0.00% in ROPE]. Precipitation constancy has a probability of 99.42% of having a negative effect on nomadism, relative to generalism (Median = -7.83, 89% CI[-13.58, -2.43] and the effect can be considered as significant [0.00% in ROPE]. Finally, precipitation contingency has a probability of 97.70% of having a negative effect on nomadism, with respect to generalism (Median = -5.97, 89% CI[-10.90, -1.15] and the effect can be considered significant [0.00% in ROPE]. Therefore, nomadism is significantly more likely to occur at higher temperature constancy and lower precipitation constancy and contingency than generalism. For all other variables there is no significant effect of environmental variability on strategy usage.

Additionally, the estimated probability of each strategy at different degrees of constancy and contingency were calculated (Fig 3.7a - d) for both temperature and precipitation. In Figure 3.7a we see that generalism becomes less common as temperature constancy increases. There may also be a slight increase in nomadism. In Figure 3.7c we can see that there is a decline in nomadism as precipitation constancy increases. Finally, in Figure 3.7d we see that generalism becomes more likely as precipitation contingency increases, while nomadism becomes less likely. For all other strategies there was no trend found between strategy and contingency/constancy.

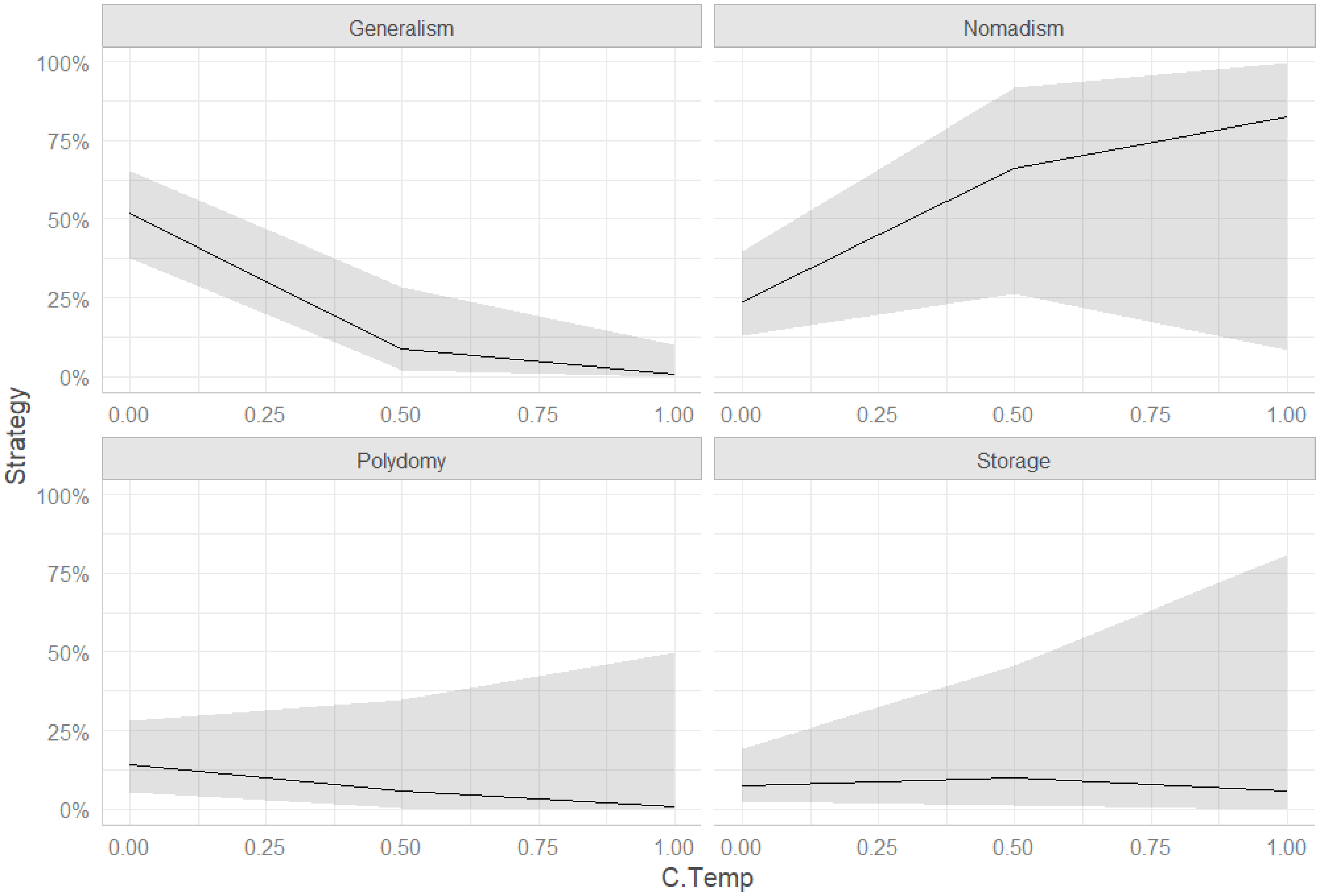


Figure 3.7a: Probability of each strategy occurring at different degrees of temperature constancy (C. Temp). Error bars represent the 89% Credible Intervals.

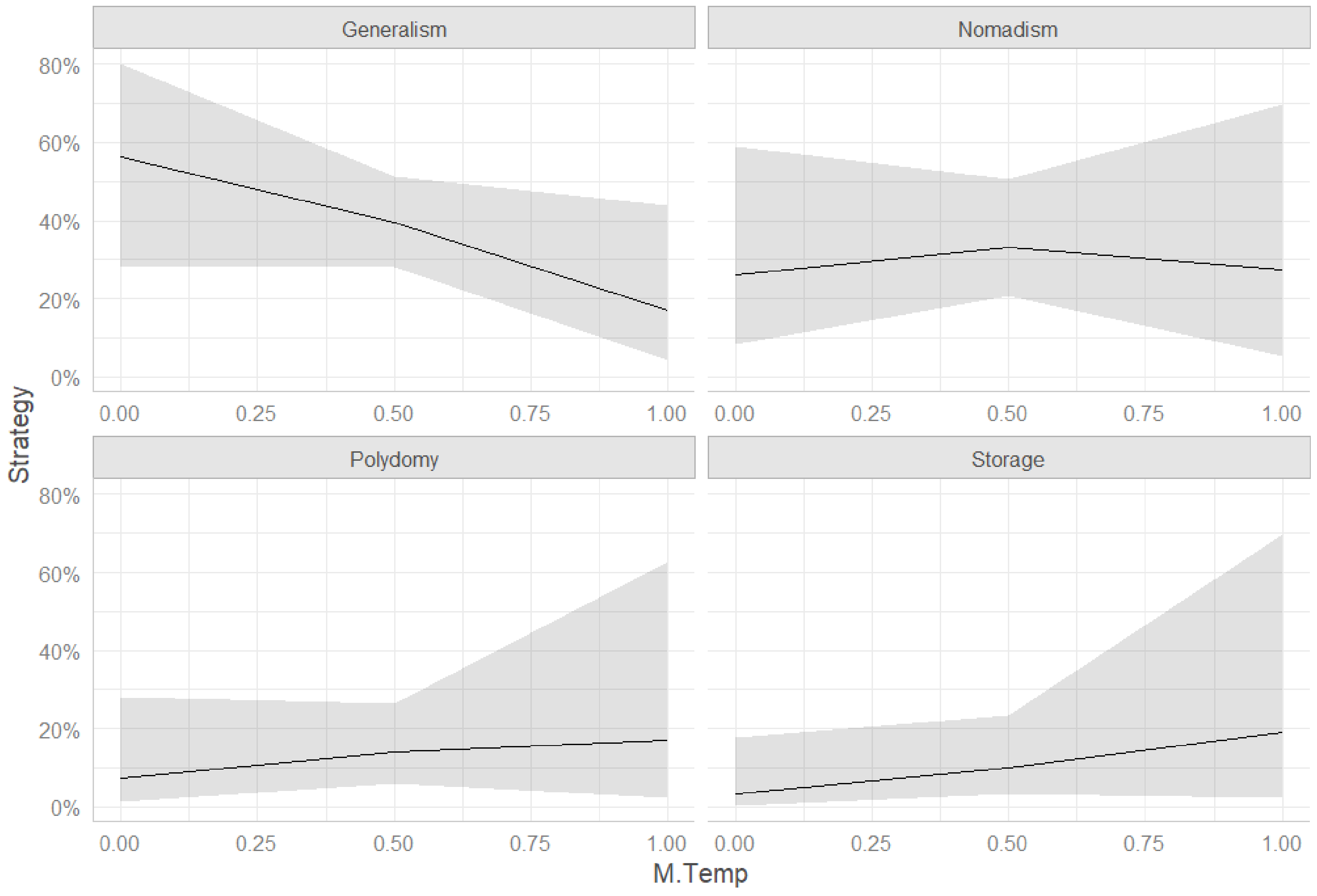


Figure 3.7b: Probability of each strategy occurring at different degrees of temperature contingency (M, Temp). Error bars represent the 89% Credible Intervals.

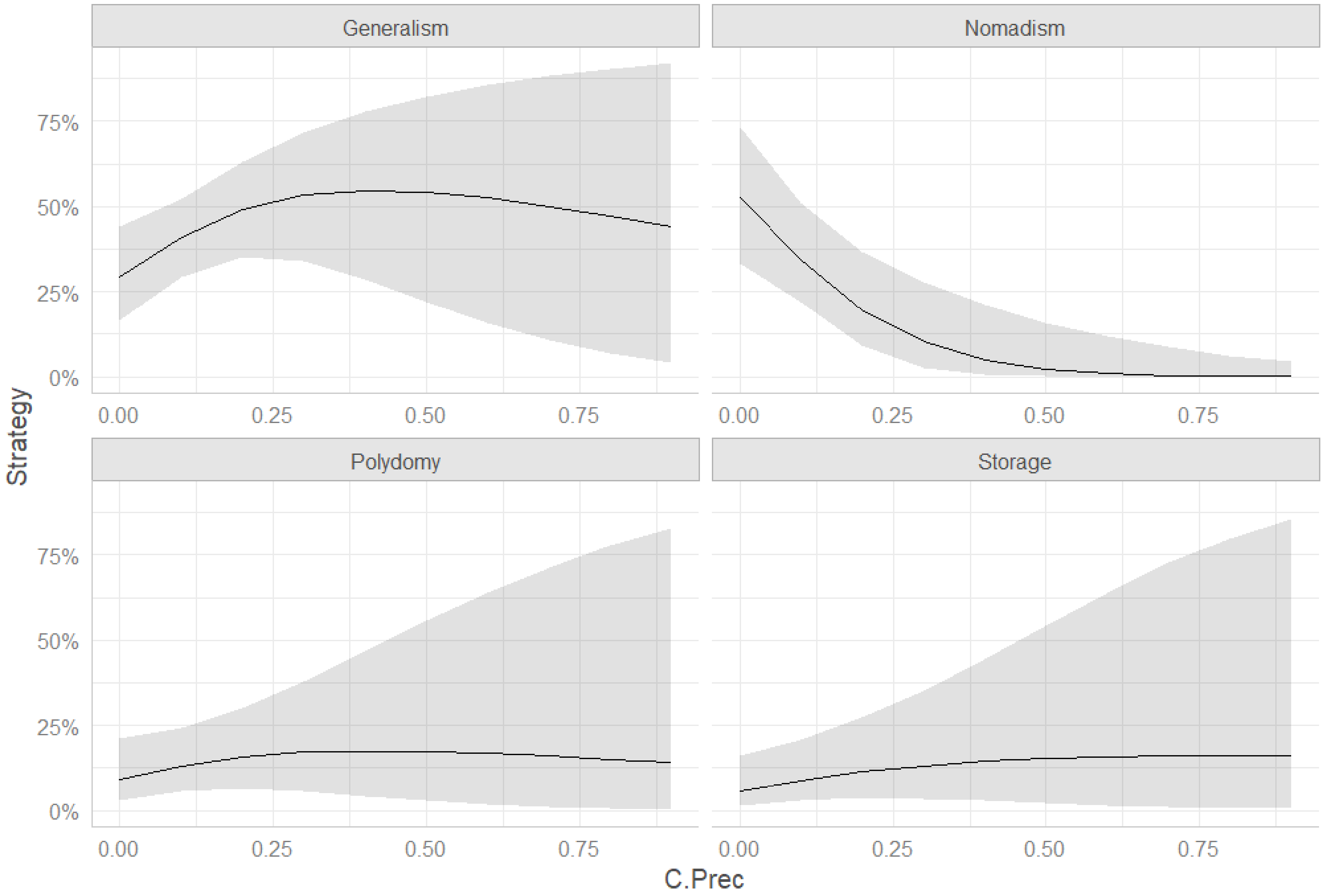


Figure 3.7c: Probability of each strategy occurring at different degrees of precipitation constancy (C. Prec). Error bars represent the 89% Credible Intervals.

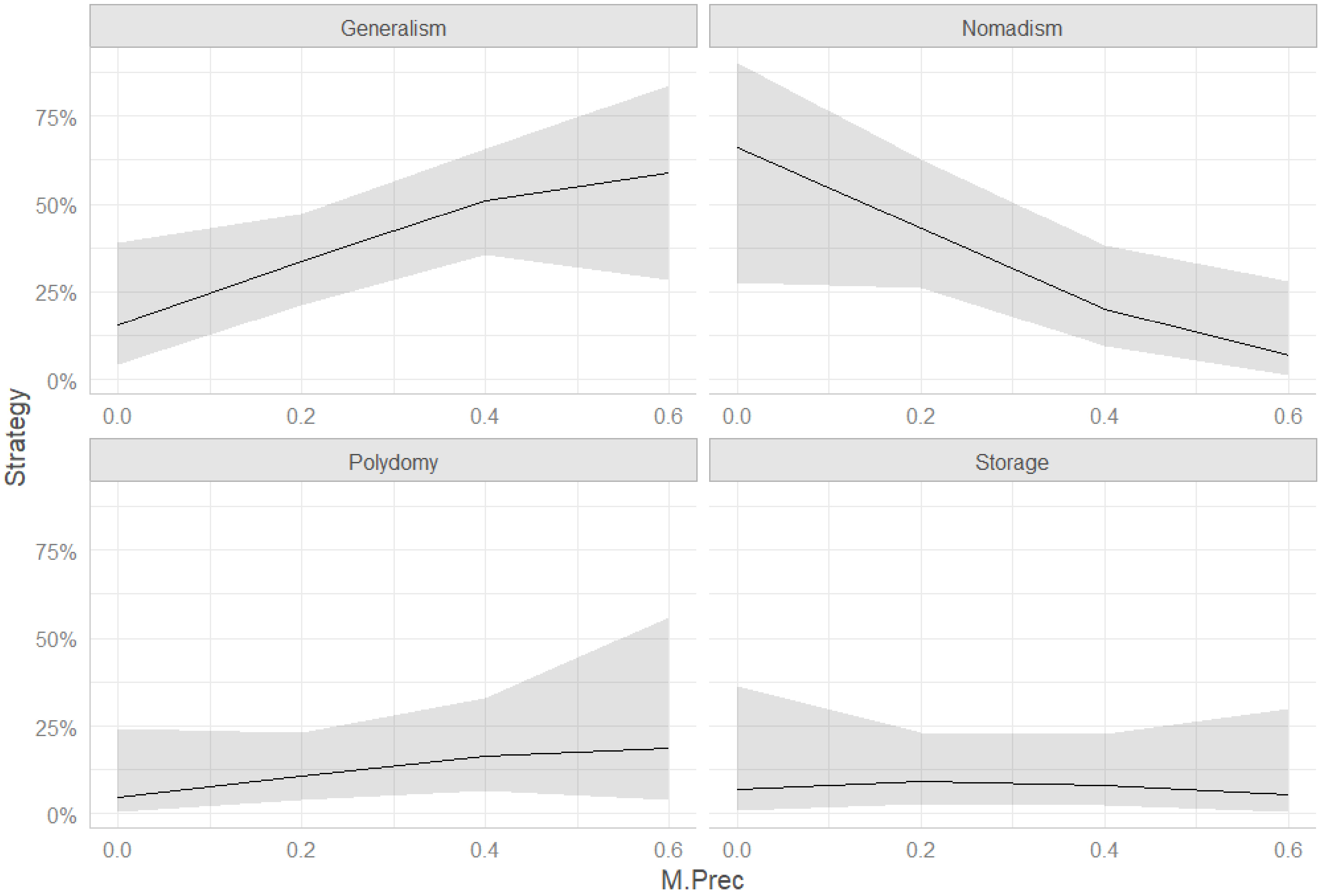


Figure 3.7d: Probability of each strategy occurring at different degrees of precipitation contingency (M. Prec). Error bars represent the 89% Credible Intervals.

4. Discussion

4.1: Ancestral State Reconstruction

Our ancestral state reconstruction provides us with an idea of the overall trends in the loss and gain of each of our strategies over time. We can see that a combination of generalism and nomadism is the most likely ancestral state for the Formicidae. Regarding generalism, this is unsurprising as we found that generalism remains extremely widespread throughout the ant family, which itself aligns with general consensus in the field that most species are generalist predators (Carroll & Janzen, 1973; Hölldobler et al., 1990; Levings, 1983). Even within species that had preferences for one or few food types, such as the flexibly specialist predator *Stigmatomma silvestrii*, which has a 90% centipede diet in the wild, will readily eat alternatives when their preferred diet is unavailable in a lab setting (Masuko, 1993). We also find generalist diets in the wider Hymenopteran order, including the early branching spheciform wasps which are most closely related to the ant taxa (Ward, 2014). The mud daubers for example, exhibit a flexible generalist diet similar to many ant species, which may specialise at an individual (or as a colony/population level in ants) but have the capacity to feed on a breadth of prey types (E. C. Powell & Taylor, 2017). Even in less immediately related wasps we see broad generalist diets (consumption of both multiple carbohydrate sources and protein sources) (Harris, 1991).

Nomadism was also an ancestral state, and like generalism, was found to be widespread across the ant family. It is important to acknowledge that here we use the term nomadism to mean a readiness to relocate, which is inclusive of a broader range of species than just the extreme nomads of the army ant species which would typically be described as nomadic. Our measure of nomadic potential was not only based on direct relocation observations, but also the nesting structure of ant colonies - i.e. ant genera without direct relocation data but which had tendencies to nest in pre-formed cavities were likely to be nomadic, while those with extensive nest excavations were not. While this assumption has a sound theoretical basis when considering the cost-benefit trade-off of relocation compared to investment in nest construction, it does encompass a wider portion of the ant family than that of direct relocation observations. This could explain why our findings contrast with opinions such as that of Levings (1983), who believed that nest relocation is an uncommon practice among most ant species, as many may establish colonies that can remain in a fixed location for multiple years - adopting a sessile existence. Even using nesting structure alone, we still do not manage to capture the full extent of relocation behaviours. Despite the expected energy trade-off many nomadic species will construct extensive subterranean nests (e.g.

Amblyopones: (Heterick, 2022)). Similarly, some species excavate complex nests but live in close or obligatory association with a frequently relocating species, which would suggest that they would also need to be nomadic themselves (Kaufmann et al., 2003). Finally, some polydomous colonies may relocate only a single nest or part of their colony (Pfeiffer & Linsenmair, 2000), therefore it could be argued as both a form of nomadic behaviour or secondary characteristic of polydomy.

Nevertheless, relocation behaviours are observed widely through the Hymenoptera and social insects (McGlynn, 2012). Taking a look again at the wasps, pipe-organ mud daubers inhabit pre-formed cavities, twigs and man-made trap nests (Barber & Matthews, 1979) although there are a variety of nesting behaviours displayed within the wider mud-dauber family, including fully constructed tunnels (Brockmann, 1980). It is primarily in the legionary army ants of the Dorylinae, the most extreme nomads of the Formicidae, that we see a distinctive loss of generalism. Other species with distinctly nomadic lifestyles, such as the mushroom harvesting *Euprenolepis procera* have narrow, and specialist dietary ranges in the wild, with 99.6% of their diets made up exclusively of foraged mushrooms (Witte & Maschwitz, 2008). This trend would suggest that the loss of generalism strengthens the selection of a nomadic lifestyle in order to sustain access to a specialised food resource.

While nomadism and generalism are more widespread within the ant family, storage and polydomy appear to dominate more specific areas of the phylogeny (Fig 3.5). Polydomy most frequently occurs in the phylogeny between the Formicidae and the Dolicherinae. This strategy appears to be the most frequently gained trait in the phylogeny, particularly compared to nomadism and generalism which have been lost more often than gained. This may be because it often originates in response to nesting constraints such as that of cavity nesters - in which case we would expect and do see the frequent co-occurrence of nomadism and polydomy (Fig 3.4) - as well as in response to secondary polygyny and reproductive budding, which themselves have evolved many times (Debout et al., 2007; Ellis & Robinson, 2015).

In areas of the phylogeny where storage behaviours are common, different sub-strategies appear to dominate clades. Within the Formicidae we see the formation of repletes (van Elst et al., 2021). Instead the Ponerinae, which frequently lack a distendable crop or physical structure allowing for internal storage, have developed behaviours such as prey-paralysis (Maschwitz et al., 1979). In the Myrmicinae the Attines are primarily fungus-growing ants (Mehdiabadi & Schultz, 2009), while the Stenammini store harvested seeds in dedicated granaries (McCopk, 1878; J. Wheeler & Rising, 1975). Larval hemolymph feeding (LHF) is a strategy which dominates the Ambyloponinae (K. Masuko, 1989). Similar to extreme nomadism, this form of storage occurs commonly in specialist predators which lack the ability to regurgitate food or form trophic eggs, and due to their specialisation may have long periods without locating new food (Ito & Gobin, 2008). Thus, the evolution of more and new storage behaviours may become most common in cases where generalism has been lost, although due to the nature of our data being represented at a genus rather than species level a clear pattern may have been obscured. Storage also seems to preclude nomadism, particularly within the fungus-growers. Even in cases where nest relocation has been observed these nest movements are not considered a dominant part of their life history and may be initiated by predation rather than lack of food resources (McGlynn, 2012; Nickele et al., 2012). Alternatively, nest migrations may develop due to limitations in long-term storage practicality. In extremely wet environments, collected organic matter will decay within a few days, which can lead to potential disease threats for ant eggs and larvae as bacteria and fungi proliferate (Freitas, 1995).

Finally, it is interesting to note that the second most common state after nomadism and generalism, which was the ancestral combination, was a combination of nomadism, generalism and polydomy. The ancestral state, and especially with the addition of polydomy is a combination that tends to be a precursor to the development of “wandering” or invasive ants (Passera, 1993). This combination is likely to be so common through the evolutionary history of the Formicidae as it excels in the occupation of new environments.

4.2: Predictability

Through our predictability analyses we have found relationships between generalism and nomadism behaviours with environmental predictability, however we do not see any relationship with storage or polydomy. As we predicted, generalism declines in probability as temperature constancy increases and similarly nomadism declines as precipitation constancy increases. We expect such patterns as an environment which has a high degree of constancy should have an abundance of food. Thus, there would be less selective pressure that would lead to the development of risk-mitigation strategies. Based on the slope of nomadism in Figure 3.7a, this strategy appears to become more common as temperature constancy increases, which would counter our expectations, however due to the large error bars we cannot draw any meaningful conclusions on whether this trend is accurate.

Under increased precipitation contingency, generalism appears to become more common, while nomadism becomes less common. Regarding nomadism, this trend meets our expectations as we would expect that nomadic behaviours develop when environmental conditions are entirely unpredictable. In a low contingency environment nomadism would allow ants to move from one location to another once a food resource becomes depleted, as is observed in the army ants (Topoff & Mirenda, 1980), compared to sessile strategies such as storage which involves keeping food which may have a finite storage period (Freitas, 1995). However, we also predicted a similar trend in generalism, as a widening of dietary preference would allow ants under highly unpredictable environments to mitigate the long-term risks to food resources by increasing the number of food types consumed. Such behaviour is observed in *Novomessor* who alter and widen their diets when their preferred seed types are less abundant.

In our ASR we found that nomadism and generalism had instances where they may preclude each other, particularly where nomadism behaviours are more extreme. Relocation events in ants may be influenced by reasons other than limited food resources. One important influence is nest desiccation and moisture level (Sanders & Gordon, 2000). Under predictable or constant precipitation levels, ants can find a suitable nesting site for their moisture level needs and develop alternative strategies for dealing with periodic changes. For example, they may create specific nesting structures and plug nest entrances such as the wall-pappering techniques of *Harpegnathos saltator* during periodic flooding (Peeters et al., 1994). If such behaviours develop there is less incentive to take up relocation, and the overall nest construction cost-benefit balance may thus weigh in the favour of sessile nesting habits despite potential food uncertainty. In which case we would expect ants to have a greater selection for other risk-mitigation strategies that counter long-term unpredictability, for example generalism. Thus, the loss of nomadic lifestyles may increase the prevalence of generalism, creating a negative correlation effect. In a similar but converse manner, generalism may enable ants to better occupy temperature variable environments, as is seen in other taxa such as coral-reef fish (Monaco et al., 2020). In turn, the dependence on generalism may reduce selection pressure on nomadism and once again the costs associated with nest rebuilding may outweigh any potential additional effects of two risk-mitigation strategies. A study considering the effectiveness of compounding the effects of strategies compared to using just one could be carried out to investigate this.

Unlike nomadism and generalism, polydomy and storage remain constant under all four of our measures of predictability. The probabilities of occurrence are also similar. Polydomy is used for the exploitation of food resources (Ellis & Robinson, 2016; Hölldobler & Lumsden, 1980), however as previously mentioned the evolution of polydomy may also be driven by many other factors less associated with environmental predictability, such as limited nesting sizes in cavity nesting ants (leading to expansion of nest in a new location), reproduction by budding (in which new queens establish nests through colony fission, which may or may not lead to full independence) and secondary polygyny (which is believed to have led to secondary evolution of polydomy in many different species) (Debout et al., 2007; Ellis & Robinson, 2015). It is more surprising that environmental predictability does not affect storage probability. Storage behaviours are common throughout the animal kingdom in preparation for seasonal dips in food abundance over winter (Hurly, 1992; McNamara et al., 1990; C. C. Smith & Reichman, 1984). It may therefore be the case then that we would need to consider other factors as measures of environmental predictability to observe any trend. Alternatively, it may depend on the form of storage we are considering. We have considered a range of storage types and some of these may be better suited to different levels of predictability, or be influenced by some environmental factors (i.e. temperature and precipitation) more than others. If the former is true, then we would need to consider conducting an analysis at sub-category level to pick apart any trends between storage types. Finally, the differences between effects seen in our four strategies may simply be due to our sample sizes. We have almost twice as many positive data points (the data points used for all our analyses) for nomadism as polydomy and storage, and even still we have large error margins on these graphs. Therefore, it may be the case that we need a larger sample set to begin to see any trends at all.

4.3: Data Distribution and Biases

Our data was reasonably well spread across the globe, with data gathered from studies which took place in every continent where ants are present (Fig 3.1). Nevertheless, there was a dominance in our dataset of English papers and samples from English speaking countries. Much of our data was collected from North America, Southeast Asia and Australia, all of which have English as a primary language. Within the African continent almost all our data was from the English-speaking countries of West Africa such as Cameroon and Gambia, or South Africa. From our distribution map in Figure 3.1 we can see that there is a gap in sampling around Northeast Africa and Central Asia. This bias is of course due to our limited language proficiencies which meant data collection in other languages required a substantially larger time commitment than data collection from English language papers. Of our 306 papers used within our studies, less than 2% were of a non-English language. The importance of inclusion of non-English literature has been studied by (Angulo et al., 2021). The study considered 15 non-English languages and found that not only did it capture a greater amount of data than English-language literature alone (2500 data points compared to 2396 data points), but also that these sources added 249 species to the study from 15 countries that were not captured in the English language sample.

Even within our set of locations it became clear that some study sites were more heavily sampled from than others. For example, if our data points had been distributed evenly over our 206 study sites we would expect approximately 5 data points per site, however the Barro Colorado Island (BCI) in Panama is represented by 15 data points, and Ulu Gombak Nature Reserve in Malaysia accounted for over ten times as many (n=56). Consistent studies at the same sites mean there is an in depth understanding of the different species making up the community within this ecosystem, but there remains many other sites and environments which are extremely understudied.

In a similar vein, there is a great variation in the degrees that different genera and species are studied. We have a good spread of data across the different subfamilies of the Formicidae (Fig. 3.2) and those subfamilies that are the most skewed from our expected sampling rate are the smallest ones, where one or two genera sampled can easily overrepresent the groups. Nevertheless, even a cursory review of the Antwiki database would reveal that many studies are focused on just a very few species and genera, with the large majority having little to no records of the biology outside of morphology. One of the few larger subfamilies that was underrepresented in our dataset was the Dorylinae. Even so, particular genera such as the *Eciton* are overrepresented (n=25) compared to what we would expect of a uniform distribution across our sampled genera (~n=6). In this example the cause of the bias can be attributed to the highly conspicuous raiding columns and the use of army ant behaviours which have been well studied, particularly at popular sites such as BCI, Panama (S. Powell, 2011; S. Powell & Franks, 2006). Species with more cryptic life histories, such as those which are primarily subterranean, are much harder to make observations on.

Finally, we had an uneven distribution of each strategy across our genera (Fig 3.3). We had data on nomadism and generalism for over 150 of the complete 285 genera we attempted to sample from. In contrast, we only found data on 67 and 61 genera for polydomy and storage, respectively. This difference is likely due to the nature of data collected. Storage and polydomy were typically recorded as present or absent, however as most of our papers were observational studies it is much easier to record the presence of data than it is to confirm the absence of a behaviour. I.e. an observed behaviour can be recorded as present in the taxa or population, but an absence of observed behaviour doesn’t equate to absence of behaviour occurring in the overall taxa or population. Instead, our nomadism data collection had both binary (relocation vs no relocation) measures and a scale (degree of nesting modification), and generalism also has a scale (degree of specialism) allowing us to determine both the presence and absence of data. Additionally, we found dietary behaviours from cafeteria experiments and information on nesting structure is common and widely noted even in preliminary studies of an ant species. Furthermore, it may be the case that behaviours which are considered to be more interesting or notable get recorded more frequently or that some behaviours are assumed to be known without direct mention. For example we have many records of more elaborate storage behaviours such as repletism, LHF, prey paralysis and fungal gardens, however observations of presence or absence of granaries in seed harvesting ants were few and only four observations of non-seed storage piles, only one of which explicitly mentioned the piling of resources for storage.

Despite the ease of finding information on nomadism, some of the data available was still difficult to interpret. We found nesting information alone could consist of very ambiguous descriptions such as “nesting in leaf litter”, “...ground” or “...in wood” without details on any degree of excavation, modification or mention of free-living/bivouacking. This led to a higher proportion of unclear samples within our nomadic dataset.

4.4: Further studies and outstanding questions

Given more time, we would have expanded our model to consider additional factors as proxies of food predictability. EM-DAT International Disaster Database (emdat.be, 2022) has a record of all major natural disasters, such as tropical storms, landslides and floods, earthquakes and wildfires that have occurred globally over the past century. With that data we could have calculated an average annual disaster rate for each location, to at least a country level specificity and used this to consider the effect of natural disasters on our strategies. Additionally, we have collected data on human disturbance at each of the locations that our data samples were from, based on whether the land was used agriculturally or was developed compared to, for example, primary forest, and whether the area was described as heavily used by humans or not. We could therefore include human disturbance as a binary yes-no variable within our model of environmental predictability.

We would also be interested in considering our strategy data in alternative ways. Based on the data we have collected, while there are patterns regarding some of our strategies precluding others, these are not fixed rules and often multiple strategies may be exploited within a single genus or even species (Fig. 3.5). We would thus be interested in understanding whether different degrees of environmental predictability influence the number of strategies used by a genus, as we would expect that the use of a greater number of strategies may have a compounding effect on the ant’s risk-mitigation potential and so be more common under lower levels of predictability. “Wandering” ants such as *Solenopsis invicta*, which are often invasive and so regularly occupy new and potentially unpredictable environments, make use of a combination of nomadism, generalism and polydomy behaviours (Passera, 1993).

Similarly, we have categorised each of our strategies into finer gradient sub-categories (Appendix B). We would therefore be interested in finding out whether considering each strategy individually at this finer scale, we find any more links between our model of environmental predictability and the use of each strategy. Additionally, the structure of an analysis like this would also allow us to make use of the negative data (information on the absence of a behaviour) as well as just the positive (presence of behaviour) data we have used in the analyses reported here. In our current design, information was lost regarding where strategies were known to not be found as we were not able to represent both positive and negative data in either our polymorphic ancestral state model or within our Bayesian categorical regression model.

4.5: A note to future researchers

During our literature search we initially carried out a keyword search in the WoS database, before proceeding with a second review of the AntWiki. For future phylogenetic reviews of the Formicidae, particularly where time is limited, we would recommend the following: We would begin with a systematic review of literature references from the AntWiki to create an initial dataset. We have found that this is much more efficient at producing a comprehensive dataset than the keyword searches we carried out. Following this initial search, we would then recommend using the WoS to carry out more specific searches based on data gaps that become apparent. Due to the breadth of the WoS database, broad search terms require extensive filtering before appropriate papers can be located. As the AntWiki is already specifically associated with the Formicidae it acts as a much more targeted repository to search from.

4.6: Summary

To summarise, we have found that the ancestral state of the Formicidae family is a polymorphic state of nomadism and generalism. This combination was the most common state throughout the evolutionary history of the Formicidae, occupying nearly a quarter of the evolutionary history of the Formicidae. The most common combinations of states over the history of the family were found to be those that are prerequisite to the transition into an invasive species, i.e. those that allow species to move into new and potentially unpredictable environments.

We did not find any association between environmental predictability and either storage or polydomy behaviours. However, we did find that as temperature constancy increases, nomadism becomes more common with respect to a generalism. Conversely as precipitation constancy and contingency increases, nomadism becomes less common with respect to generalism. These two strategies appear to be inversely correlated in their presence at different levels of predictability. This could be due to the fact they should mitigate similar types of unpredictability, and therefore it may only be necessary to focus primarily on one of these strategies.

Overall, it appears that there may be some effect of environmental predictability on nomadism and generalism risk-mitigation strategies. However, all our strategies are also affected by other factors unrelated to predictability and food risk (e.g. polygyny, nest desiccation), which must be taken into account when attempting to predict the effects of environment on strategy preference. Further studies outlined in the discussion should be carried out to expand on the initial findings we have made here.

Appendices

Appendix A: A list of keywords used in our literature search of the Web of Science, in addition to future recommendations on keywords to include (underlined). Terms are followed by WoS-ready input terms. All WoS terms follow the suffix "Ant AND ".

Nomadism:
Relocation (Relocat* AND Food)
Nomadism (Nomad*)
Nest movement (Nest movement*)

Storage:
Internal Storage (Internal Stor*)
Stockpile (Stockpil*)
Storage (Stor* + Food)
Honeypot (Honeypot*)
Replete (Replete*)
Trophic Eggs (Trophic AND Egg*)
Prey Paralysis (Prey AND Paralysis)
Fungus Growing (Fungus AND Grow*)
Larval Hemolymph feeding (Larval Hemolymph Feeding)
Corpulent (Corpulent*)

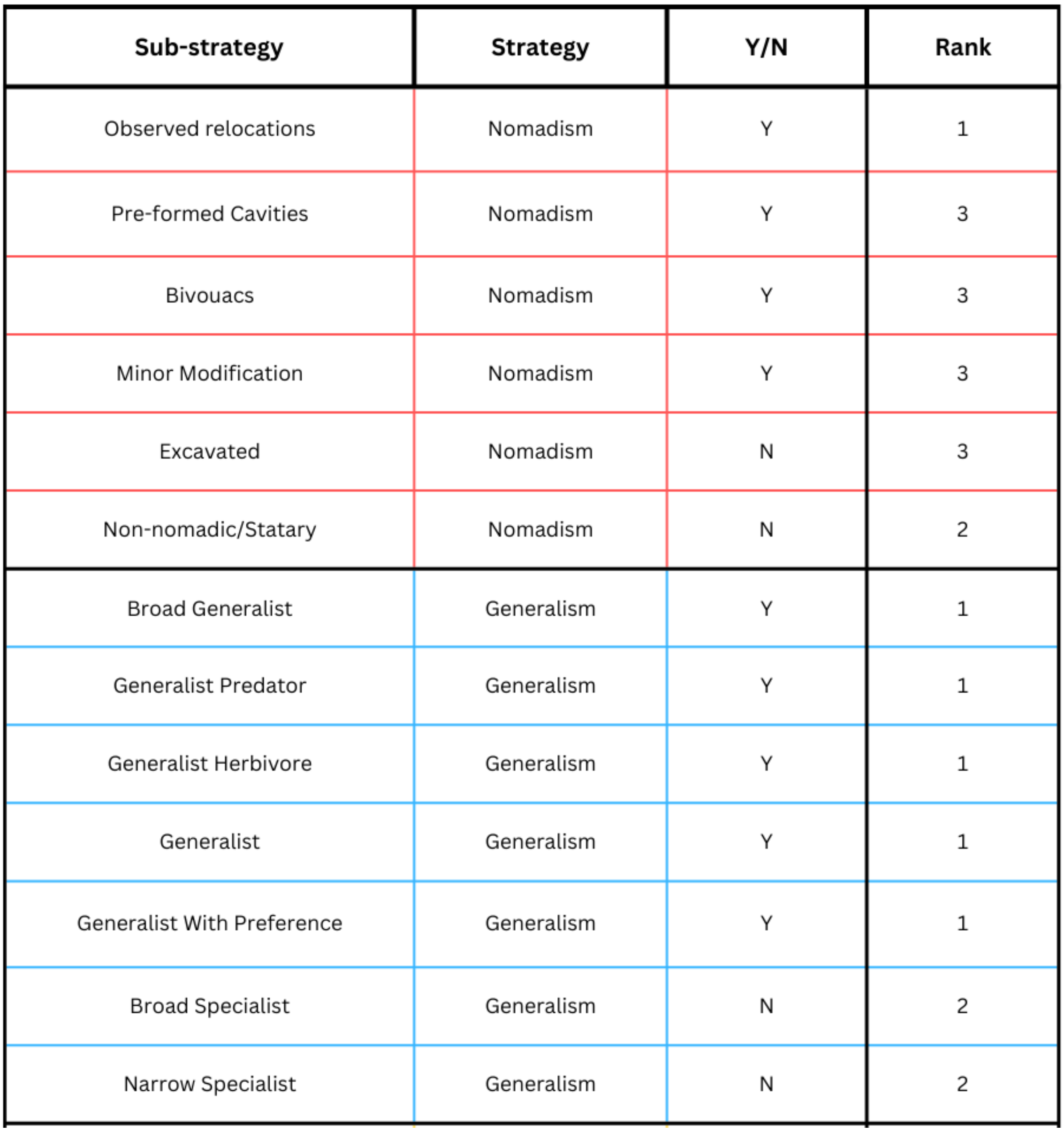
Polydomy:
Exchange (Exchange AND Food)
Cooperation (Cooperation AND Food)
Polydomy (Polydom* AND Food)
Multidomy (Multidom*)
Polycaly (Polycal*)

Generalism:
Generalism (Generalis* AND Food)
Specialism (Specialis* AND Food)
Oligophagy (Oligophag*)

Other:

Resource (Resource* + Predictability

Appendix B: A list of the sub-strategies/sub-categories that were identified and used to assign each datapoint to a strategy category. Y/N represents whether or not the strategy was found to be present or absent in a genus respectively. The rank system was used in the cases where our data fitted multiple sub-categories. In such cases a lower rank number overrides a higher rank number in determining whether or not a strategy was labelled as present or absent for a genus.



Sub-strategy	Strategy	Y/N	Rank
Observed relocations	Nomadism	Y	1
Pre-formed Cavities	Nomadism	Y	3
Bivouacs	Nomadism	Y	3
Minor Modification	Nomadism	Y	3
Excavated	Nomadism	N	3
Non-nomadic/Statary	Nomadism	N	2
Broad Generalist	Generalism	Y	1
Generalist Predator	Generalism	Y	1
Generalist Herbivore	Generalism	Y	1
Generalist	Generalism	Y	1
Generalist With Preference	Generalism	Y	1
Broad Specialist	Generalism	N	2
Narrow Specialist	Generalism	N	2

Described Polydomous	Polydomy	Y	1
Multiple Nests W/ Exchange	Polydomy	Y	3
Non-Hostile Workers	Polydomy	Y	3
Many Partial Nests (Missing Queens or Larvae etc.)	Polydomy	Y	3
Multiple Nests W/O Exchange	Polydomy	N	4
Non-Polydomous	Polydomy	N	2
Larval Haemolymph Feeding	Storage	Y	1
Granaries/Food Piles	Storage	Y	1
Dried Insects	Storage	Y	1
Preservation	Storage	Y	1
Prey Paralysis	Storage	Y	1
Repletism	Storage	Y	1
Planned Cannibalism	Storage	Y	1
No Storage	Storage	N	2

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