Chapter 3

Geographic Gradients

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3.1 Introduction

Linnaeus, upon travelling north from southern Sweden, was struck by the differences between that colder land and his homeland. The differences in the composition of species begged explanation. Ever since (and probably before), naturalists, ecologists, and biogeographers have sought to understand why species and the communities they make up differ from place to place. Why does body size, both within and among species, vary geographically? Where are there more species and why? The ease of posing such questions has attracted generations of biologists – each lured by the possibility of finding elegant answers to superficially simple problems. But to date, consensus explanations remain elusive. And so how should we move forward? Major headway, we suspect, will come not from the search for general explanations of ecological gradients, but instead through the careful study of a few focal taxa and the factors that influence their distribution along gradients. The most obvious focal taxa are likely to be vertebrate groups (e.g. birds and mammals). But because most animal species are insects, having even a single well-studied insect taxon whose ecological gradients are well understood would be disproportionately valuable. To date, the best candidate for such intensive focus is ants. They are relatively easy to sample (see Box 3.1), well known, ecologically important and have been the subject of gradient studies for nearly 50 years.

In this chapter, we review our current understanding of gradients in ant diversity, body size, range size, and other life-history traits. We examine the underlying causes of these gradients and discuss their consequences for some of the processes ants mediate, such as predation and seed dispersal. We start with the patterns themselves by reviewing latitudinal and elevational gradients in ant diversity at multiple spatial and taxonomic scales. Then, we move on to two other common gradients in ants – gradients in body size and range size. For each gradient, we explore some of the potential underlying mechanisms.

3.2. Empirical patterns along gradients

3.2.1 Species diversity and latitude

Since as early as the work of Forster and von Humboldt in the early 19th century (see Hawkins 2001), scientists have been aware of latitudinal gradients in diversity, particularly for vertebrates and plants (Brown and Lomolino 1998; Rosenzweig 1995; Willig and Lyons 1998; Willig et al. 2003). Generally, diversity declines with latitude and ants are no exception. Kusnezov (1957) was the first to attempt to quantify the latitudinal gradient in ant diversity by compiling total species lists for regions (e.g. Alaska, Iowa, Utah, Cuba, Trinidad, parts of Argentina, and Brazil). His finding that ant species richness decreased with latitude was among the first clear demonstrations of a latitudinal diversity gradient in insects. In the 1970s, similar results were reported based on data compiled from the ants of the British Isles and northern Europe – a decline in species diversity with latitude (Baroni-Urbani and Collingwood 1976, 1977). Cushman et al. (1993) followed these earlier leads and compiled species lists and museum data to examine whether there was a latitudinal gradient in ant diversity in...
Box 3.1 Field techniques for sampling ants
Brandon Bestelmeyer and Leticia Rios Casanova

Ants occur in most environments and ecologists ask a diverse array of questions involving ants. Thus, a key consideration in ant studies is to match the environment and question (and associated environmental variables) to the ant sampling technique. Since each technique has distinct limitations, using a complementary suite of techniques is often beneficial (Agosti and Alonso 2000). For further details, see Bestelmeyer et al. (2000) and newer applications.

There are two general questions that an investigator should consider in choosing one or more techniques to sample ants: (a) What distinct microhabitats or sampling strata are available or of interest in a study area? And (b) What is the ant variable of interest? From top to bottom, distinct sampling strata include: (a) large trees including emergents (>5 m tall), (b) small trees and/or shrubs (0.5–5 m), (c) small shrubs and/or herbs (<0.5 m), (d) rotting wood, (e) leaf litter and/or humus, (f) ground surface, and (g) subsurface soil. There are three general types of variables used to represent ant species and communities: (a) abundance, some measure of the number of individuals of a species within samples, or frequency of occurrence across samples; (b) richness, number of species in a sample, also presence or absence; and (c) behaviour, observations of species interactions or foraging that can be used to quantify behavioural dominance. Certain techniques also estimate forager or colony density. A subjective ranking of the value of technique types for sampling different strata, with respect to the type of data best produced by that technique, is indicated in Table 3.1.1 (see also Bestelmeyer et al. 2000). Brief descriptions of the classes of techniques follow.

Canopy fogging samples ants from the canopy of large trees. Fogging involves four steps that include (a) identification of tree species to be sampled and replication, (b) placement of collection funnels under trees (with a standard size, number, and arrangement), (c) fogging of the tree for a fixed period (e.g. 4 min) using an insecticide (often pyrethrum), and (d) collection of specimens that fall from the tree after a fixed time period (e.g. 90 min). Only ants active on the tree surface are collected using this technique. Ant behaviour (e.g. ants living in epiphytes) and the time period at which fogging takes place will influence the likelihood of ant species’ records in samples (Schulz and Wagner 2002).

Beating samples ants from large to small woody plants within reach of poles. Ants dislodged from vegetation struck by the pole fall onto a sheet (e.g. 2 m x 2 m) where they are collected (e.g. Majer et al. 1994). Beating can also occur in conjunction with the use of direct searching (see later) for ant species inhabiting bark and twigs that may be missed by beating. As with canopy fogging, ant behaviour and time period will influence the collection of particular species.

Sweeping and vacuuming are typically used to estimate abundance from low woody and herbaceous strata. Sweeping involves moving a sweep net through vegetation to dislodge and collect ants in the net. The number of sweeps, extent sampled, and pattern of sampling is standardized for comparison (e.g. Andersen et al. 2007). Plant substrates can also be vacuumed. Philpott et al. (2006) used a garden vacuum to suck arthropods into plastic bags where they were killed with ethyl acetate. Samples were compared using the number of individuals per gram of foliage. The ground surface can also be vacuumed to provide a density value for high-density foragers (Abbott 2006). There are similar considerations regarding ant behaviour and period of sampling as discussed earlier.

Bait sampling encompasses a diverse array of techniques used to evaluate the presence and behaviour of active ant foragers on the ground surface, below ground, or in vegetation. Baits are protein-, fat-, or carbohydrate-rich food substances that attract foraging ants to points where they are observed and/or collected. Baits are used to indicate which ant species are present, especially where other methods cannot be used (e.g. pitfall traps in rocky terrain). Changes in the abundance and species of ants at baits as well as interactions over time can be used to determine dominance (Andersen 1992; continues)
Table 3.1.1  A qualitative ranking of the utility of different methods for sampling ants in different strata (from + to ++++) and the types of data provided by each method other than species presence or absence (that is common to all methods).

<table>
<thead>
<tr>
<th>Method</th>
<th>Canopy fogging</th>
<th>Beating</th>
<th>Sweeping/vacuum</th>
<th>Bait sampling</th>
<th>Pitfall trapping</th>
<th>Quadrat count</th>
<th>Colony sampling</th>
<th>Direct sampling</th>
<th>Litter extraction</th>
<th>Soil sampling</th>
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<tbody>
<tr>
<td>Data type</td>
<td>Abundance, richness</td>
<td>Abundance, richness</td>
<td>Abundance, richness</td>
<td>Behaviour</td>
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<td>Abundance, richness behaviour</td>
<td>Abundance (colonies)</td>
<td>Behaviour</td>
<td>Abundance, richness</td>
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<td>Stratum</td>
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<td>Small tree/shrub</td>
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<td>Small shrub/herbs</td>
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<td>Litter/humus</td>
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<tr>
<td>Ground surface</td>
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\(^a\)If using a canopy crane.

continues
see Chapter 5). Ant contributions to ecosystem processes, such as myrmecochory, can be measured using seed baits. Finally, baiting is an excellent tool for measuring behavioural attributes. Differences in behavioural dominance, foraging behaviour, and preferences for food items will often result in an incomplete representation of the larger ant community.

Pitfall trapping is the most common method for sampling ground-active ants, although traps may also be used on woody strata. Open containers are placed flush with the surface. Ants fall into them and are usually killed and preserved in a liquid such as propylene glycol. Trap diameter and trapping duration (e.g. 1–4 days) need to be considered when using this technique. Trapping is relatively simple, integrates the sample across daily periods used by different ant species, and is perhaps the most commonly used method to evaluate ant community structure across broad areas and in situations where leaf litter is not deep. Differences in ant movement rates among habitats can bias the data (Melbourne 1999).

Quadrat sampling can be used for sampling surface-active ants, typically in open habitats. Behavioural observations can also be gathered, such as food items collected by the ants. A quadrat is used to delineate the observation area. In cases where activity is very high, the quadrat may be a small (e.g. 10 × 10 cm) card. Species of ants seen inside or entering the quadrat over a fixed time interval are counted and/or collected, and identified either in the field or back in the laboratory. Quadrats provide data similar to those of pitfall traps without trap-related biases. The method requires great skill in identification when ant activity is high and some species may be impossible to distinguish in the field. Observations may need replication at different times of day.

Colony sampling enumerates ant colonies in a defined area, providing a measure of abundance or density based not on individual ants but on colonies as units. Ants with characteristic nest structures facilitate direct enumeration and even mapping (Schooley and Wiens 2003). In habitats where most nests are inconspicuous, examination of soil under rocks, litter, nuts, and twigs or branches is necessary. Multiple nest entrances may overestimate colonies, especially when ants are polydomous. This method can provide a population-oriented perspective on ant communities and a distinct community characterization when compared to pitfall trapping (Schlick-Steiner et al. 2006a).

Direct searching records the presence of ant species inhabiting a habitat element or area. Different microhabitats or habitat elements (e.g. trees, foliage, and especially inside rotting wood) are systematically searched and ant foragers (or entire colonies) are collected. Ant behaviour within microhabitats (e.g. at extrafloral nectaries) can also be directly observed and quantified (Oliveira et al. 1999). Collections can be performed for fixed time periods to aid standardized comparisons of richness or composition. Nonetheless, standardized comparison across investigators can be difficult due to differences in ability. Direct sampling permits a complete list of the ant fauna in relatively little time by experienced collectors, but abundance is difficult to estimate. It is often used as supplementary technique or in cases where other methods are impractical.

Litter extraction measures abundance and richness of ants inhabiting a volume of leaf litter. A quantity of moist leaf litter is collected and placed in an extraction apparatus. Ants migrate from the litter and fall into a collecting receptacle. The migration behaviour of ants can be caused by disturbance (Winkler sack) or changes in microclimate (Berlese funnel). Litter techniques are needed for complete and cost-effective community characterization where litter horizons are deep, as in many tropical forests wherein the bulk of non-arboreal species inhabit the leaf-litter column (Fisher 1999b).

Soil sampling for subterranean ants is accomplished by excavating and searching a volume of soil for ants. Alternatively, chambered, tubular soil probes can be installed into the soil using an auger wherein baits placed in the chambers attract ants into the chambers to measure presence (Ryder Wilkie et al. 2007). This technique allows ants to be associated with particular soil horizons or depth increments in a cost-effective way.
Europe and found that species diversity declined with latitude.

The advantage of such large-grain, large-scale, geographic approaches is that they consider the spatial grain at which speciation and often extinction occur. The disadvantage of these scales and grains is that data on species are necessarily crude because it is easier to collect all the species in a metre square or even a hectare than in an entire geopolitical region. There are very few regions on earth where the species-level faunas of ants or any other insect taxon are completely known. To avoid the difficulties associated with generating species lists at large spatial grains, Jeanne (1979) collected ants at 10 sites, from Minnesota to Brazil. He was the first to show that the number of ant species in local communities increased towards the tropics, just as earlier authors had observed at larger sampling grains. Similarly, Kaspari et al. (2003) compared 49 New World sites that span similar conditions to those considered by Kusnezov (1957) (tropical forest to arctic), but with a bias towards the northern hemisphere. At both the plot (m$^2$) and transect (30 samples from a 330 m transect) grains, species diversity decreased with increasing latitude (Kaspari et al. 2003). In a related study – based on leaf-litter ant samples from 96 sites from Australia, Madagascar, North America, and South America – Kaspari and colleagues also found a strong latitudinal gradient in ant species diversity (Kaspari et al. 2004).

In sum, as for nearly all major groups of organisms (Hillebrand 2004; Willig et al. 2003), ants exhibit a strong latitudinal gradient in diversity. However, broad similarity in patterns of diversity among grains does not preclude more subtle differences in the form (e.g. quadratic versus linear) or parameterization (magnitude of coefficients) of the relationships between latitude and diversity (Levin 1992). Similarly, the relationship between diversity and latitude differs between hemispheres for some other taxa, with more species for a given latitude in the southern hemisphere (Chown et al. 2004). Such a possibility remains poorly explored for ants (but see Dunn et al. 2009). Further, patterns of ant diversity with latitude may differ at different scales, or depending on how diversity is measured (although see Kaspari et al. 2003). Understanding differences in diversity gradients among grains, and, in particular, patterns of beta diversity (turnover in species composition among focal sampling units, such as plots or grid cells) along gradients represent interesting areas for future work. Where it has been studied in other taxa, beta diversity has been shown to decline with distance from the equator (Qian 2008; Qian et al. 2009; Soininen et al. 2007; Stevens and Willig 2002), although sometimes only weakly (Gaston et al. 2007). Similar variation in beta diversity with latitude (and elevation) might be predicted for ants (Soininen et al. 2007).

### 3.2.2 Elevational gradients

Elevational gradients have long been seen as analogous to latitudinal gradients (e.g. von Humboldt 1808), because many of the processes that shape latitudinal gradients may also operate along elevational gradients. For example, temperature declines with distance from the equator and might decline similarly with elevation. Such environmental gradients can be logistically easier to study on elevational gradients than on latitudinal gradients because a much greater range of conditions can be encountered in a much smaller distance. While mean annual temperature decreases, on average, approximately 0.7°C/100 km of latitude, it decreases with elevation much more steeply, at approximately 0.6°C/100 m elevation (Colwell et al. 2008). It is not surprising then that patterns of ant diversity along elevational gradients often mirror the larger-scale latitudinal patterns. Ant species diversity typically declines with elevation (e.g. Atkin and Proctor 1988; Brown 1973; Cole 1940; Collins 1980; Janzen 1973; Janzen et al. 1976; Weber 1943) as it does with latitude, though with some interesting exceptions.

Most studies of ants along elevational gradients have been in the tropics. Several of these studies found no species at the highest elevations surveyed (e.g. 3,380 m in Costa Rica, Janzen 1973; 3,200 m in Sudan, Weber 1943). While these studies were modest in their sampling, they revealed that richness generally declines with elevation, a pattern that has been observed elsewhere. Species diversity of leaf-litter ants in a Malaysian rainforest decreased exponentially with increasing elevation (500–2,600 m; Brühl et al. 1999). Similarly, monotonic
declines in leaf-litter ant species richness with increasing elevation have been found in Panamanian rainforest (Olson 1994), Costa Rica (30–2,900 m; D. Olson personal communication; Colwell et al. 2008), Madagascar (Fisher 1996), and Tanzania (Robertson 2002). Finally, in the only study to consider correlates of canopy ant diversity, ant diversity decreased linearly with elevation (Majer et al. 2001).

A handful of other studies of tropical elevation gradients have detected peaks in species richness at mid-elevations (Fisher 1999a; Olson 1994; Samson et al. 1997). In two of these cases, it has been suggested that the drop in diversity at the lowest elevations may be due to sampling incompleteness at low elevations (e.g. Olson 1994; Samson et al. 1997) or higher rates of disturbance at lower elevations making habitat less suitable. In the third study, the lowest elevation sampled was relatively high (430 m; Fisher 1999a), leaving open the possibility that the lowest elevations might still be the most diverse.

Just as for tropical regions, temperate regions also often show negative relationships between various measures of ant diversity and elevation, whether for eastern USA (Cole 1940; Lessard et al. 2007; Sanders et al. 2007b), Austria (Glaser 2006), or Japan (Ito et al. 1998). Three exceptions to this pattern are gradients for which low elevations are dominated by (or at least include) arid biomes (Botes et al. 2006; Sanders 2002; Sanders et al. 2003b). In each of these cases, ant diversity exhibits more of a mid-elevational peak, an observation to which we will return to later. These exceptions notwithstanding, the relatively consistent linear relationship between any of the variety of measures of ant diversity and elevation contrasts with results for the elevational diversity gradient literature in general (Rahbek 2005; Rahbek et al. 2007), where a large percentage of invertebrates and other taxa show peaks of diversity at mid-elevations.

3.3 Explanations for latitudinal and elevational gradients in ant diversity

Patterns of diversity of ants along elevational and latitudinal gradients are both strong and relatively consistent. The key question then is why do these gradients exist? What causes the decline in ant diversity with elevation and latitude? There are no fewer than 30 hypotheses to explain patterns of diversity in space (Clarke and Gaston 2006; Evans et al. 2005; Willig et al. 2003) and additional hypotheses continue to be put forth (surveyed in Dunn 2008b). Fortunately, a smaller number of hypotheses have been the focus of recent research (Willig et al. 2003). We focus on six of those hypotheses here, but acknowledge that essentially none of the more than 30 explanations for large-scale patterns of diversity have been conclusively rejected (Dunn 2008b). Three of the six hypotheses on which we will focus are related to speciation and extinction differences among regions: the hypotheses of temperature-dependent kinetics (Allen et al. 2002; Rohde 1999); effective evolutionary age (Pianka 1966); and geographic area (Rosenzweig 1995). One hypothesis relates most directly to differences in extinction rates among regions: species-energy theory (Srivastava and Lawton 1998). Finally, two hypotheses, the geometric constraints models (GCMs) (Colwell et al. 2004) and niche conservatism models (Wiens and Graham 2005) relate to the consequences of random places of geographic ranges (GCMs) and random or biased placement of species’ environmental niches in space (niche conservatism models), respectively. Here we briefly review some of the theory relevant to gradients in diversity, and highlight the extent to which each theory has or has not been tested for ants.

3.3.1 Speciation and extinction rate differences

Several theories predict differences in rates of diversification among regions due to differential rates of speciation or extinction, differences in the time for speciation, and the influences of area on speciation and extinction. We consider each of these bodies of theory in turn.

Speciation rates: temperature-dependent kinetics hypotheses

Temperature-dependent kinetics hypotheses posit that, all else being equal, speciation rates are faster in warmer places than in colder places due to the effects of higher metabolism on mutation rates (Allen et al. 2002; Rohde 1999). Evidence for at least one prediction of the temperature-dependent
kinetics hypothesis appears to be growing. Several taxa, including butterflies (Cardillo 1999), birds (Cardillo 1999; Cardillo et al. 2005; Ricklefs 2006), primates (Bohm and Mayhew 2005), and foraminifera (Buzas et al. 2002) have been shown to have higher net diversification rates in tropical latitudes. However, it is unclear whether the magnitude of the difference is sufficient to explain contemporary patterns of diversity (Evans and Gaston 2005). In addition, the differences in net diversification among regions could reflect either differences in speciation rates or extinction rates. Rates of molecular evolution do not appear to differ with latitude (Bromham and Cardillo 2003), but would be expected to if differences in diversification rates with latitude were due solely to differences in the rate of speciation. The all-encompassing Metabolic Theory of Ecology (MTE), like the original temperature-dependent kinetics hypothesis (Allen et al. 2002; Rohde 1999), predicts speciation rates should be a positive function of temperature. However, the MTE predicts not only that temperature should influence diversity via its effects on speciation, but also that the effect should be so great and universal that there is a globally consistent slope of the relationship between temperature and diversity, independent of the study taxon or scale of study (Allen et al. 2002; Brown et al. 2004). This more extreme formulation of the temperature-dependent kinetics hypothesis has not been supported for ants (whose empirical slopes deviate from MTE predictions (Hawkins et al. 2007; Sanders et al. 2007b), or other taxa more generally, where slopes vary wildly among domains and taxa (Hawkins et al. 2007).

**Extinction rates**

Biodiversity theories typically focus on how differences in speciation rates in space affect net diversification and ultimate diversity gradients, but extinction rates may also vary in space. For example, the increased rate of net diversification in the tropics sometimes observed for birds and mammals may be due to the decreased extinction rates in the tropics rather than increased speciation rates (Weir and Schluter 2007). Speciation rates (as opposed to diversification rates) as determined by recent cladogenesis events, were found to be higher in cold, high-latitude regions suggesting that higher net diversification in the lower latitudes must be due to lower extinction rates (Weir and Schluter 2007), as has been observed from marine bivalve fossil data (Jablonski et al. 2006). Very little is known about extinction rates in ants (see Chapter 2), particularly with regard to how extinction rates vary in space. It is, known, however, that a number of ant taxa such as lineages of Myrmecinae, Oecophylla, and other genera have gone extinct from northern habitats of the northern hemisphere (Archibald et al. 2006) in line with the idea that extinction rates are higher in cool climates. However, Dunn et al. (2009) have recently argued that these extinctions may be more strongly linked to the change in temperature in the northern hemisphere since the Eocene, rather than current lower temperatures per se.

**The effective evolutionary age hypothesis**

One way that diversity might vary among regions independent of diversification rates is if the time for diversification has differed between those same regions. The concept of effective evolutionary time posits that diversity should be greatest where the time for speciation has been longest, that is in the regions that have been least climatically stable over millions of years (Pianka 1966). While many of those scientists actively studying diversity gradients believe effective evolutionary time to be important (surveyed in Dunn 2008b), it is a difficult model to study empirically and perhaps for that reason has been less thoroughly explored than have other hypotheses, whether for ants or any other taxon. The biggest difficulty is estimating the age of different biomes or climatic conditions, and while palaeoclimate data continue to be gathered, it is likely to be difficult always to estimate the age of different biomes with any accuracy. Perhaps the best (albeit still anecdotal) evidence that the age of biomes, or at least their relative stability, is important to contemporary diversity comes from a recent study by Dunn et al. (2009). Dunn et al. (2009) found that even after accounting for climate that local ant communities were more diverse in the northern than in the southern hemisphere. This difference is in line with what might be expected if the greater climate change in the northern hemisphere since the Eocene was associated with higher extinction rates.
The geographic area hypothesis
In reality, the diversity of a given region or site is undoubtedly a reflection of speciation rates, extinction rates, and the time between major pulses of extinction. In practice, however, these aspects of diversity tend to be treated separately. The area hypothesis is one of few theories that considers the effects of both speciation and extinction (though it ignores evolutionary age). It argues that speciation rate increases with the area of continents because larger continents are more likely to be subdivided by random processes or dispersal barriers (e.g. rivers and mountains; Rosenzweig 1995; Rosenzweig and Sandlin 1997). In addition, species inhabiting larger habitats and biomes are predicted to have the opportunity of having larger spatial extents for populations and ranges, and hence lower per species rates of extinctions. However, empirical evidence to date for a positive relationship between the spatial extent of species’ geographic ranges and speciation rate is limited. Some evidence points toward a unimodal relationship between range size and speciation probability (Gaston 1996; Gaston and Blackburn 1997), though the shape of the relationship undoubtedly depends on the size of the domain being considered.

As has been pointed out by many authors, rewinding the evolutionary tape is impossible, and no experiments could confirm or reject any of these hypotheses about diversification, speciation, or extinction, at least at global scales. Furthermore, the key independent variables pertaining to different theories are correlated such that tropical forests, for example, are hot, have high Net Primary Productivity (NPP), are large and relatively old, and so would be predicted to be diverse under essentially every theory. Given that elevational gradients may mirror latitudinal gradients, carrying out experiments aimed at elucidating the underlying mechanisms and predictions of some of these evolutionary models may be tenable. Yet, it is reasonable to question whether short-term responses of species or taxa to experiments along elevational gradients are sufficient tests of theories meant to apply over global spatial scales and temporal scales of millions of years. Arguably, the theories most testable using experiments along elevational gradients are those related to energy and coexistence, an area of theory broadly referred to as species-energy theory, to which we now turn.

3.3.2 Species-energy theory
In the quest for mechanistic links between climatic conditions and patterns of local (or regional) biodiversity, many recent studies on a variety of taxa have tested a body of theory that is sometimes called species-energy theory (see Clarke and Gaston 2006). Species-energy theory is based on the premise that large-scale patterns of biodiversity occur because diversity tracks patterns in the density of individual organisms and patterns in the density of organisms track the energy available per unit area per unit time (typically g C/area/time) (Hutchinson 1959; Pianka 1966; Wright 1983). Theory posits that where more energy is available there are lower local extinction rates because more individuals of all species can be sustained per unit area by the greater flux of resources. Lower local extinction rates are predicted to, in turn, lead to lower rates of local extinction and hence higher diversity.

If energy availability determines local ant diversity, then NPP, or some proxy of NPP, should be the best predictor of local ant diversity. However, access to resources may be mediated for ants by more than simply the total energy available. The energy available to ants is affected by any variables that affect when and how long ants forage. Because ants are thermophilic, temperature (along with other variables) should limit the resource availability above and beyond the limits imposed by NPP. Depending on the relative importance of temperature and NPP, and whether the region being considered is temperature limited (with temperature likely to limit ant fitness, foraging, and abundance at lower temperatures than those at which it affects plants) or precipitation limited (with precipitation likely to limit plants before ants), the local relationship between ant diversity and climate might be complex and vary among regions (Kaspari et al. 2003).

Several studies have now found patterns broadly reconcilable with some form of species-energy theory. Ant species diversity was positively correlated with light availability, length of the growing season,
and July temperatures (which are all correlated with each other) in the British Isles and northern Europe (Baroni-Urbani and Collingwood 1976, 1977). Kaspari et al.’s studies (2000, 2003) of New World ant communities revealed that ant diversity patterns at smaller grains (plot and transect) were best explained by differences in the density of ant colonies. At the largest grain (with diversity measured as Fisher’s z, which accounts for differences in abundances), temperature and ecoclimatic area were the two best predictor variables. Similarly, Sanders et al. (2007b) in the Great Smoky Mountains National Park in the eastern United States showed that ant diversity at small grains (m²) was best explained by abundance and temperature. At progressively larger scales, temperature was a progressively better predictor of diversity than was abundance. Most recently, Dunn et al. (2009) found that temperature was the single strongest predictor of local ant diversity when more than 1,000 samples from all over the globe were considered.

However, even if temperature and energy are consistently good predictors of local ant diversity, the relationship remains correlative (and could, for example, also support a link between temperature and speciation and extinction). There was initial enthusiasm for a ‘more individuals’ mechanism linking energy availability to species diversity (Kaspari et al. 2000b), but that enthusiasm has waned of late (Clarke and Gaston 2006) for a variety of reasons. First, it remains unclear why more energy should lead to more individuals of different species rather than just larger population sizes of the species already there. Second, the ‘more individuals’ hypothesis predicts that diversity increases as a function of increases in the total number of individuals summed across species. In general, energy and diversity seem better correlated than do energy and the density of individuals, the opposite of what would be predicted were energy to directly affect individual density (e.g. Clarke and Gaston 2006). For ants, the links between ant density (individuals per area) and energy are difficult to explore because it is not obvious whether the variable that should be considered as a test of theoretical predictions is nest density or individual density. However, in the one case where the density of ant nests was compared to NPP (Kaspari et al. 2003), ground-foraging density was well correlated with NPP as well as temperature and temperature seasonality. Experiments are sorely needed that examine the mechanisms linking climatic conditions and energy availability to ant diversity at a variety of scales. But the good news is that species-energy theory is, unlike other diversity theories, actually amenable to small-scale experimental tests.

3.3.3 Mid-domain null models

**Geometric constraint models**

Latitudinal and any other large-scale spatial patterns of diversity are ultimately a result of the overlap in the distribution of species’ ranges. As a consequence, some have argued that it is not only interesting, but necessary to examine the pattern of diversity that would result were species’ ranges to be randomly arranged on the domain being studied. What would happen, for example, if a lineage started in some random position on a continent and then diversified, with new species no more likely to occupy any one part of the continent than any other?

Models that simulate the expected pattern of species diversity in space where species’ ranges to be arranged at random are usually called Geometric Constraints Null Models (GCMs) (see Colwell et al. 2004). The random process simulated in most of the many null models employed to date is the random arrangement of geographic or elevational ranges along the study gradient (Colwell and Hurtt 1994; Colwell and Lees 2000; Colwell et al. 2004). These models have also been generalized to other domains, such as the distribution of riparian plants along rivers (Dunn et al. 2006), phenologies of plant species through time (Morales et al. 2005) and most recently the seasonal activity patterns (Dunn et al. 2007c) and reproductive phenologies of ants (Dunn et al. 2007b). Just as a pile of pancakes is almost always higher in the middle of a plate as a consequence of the overlap of pancakes, GCM randomizations almost always produce a hump-shaped pattern in diversity, with the highest number of species at the middle of the domain (i.e. the ‘mid-domain effect’; Colwell et al. 2004), whether it is one-dimensional spatial domain (examples in
Colwell et al. 2004), a temporal domain (examples in Dunn et al. 2007b,d), or a two-dimensional domain (examples in Colwell et al. 2004). Thus, hump-shaped patterns of species diversity (e.g. the latitudinal gradient in species diversity) are predicted by GCMs in the absence of spatial variation in climate, biogeographic history, etc. When the domain considered is an elevational gradient, GCMs also predict hump-shaped patterns, with highest species diversity at mid-elevations.

To date, there have been only a handful of tests of the utility of GCMs as explanations of ant diversity along latitudinal or elevational gradients. GCMs alone accounted for 13% of the variation in ant species diversity along a regional elevational gradient in Colorado, 91% of the variation in Nevada, and 37% of the variation in Utah (Sanders 2002). In contrast, there was no support for GCMs in a study of leaf-litter forest ants along an elevational gradient in the southern Appalachians (Sanders et al. 2007b), nor was there for continental-scale patterns of ant diversity in North America (Kaspari et al. 2004). Thus, of the elevational studies of ant diversity to date, the only datasets that seem to coincide well with null model predictions are those from areas where low-elevation conditions are hot and exceedingly dry, and high-elevation conditions are, like everywhere, colder than low elevations. We suspect that ant diversity patterns will tend to consistently differ from null expectations of GCMs except in those cases where climatic predictions and null models overlap. Such cases represent the coincidence of null model predictions and climatic effects.

Independent of the question of whether ant diversity patterns deviate from the expectations of GCMs is the question of whether GCM null models represent a useful approach to considering patterns of diversity. GCMs have been strongly criticized on the grounds that they are biologically unrealistic and make inappropriate assumptions (Hawkins and Diniz 2002; Hawkins et al. 2005; Zapata et al. 2003, 2005). Disagreements involving the specifics of GCM simulations and their biological plausibility may, we suspect, be resolved by altering aspects of the models themselves, in particular by considering GCM models as diversification models in which speciation and extinction are considered to be random with respect to geography and history. More realistic models can be created by adding additional realism where useful, whether that realism is more sophisticated models of speciation or aspects of phylogenetic niche conservatism.

Niche conservatism models
Phylogenetic niche conservatism is the idea that species traits evolve relatively slowly, such that related species are more similar to each other than are any two random species. Such similarity includes not only morphological and behavioural traits but also traits related to environmental tolerance and hence the conditions in which a species can live and its geographic range. As such, one can imagine that each lineage begins in some point of origin with a given set of climatic conditions. Over time, new species will arise that will tend to have similar climatic preferences to the original species. Slowly, climatic preferences (niches) will shift, but initially the centre of diversity for the lineage in question will be centred near the niche preferences of the first species. Given enough time, lineages will spread from their original conditions and begin to fill the domain being studied (as they do niche conservatism models will begin to look very similar to geometric constraints models).

Some assumptions of niche conservatism models can be tested. For example, one can examine whether niches tend to be conserved by plotting measures of niche space on a phylogenetic tree. However, niche conservatism models differ (along with GCMs, to some extent) from other diversity models in making no single prediction of what the ‘correlates of diversity’ should be. Instead, niche conservatism models have lent themselves to simulation and in particular to GCM-like models of diversity patterns. Recent work has explored the patterns of diversity resulting simply from assuming that lineages exhibit niche conservatism (Rahbek et al. 2007; Rangel et al. 2007). These new models are essentially GCM models into which more biology has been added and such models may represent an important new step forward in considering patterns of diversity. While these simulation approaches seem a productive avenue for exploring the consequences of niche conservatism, they may also offer an important means to better understand
the predictions and assumptions of diversity theories more generally.

3.4 Diversity of higher taxonomic levels and phylogenetic diversity: an example

To date, studies of ant diversity patterns have focused on species diversity. Ultimately, our understanding of ant diversity will likely depend upon additional insights about diversity at higher taxonomic and phylogenetic levels. What are the spatial patterns of species, genus, and subfamily diversity and how are they related? Do similar processes explain patterns at different taxonomic scales? Do phylogenetically independent clades track environmental variables similarly? Answers to these questions may help us understand not only patterns of diversity, but also the evolutionary processes underlying the patterns.

The study of diversity patterns of higher taxa, such as genera, has a long history in the palaeontological literature where complete sampling and identification of species are problematic (reviewed in Willig et al. 2003). Generic and higher taxon diversity has also been useful for diverse modern groups such as plants (Qian 1998) and copepods (Woodd-Walker et al. 2002) and, here, ants. Although it is possible to compare the diversity of sampled plots across biomes, knowing the diversity for larger grain sizes for comparisons that include the tropics remain a formidable challenge, because a large proportion of ant species remain undescribed. However, genera are relatively well described, even in areas such as the tropics where study is difficult and diversity high. Although new genera remain to be found (see, for example the recent discovery of a new ant subfamily and genus, Rabeling et al. 2008), the discovery of a new ant genus is now relatively rare. Furthermore, new genera are likely to be geographically rare and consequently have little influence on overall diversity patterns. Therefore, if ant species diversity is correlated in space with generic diversity, as is the case for many other taxa (e.g. trees; Enquist et al. 2002), we may be able to use generic diversity as a proxy for species diversity in examining truly global patterns of regional diversity and endemicity. See Box 3.2 for a description of ant databases that may facilitate such analyses.

A strong correlation between generic and species diversity bodes well for using patterns of generic diversity as a proxy for patterns of species diversity. In the Great Smoky Mountains in the eastern United States, genus and species diversities were highly correlated ($R^2 = 0.89$, Ordinary Least Squares Regression) (data re-analyzed from Sanders et al. 2007b). A similarly strong relationship exists between species diversity and generic diversity in well-studied political regions in North America (exclusive of México) and Europe (Guénard et al., unpublished data; see Figure 3.1). Even if species diversity and generic diversity are not always well-correlated (as is likely to be the case in Australia, where generic diversity is highest in the tropics, but species diversity appears highest in drier regions; Shattuck 1999), the genus may represent an interesting taxonomic level to explore in its own right.

One of us (B. Guénard) has compiled distribution data on ant genera for the better-studied countries and political regions of the world (described in more detail in Figure 3.1). This work enables an exploration of whether patterns of diversity differ for ants

![Figure 3.1](image.png)
Most of what is known about global patterns of diversity is based on birds, plants, and to a lesser extent, reptiles and butterflies. However, it is little appreciated that ants were among the first taxa to be examined through a macroecological lens. Wheeler (1910) wrote: 'The great importance of ants in the study of geographical distribution has not been overlooked by students of this fascinating subject', and Gregg (1963) discussed the 'macroecology' of Colorado ants. Despite this head-start in macroecological studies, quantitative studies of global patterns of ant diversity are still in their infancy. Kusnezov (1957), Jeanne (1979), Kaspari et al. (2000b), and Ward (2000) were pioneers in the study of global ant diversity. With the exception of Kusnezov, each relied on his own field collected data. However, ecologists working on other taxa often take advantage of massive databases that are, for the most part, freely available online. Could ant ecologists do the same? The answer seems to be yes, as a number of exciting databases provide freely available data on the distribution and diversity of ants.

The Global Ant Community Database that Dunn and colleagues have compiled will no doubt be useful (see Chapter 3). It is a growing database that includes information on ant biodiversity from over 3,000 ant assemblages around the globe (Figure 3.2.1; www.antmacroecology.org). In addition, the database also includes whether the assemblage has been invaded by exotic ants, whether it has been disturbed (either naturally or otherwise), and the type of habitat the assemblage is situated in. It is possible the Global Ant Community Database of Dunn and colleagues is the largest of its kind, for any taxon.

The Global Biodiversity Information Facility (GBIF) (www.gbif.org) is intended to be a georeferenced database for the diversity of all life on the planet. There are at least 187,401 records of ants (locations at which a species has been collected) for species in >280 genera. To my knowledge, only one study on ants (Geraghty et al. 2007) has used information from GBIF. Though the distribution of the data is spatially and taxonomically patchy, it is possible to estimate the northern and southern latitudinal extent of species ranges, especially in well-sampled areas, as was done by Geraghty et al. (2007) in their study on the relationships among body size, colony size, and range size in ants of eastern North America.

The web site AntWeb (www.AntWeb.org) ‘provides tools for exploring the diversity and identification of ants’ with the ultimate aim of describing and providing a high resolution

continues
relative to other taxa, and also whether patterns of ant diversity along these large gradients differ among taxa. Ant generic diversity decreases in diversity with latitude (see Figure 3.2), just as does species diversity in local plots. Generic diversity is highest in the broad latitudinal band of the tropics in the Americas, in Africa and Europe, and in Australasia and is higher in the southern than the northern hemisphere for comparable latitudes. There is a dip in diversity in North Africa commensurate with what might be

Box 3.2 continued

Very recently, www.plazi.org has been launched as follow-up of antbase.org. It allows for searching full text for published ant descriptions. Furthermore, distribution data from original publications now directly feed into GBIF, and thus can be harvested for global biodiversity studies.

At more regional scales, Klingenberg and Verhaagh (2005) provide a valuable compilation of a growing number of web sites covering mainly regional-scale fauna studies and species lists. With more databases on the horizon, they finally quantify what Wheeler (1910) and Gregg (1963) knew so long ago — ants are an ideal taxon with which to document and understand global patterns of biodiversity and macroecological processes.

Figure 3.2 Generic diversity of ants in each political region in the Americas, Asia + Australia, and Africa plotted against latitude. Lines show best-fit polynomials.
expected, given the extreme climatic conditions for that region (see Figure 3.2). The overall patterns are nearly identical when differences in area are corrected for by plotting the residuals of the area × genus diversity regression against latitude instead of raw genus diversity (see Figure 3.2). The decline in diversity with latitude appears asymmetrical, as has been shown for some other taxa (reviewed in Chown et al. 2004) and as was also recently shown for local ant diversity (Dunn et al. 2009), where diversity is lower in the northern than in the southern hemisphere.

When generic diversity is regressed on mean annual temperature, most of the global variation in generic diversity is accounted for (see Figure 3.3). While the relationship between temperature and diversity is very similar for the Americas and Asia, high-temperature sites are less diverse in Africa than in other regions (see Figure 3.3). In part, this might be due to the relative dryness of Africa. However, it appears even tropical countries with tropical forest in Africa are less diverse than their counterparts in Asia or the Americas. Diversity is also lower in Africa relative to the Americas and Asia in amphibians (Buckley and Jetz 2007), and birds (C. Rahbek, personal communication), but not for plants (Kreft and Jetz 2007), even after accounting for differences in climate.

Plotting the most diverse higher groups of ants separately (Myrmicinae, Formicinae, and Poneroids) shows that these groups differ both in their absolute diversity (as would be expected) and also in their patterns of diversity relative to temperature. The subfamily Myrmicinae contains the highest number of genera, and drives the overall pattern of generic diversity (as it probably does in most studies of ant species diversity along gradients). The Poneroids, in which most species forage at higher trophic levels (see Figure 3.4) show more peaked patterns of diversity with latitude and represent a much higher proportion of generic diversity at higher temperatures. The most generalist ant groups considered (Formicininae in Figure 3.4, and Dolichoderinae, not shown) show weak and more inconsistent relationships between diversity and temperature. Regardless of the cause of the differences among taxa, it is clear that although temperature seems to be consistently important, its effect is not identical among taxa. From the perspective of naturalists, this is perhaps an obvious result, but from the perspective of theory, this difference follows from several, but not all hypotheses, meant to explain global patterns of diversity. Under metabolic theory, for example, the effects of temperature on kinetics and ultimately speciation are not expected to differ among ectothermic taxa or trophic levels.
3.5 Patterns of range size

Ultimately, one would hope to be able to predict not just patterns of species diversity, but also patterns of endemicity and range size. With respect to conservation, it is often not species diversity per se we care about, but rather the diversity of rare, evolutionarily unique, or regionally restricted species (see Chapter 4).

To date, studies of range size and endemicity patterns in ants have focused on analyses of Rapoport’s rule. Rapoport’s rule asserts that range size decreases with elevation (Stevens 1992) and latitude (Stevens 1989). Because conditions at high latitudes and/or elevations are more seasonal than those at lower latitudes and/or elevations, Stevens (1989) predicted that species at high latitudes and/or elevations would have large ranges as a consequence of their necessarily broader environmental tolerances. Support for the rule as an explanation for such patterns is mixed at best (Colwell and Hurtt 1994; Gaston et al. 1998; Rohde 1996; Taylor and Gaines 1999).

Two studies of ants have considered patterns in geographic range size among species and both have been limited to parts of North America. In both the Great Smoky Mountains National Park (Geraghty et al. 2007), and in Colorado, Nevada, and Utah, ant species at lower elevations tended to have smaller ranges than those species at higher elevations (species with larger ranges also have higher elevational range midpoints; Sanders 2002) in accordance with Rapoport’s rule predictions. Neither study explicitly considered whether Rapoport’s rule would explain patterns of diversity, and too few studies have examined the causes of
variation in the range sizes of ant species for us to say whether the results are general. In the Great Smoky Mountains study (Geraghty et al. 2007), the size and position of elevational and latitudinal ranges were correlated (e.g. species with big elevational ranges had big latitudinal ranges). While the idea that latitudinal and elevational ranges should be correlated makes intuitive sense, it has seldom been tested.

An alternative approach to considering patterns of range size and rarity is to explicitly model the correlates of diversity of small-ranged or rare species. For other taxa, such as birds (Jetz and Rahbek 2001) the correlates of diversity for narrow- and wide-ranging species are very different. Because widespread species drive large-scale patterns of diversity, simply considering total diversity can mask patterns of rare and/or small-ranged species diversity, unless the two are considered separately. Any of a variety of processes might lead to differences in the diversity patterns of wide- and narrow-ranged species. Recent work (Dynesius and Jansson 2000; Jansson and Dynesius 2002) suggests climatic history, for example, may have a much stronger impact on the distribution of rare species than it does on overall patterns of diversity. We know of only a handful of studies of patterns of diversity in rare ant or small-ranged species. Diversity of rare ant species in Great Smoky Mountains National Park in the eastern United States was concentrated in the warmest sites, just as for species diversity overall (Lessard et al. 2007). Similarly, along an elevational gradient in Costa Rica, nearly all small-ranged ant species were found at low elevations (Colwell et al. 2008). In the Philippines, only 2 of the 77 species encountered were found at either of the two high elevations sampled (1,550 m and 1,750 m) and only one of those species was restricted to those elevations (Samson et al. 1997). In Madagascar, a high proportion of the species found at the highest elevation sites (1,800–2,000 m) was found only at those sites (50% compared to 24% at the lowest elevation site), but the absolute number of species restricted to the highest elevation was still small (10 species of 273 total; Fisher 1996). In general, rare and narrow-ranged ant species seem much more likely to be at low than at high elevations.

These patterns may not hold, however, for other regions and deserve better testing.

One final approach to considering Rapoport’s rule, or more generally, patterns in species distributions, would be to directly compare the niches, and in particular one aspect of the niche, the climatic tolerance of species with latitude or elevation. The idea that niche sizes might be smaller in the tropics pre-dates Rapoport’s rule by many years (Klopf er and MacArthur 1961) but remains untested. Are, for example, species in tropical forests constrained to live in a narrower range of temperatures than are species in temperate forests? For the moment, this question remains unresolved in general, not just with regard to ants.

3.6 Patterns of life history and morphology

There is a long history of the study not only of variation along gradients in diversity but also in traits and their distribution. To date, the limited work on variation in ant life history has focused on colony and body size, but we also consider here other traits, such as the prevalence of social parasitism, that might vary along gradients.

One of the best-explored patterns in a life-history trait along gradients is Bergmann’s rule (James 1970), which stems from the observation that body size tends to increase with latitude, and by analogy, elevation. Bergmann’s rule was first applied to variation in body size among species along gradients, but has also been considered within species. Just as for the latitudinal diversity gradient, in practice Bergmann’s rule refers primarily to the pattern of body size along gradients (larger body size at higher latitudes and elevations), rather than to a particular mechanism underlying that pattern. The first question we consider is whether ants show the pattern referred to as Bergmann’s rule. Unlike for solitary animals, for ants and other social insects, body size can vary along gradients either as a function of the body size of individual (e.g. a worker ant) or as a function of the ‘body size’ of colonies, where colonies are considered to be the scale at which investment decisions are made.
3.6.1 Colony size

Analyses of relationships between colony size and latitude reveal mixed results. In the Americas, ground-dwelling tropical ant species have smaller colonies than do temperate ant species (Kaspari and Vargo 1994). Kaspari and Vargo (1994) argue that larger colony size in colder environments facilitates overwintering ability because larger colonies are thought to have a greater ability to withstand attrition due to winter mortality. However, their results are reconcilable with alternative explanations. Perhaps, for example, ant species in the tropics are more likely than temperate ant species to occupy the litter, and for any of a variety of reasons, leaf-litter lifestyle necessitates smaller colonies. Large colonies are at least not a requirement of cold climates since among those species that inhabit the coldest realms (Francoeur 1997), colonies often include no more than tens of individuals. If larger colonies are advantageous as buffers to winter mortality or are in any other way more advantageous at higher latitudes and elevations, then one would expect species found in colder climates would have larger colonies, but also that within species, populations from colder climates would have larger colonies. However, there is no relationship between latitude and colony size in the holarctic ant, *Leptothorax acervorum* (Heinze et al. 2003), and work on a different *Leptothorax* species has shown no relationship between winter mortality and colony size (Herbers and Johnson 2007).

With results limited to one study, the relationship between elevation and colony size remains ambiguous. Geraghty *et al.* (2007) found no correlation between colony size and elevation among ant species in the Great Smoky Mountains National Park. A strong effect of elevation on colony size might not be expected within temperate regions, if the primary driver of the latitudinal colony size gradient is variation in the proportion of species living in the litter. An alternative explanation for the discrepancy between elevational and latitudinal studies has to do with differences in species turnover. In the Great Smoky Mountains, for example, the pattern of species distribution and diversity with elevation is nested (Lessard *et al.* 2007) such that the species found at high elevation are, for the most part, a cold-tolerant subset of those at low elevations. In contrast, as one goes north, even from the Great Smoky Mountains, one encounters a new set of species. Diversity is not typically nested with latitude. Thus, while the northern latitude endemic species may adapt to local conditions, the species found at high elevations in the Great Smoky Mountains are also found at low elevations and so likely have selection for one colony size at high elevations and another colony size at low elevations. Whether these distinctions generalize to other regions is an open and interesting question.

3.6.2 Body size

In addition to variation in colony size, the size of individual ants might also be expected to decrease with increasing temperature along the climatic gradients for which elevation and latitude are proxies. Just as colony survival may depend on the adaptiveness of a particular nest size for a particular climate, survival of individual ants may also vary with climate as a function of body size, with consequence for spatial patterns in body size along gradients. Results for body size, like for colony size, suggest ant species tend to be larger at higher latitudes in the northern hemisphere (Cushman *et al.* 1993). This pattern is mirrored by variation in individual body size within species. For example, colonies of *Leptothorax acervorum* at higher latitudes had larger individuals than those at lower latitudes (Heinze *et al.* 1998). Just as for colony size, a variety of mechanisms related to phylogenetic history, migration ability, and starvation resistance might explain this pattern. An interesting next step would be to conduct laboratory studies on the relationship between body size and survivorship for a large number of species.

3.6.3 Other ant-related life-history patterns

Reproductive strategies can vary with latitude and elevation. Such variation is perhaps best characterized for marine invertebrates (Rohde 1999), and birds (Lack 1947; McNamara *et al.* 2008) in which both species and individuals at higher latitudes produce fewer offspring than those at lower
latitudes (McNamara et al. 2008; Rohde 1999). For birds, it has been suggested that smaller clutch sizes (with more investment in each offspring) result from the greater seasonality (and hence urgency for rapid development) in high latitudes. We know of no work comparing egg production by queen ants along gradients, but the study of reproductive investment along gradients in general would be an interesting area of inquiry.

However, apparent empirical spatial patterns in rates of social parasitism (any of a variety of systems whereby individuals of one ant species take advantage of colonies of another ant species during some part of their life cycle) have long attracted attention. Most of the more than 300 social parasite species (Buschinger 1990, 1991) known today are found under temperate climates and at high elevations. Many of these social parasites, especially among inquilines, have been described from extreme environments such as mountainous or arid regions. This observation has led to the idea that low temperatures found in higher altitude or latitude could favour the emergence of social parasitism, perhaps because just as has been suggested for benthic invertebrates (Rohde 1999), mortality associated with independent colony foundation is greater at those latitudes. Some have argued that social parasitism may be far more common in the tropics than is now appreciated (Feitosa and Brandão 2008; Wilson 1984), but the overall pattern in social parasitism seems unlikely to change.

As latitude increases, plants flower later, are reproducitively active for a shorter period of time, and are older at the time of first reproduction (Olsson and Agren 2002). Similar patterns in reproduction might be expected for ants along elevational or latitudinal gradients. There is some suggestion that in tropical forests reproductive flights of ants are more continuous than they are in temperate forest ecosystems (Dunn et al. 2007b; Kaspari et al. 2001a,b). Further, within temperate regions, reproductive flights are more continuous at lower elevations than at higher elevations (Dunn et al. 2007b). These two patterns suggest that there may be general patterns in reproduction along environmental gradients, but we have barely begun to explore. A study comparing reproductive strategies of a suite of ant species along an elevational or latitudinal gradient would contribute greatly not just to our understanding of ants, but also to the responses of species to gradients more generally.

### 3.7 Consequences of gradients in ant communities

It has been suggested that rates and types of interactions might differ with elevational and latitudinal gradients. Biotic interactions have been speculated to be more important in low latitudes and abiotic drivers more important in high latitudes. In the broader literature, support for such gradients is strong in the few cases where they have been examined (reviewed in Rohde 1999). Perhaps the strongest evidence for gradients in biotic interactions in terrestrial organisms comes from ants, where predation rates and interactions with some mutualists appear to vary along gradients. Predation rates in forests, particularly in the forest canopy (Jeanne 1979) decrease with latitude (Jeanne 1979; Novotny et al. 2006), possibly due to concomitant decreases in ant diversity with latitude. Figure 3.5 suggests such a relationship for ground-foraging ants in forests.

Seed dispersal of myrmecochorous plants also changes along environmental gradients across which ant communities vary (Gove et al. 2007; Zelikova et al. 2008). Finally, the decline in the

![Figure 3.5 Days to discovery of baits (larval wasps) by ants from samples along a latitudinal gradient. Figure derived from data in Jeanne (1979). Each point represents a site where baits were observed.](image-url)
proportion of treehopper species dependent on ants with elevation is thought to be due to the decline in the diversity and abundance of ants with elevation (Olmstead and Wood 1990). Other ant mutualists might be expected to show similar patterns.

3.8 Climate change and gradients of diversity

What can theory and empirical patterns tell us about the potential for change in patterns with climate change? Given that ant communities and species are influenced strongly by climate, and in particular temperature, ants may be particularly predisposed to respond directly to the temperature changes associated with climate change. However, to date, studies that focus on the relationship between climate change and ant communities are scarce and restricted almost exclusively to the future distributions of invasive species (Levia and Frost 2004; Morrison et al. 2005; Chapter 13). No studies have yet examined whether historical shifts have occurred in ant distributions with climate change (see reviews for other taxa in Hughes 2000; Parmesan and Yohe 2003), though the long history of ant collecting in many of the regions that have experienced the greatest climate change makes ants a good candidate for such work. However, our knowledge about the patterns in ant communities along gradients allows us to make strong a priori predictions as to what might be expected in ant communities as climate changes. For example, to the extent that ant diversity, abundance, and ecological roles all increase with temperature, in many regions increases in temperature with climate change seem likely to increase the local diversity, abundance, and relative importance of ants.

That the abundance of some ants will increase in a warmer world seems very likely. Less clear is which ant species and lineages will become more abundant and widespread. For example, in regions like southwestern Australia and South Africa, which currently have relatively wet and cool winters but are surrounded by larger more arid habitats, the regional species pool may account for many of the ‘new’ colonists under warmer conditions. Conversely, for other regions, particularly islands and mainland habitats in which there are no adjacent species pools corresponding to future climatic conditions, source pools are less clear and may be dominated by invasive and introduced species (Colwell et al. 2008). The tip of Florida, in the United States, is a small patch of very isolated subtropical habitat, in which reside no fewer than 50 introduced ant species (e.g. Deyrup 2003). With climate change, subtropical conditions are predicted to expand through the south-eastern United States and the introduced species at the tip of Florida may spread. If invasive species are able to colonize new, warmer habitats faster than migrating native species they may preempt the arrival of natives or, at the very least, reduce their ability to track shifting climates. Thus, although our most general prediction is that higher temperatures will increase ant abundance, diversity, and impacts, locally there are regions where such changes will be pre-empted or altered by invasive species.

Nailing down which species will be negatively affected by to climate change is difficult. Studies of vertebrates suggest that endemic species found mostly in cool climates (at high elevations and latitudes) are likely to be most affected by climatic warming (McDonald and Brown 1992). However, for ants, at least in temperate systems, there are few high-elevation endemic species (see the earlier discussion; Lessard et al. 2007). Even in tropical systems, a smaller percentage of ants than other taxa seem confined to high elevations (comparisons in Colwell et al. 2008; Samson et al. 1997). If the elevational gradients studied to date are indicative, ant populations may be less at risk of extinction at high elevations than is the case for other taxa. Detailed studies of not just the diversity of ants along elevational and latitudinal gradients, but also the patterns of range size would help to understand the relative risk of high-elevation ants. Low-elevation tropical species also may be at risk due to climate change because as tropical habitats warm, such species will find themselves in much smaller areas of habitable forest (mid-elevations occupy a smaller area than do low elevations, in general, since area declines with elevation) (Colwell et al. 2008). Key to this prediction is the idea that tropical species, at least on average, are poorly able to tolerate conditions warmer than those they currently
inhabit. Physiological tests suggest that tropical insects do tend to have narrower thermal tolerances than do temperate species (Deutsch et al. 2008), though this pattern deserves much better exploration.

As species distributions shift with climate change, trait groups should also shift. If high-latitude and high-elevation species tend to have large bodies and large colonies, the first species to be affected by climate change can be predicted to have the same traits (see Bergmann’s rule in Section 3.6). Similarly social parasites, because of their cool-climate bias and relative rarity may also be at disproportionate risk. The ecological consequences of ants in communities may also shift. At high elevations and latitudes, expansion of ant populations and communities may dramatically affect predation and other processes mediated by ants, in general accelerating them. At low elevations, the effect might be more idiosyncratic.

Ultimately, understanding the effects of climate change on ants will be an important test for our understanding of the relationship between ants and environmental gradients more generally. The consequences of gradients in environmental conditions have long been interesting to ecologists in general and ant ecologists in particular. The practical value of such understanding has, however, been limited. Climate change represents an opportunity in which macroecological relationships can prove useful to conservation and application. It may be that in testing the utility of our current understanding of gradients and ants, we also come a great deal further in understanding the robustness of that understanding.

3.9 Future directions

In traditional models of science, progress ultimately relies on rejecting hypotheses, and the hypothesis with the most support might be arrived at through winnowing of possibilities. To date, few or perhaps no serious explanations for gradients in diversity or other attributes of ecological communities have been completely rejected. The reasons for these difficulties are straightforward. Most studies of patterns in community composition have been correlative. Most of the existing explanations for patterns of diversity, for example, make similar predictions with regard to spatial patterns of diversity – that diversity should be high or highest in the tropics, or that diversity should be positively correlated with temperature. As such, rejecting hypotheses may depend on testing secondary predictions of the hypotheses. Unfortunately, for all but a few of the hypotheses, secondary predictions are poorly resolved or variable. For example, one version of the temperature-dependent kinetics hypothesis predicts a precise slope for the relationship between species richness and temperature (Brown et al. 2004). The universality of that slope has been rejected (Hawkins et al. 2007; Sanders et al. 2007b), but there remain other versions of the temperature-dependent kinetics hypothesis that do not assume a universal slope. So even when secondary predictions can be clearly rejected, hypotheses do not disappear, they just change.

We propose that there are three key approaches to better understanding not just the patterns, but the causes to gradients in animal communities, whether for ants or any other taxon. First, we need a better understanding of how patterns of composition of communities have changed through time and how patterns of diversification and, separately, speciation and extinction, vary in space. Well-sampled, dated phylogenies will help both of these endeavours, particularly if they can be coupled with analyses of changes in the ant fossil record. A second important approach will be to simulate patterns of diversification and the diversification of traits under the assumptions made by different hypotheses (Rangel et al. 2007). Such models help to understand what patterns of diversity and community structure are conceivable given different hypotheses and may make clear that some hypotheses are unable to produce observed patterns of diversity given realistic parameters. In addition, the process of simulating diversification helps to make obvious which hypotheses do and, in the far more common scenario, do not, make explicit predictions about extinction rates, speciation rates, and rates of dispersal. Finally, we suggest that, under some circumstances, experimental manipulations of potential driving variables might help elucidate the underlying causes of some diversity gradients.
3.10 Summary

Generally, ant diversity tends to decline with latitude and elevation. To date, results for latitudinal studies, elevational studies, and an ongoing global study of genera can be reconciled with the notion that temperature limits resource availability, access to resources, and ultimately, diversity of ants. However, critical mechanistic links remain missing, including tests of the relationship between abundance and extinction. In addition, energy variables might also have direct effects on speciation and hence regional species pools, but this possibility remains untested. Because the recent continental-scale studies of ant species diversity have focused on relatively small sampling grains (with the exception of the generic analysis herein), the importance of area as a determinant of large-scale diversity patterns also remains poorly tested. Work on elevational gradients suggests area may indeed have strong direct (Sanders 2002) and indirect (Romdall and Grytnes 2007) effects on ant diversity (though the effect on generic diversity at big spatial grains is minimal). In general, and perhaps more so than other taxa, we find ant diversity patterns deviate from the expectations of geometric constraints models due to aspects of climate associated with energy. Additionally, broad-scale patterns in body size and colony size, and their underlying causes, are in need of more attention.

Understanding the causes of those patterns is more difficult whether for ants or for other taxa. Phylogenetic work and experiments may help us to better understand causal mechanisms. In the meantime, observed patterns in ant communities allow us to make clear predictions regarding the consequences of climate change for ants. In many areas, ants are likely to form a larger part of the overall fauna in terms of biomass. Native ant species may also become more locally diverse, though this may be pre-empted by invasive species. Ants appear likely (because of their thermophilic bias in distribution) to be less negatively influenced by climate change than other taxa.

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