

# Temporal patterns of diversity: assessing the biotic and abiotic controls on ant assemblages

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In this study, we use 12 months of data from 11 ant assemblages to test whether seasonal variation in ant diversity is governed by either the structuring influences of interspecific competition or environmental conditions. Because the importance of competition might vary along environmental gradients, we also test whether the signature of competition depends on elevation. We find little evidence that competition structures the seasonal patterns of activity in the ant assemblages considered, but find support for the effects of temperature on seasonal patterns of diversity, especially at low-elevation sites. Although, in general, both competition and the environment interact to structure ant assemblages, our results suggest that environmental conditions are the primary force structuring the seasonal activity of the ant assemblages studied here. © 2007 The Linnean Society of London, *Biological Journal of the Linnean Society*, 2007, 91, 191–201.

**ADDITIONAL KEYWORDS:** ant diversity – competition – Great Smoky Mountains National Park – mid-domain effect null models – phenology – southern Appalachians.

## INTRODUCTION

Spatial diversity gradients arise from the overlap of the geographical ranges of species (Arita & Rodriguez, 2002). Similarly, temporal diversity gradients arise from the overlap of phenological ranges of species. Although ecologists have focused on the causes of spatial diversity gradients (Kaspari, O'Donnell & Kercher, 2000; Jetz & Rahbek, 2001, 2002), temporal diversity gradients and their causes have received little attention (Morales, Dodge & Inouye, 2005). To understand the mechanisms shaping patterns of temporal diversity, it is first necessary to understand the factors that govern the phenological ranges of species.

The null expectation for patterns of species distribution over time is that the phenological ranges of species (the period from their first to last occurrence during the year) are random with respect to one another (Pleasants, 1990). If phenological ranges

evolve independently of both one another and environmental conditions, diversity can be expected to peak in the middle of the activity season, as a consequence of the random overlap of ranges (Pleasants, 1990; Colwell & Hurtt, 1994). Alternatively, distributions of different species in time might not be independent of one another. Such a nonrandom pattern might result from interspecific interactions among species. For example, the theoretical framework for interspecific competition predicts that phenological ranges of competing species should overlap less than expected by chance (Kronfeld-Schor & Dayan, 2003; Pleasants, 1990), so as to reduce the effects of competition. Alternatively, phenological ranges of species might overlap more than expected by chance during times of favourable conditions if different species track similar environmental conditions, despite the potential costs of competition. If phenological ranges evolve non-independently due to competition or shared environmental preference, patterns of diversity will differ from the null expectation as a consequence of those nonrandom patterns of overlap.

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Our objective in the present study is to examine the determinants of phenological range overlap and consequent patterns of diversity in ant assemblages, and the consequent temporal patterns of ant diversity. Specifically, we ask three questions: (1) do patterns of species diversity over time differ from null model expectations; (2) do patterns of phenological range overlap differ from null model expectations and are those differences (for both questions 1 and 2) more consistent with competition or environmental drivers; and (3) do the relative influence of environmental constraints and competition on phenological patterns vary with elevation?

Seasonal patterns of activity are well studied in ants (Schumacher & Whitford, 1976; Lynch, Balinsky & Vail, 1980; Whitford *et al.*, 1981; Fellers, 1989; Suarez, Bolger & Case, 1998; Albrecht & Gotelli, 2001; Sanders, Barton & Gordon, 2001), although few studies have examined patterns for entire communities for an entire year (Fellers, 1989; Albrecht & Gotelli, 2001). Just as for other taxa, seasonal patterns of ant activity are typically attributed to either species-specific environmental preferences for specific windows of temperature (Lynch *et al.*, 1980; Albrecht & Gotelli, 2001), humidity (Levings, 1981; Kaspari, 1993; Kaspari & Weiser, 2000), or available resources (Bernstein, 1979), or to competition (Davidson, 1977; Human & Gordon, 1996). A growing number of studies employ null model analyses to examine whether patterns of co-occurrence, body size, diversity, and other features of ant assemblages differ from the patterns expected at random (Simberloff, 1983; Albrecht & Gotelli, 2001; Gotelli & Ellison, 2002; Gotelli & McCabe, 2002; Sanders *et al.*, 2003) after several decades of use in the study of the communities of other groups of organisms (Gotelli & Graves, 1996; Weiher & Keddy, 1999). No studies, however, have compared

seasonal patterns of ant activity (when species are active with respect to one and other) to a temporal null model.

In the present study, we examine the seasonal patterns of ant diversity in 11 ant assemblages over 12 months in the southern Appalachian Mountains, USA. By comparing the results obtained from assemblages that span an extreme environmental gradient in the southern Appalachians, we also examine whether the signature of competition on seasonal patterns of diversity and co-occurrence is more apparent at lower elevations than at the higher elevations where environmental conditions are more severe. A key prediction of early work by Fischer (1960) is that assemblages occurring at either high latitudes and elevation are more likely to be structured by abiotic constraints, and assemblages occurring at low latitude or elevations are more likely to be structured by biotic interactions, such as predation and competition. This hypothesis has not been extensively tested, although the evidence for a latitudinal gradient in one biological interaction, predation by ants is growing (Jeanne, 1979; Kaspari & O'Donnell, 2003). We explicitly test whether high-elevation sites are less likely than low-elevation sites to show the structuring effects of competition on patterns of overlap in species phenological ranges and diversity.

## MATERIAL AND METHODS

### STUDY SITES AND ANT SAMPLING

Ants were sampled at eight forested and three open (e.g. grassland and high-elevation shrublands – henceforth ‘balds’ *sensu* Whittaker, 1962) sites (Table 1) within the Great Smoky Mountains National Park (GSMNP) in eastern Tennessee and western North Carolina, USA, as part of an All Taxa Biodiversity

**Table 1.** Description of the 11 field sites

Site	Elevation (m)	Vegetation type	Temperature	
			January, minimum (°C)	July, maximum (°C)
Cades Cove	521	Old Field	−5.8	27.8
Twin Creeks	594	Poplar–Hemlock	−6.3	23.4
Goshen Prong	896	Cove Hardwood	−8.5	17.7
Snakeden Ridge	993	Hemlock	−8.7	23.1
Albright Grove	1033	Montane Cove	−9.3	21.8
Cataloochee	1380	Mesic Oak	−10.8	21.0
Brushy Mountain	1443	Heath Bald	−12.1	16.2
Purchase Knob	1530	Northern Hardwood	−11.4	20.7
Indian Gap	1673	Beech Gap	−12.9	18.7
Andrew's Bald	1728	Grassy Bald	−12.6	15.7
Clingman's Dome	1944	Spruce–Fir	−15.8	17.6

Inventory (<http://www.dlia.org/atbi/>). The GSMNP elevation is in the range 256–2025 m. We sampled across 79% of the gradient in elevation within the park and included the highest forested area within the park. At each site, ten pitfall traps were placed 3 m apart along an approximately 30-m transect running parallel to the elevational gradient. Traps were 6-cm diameter plastic cups buried flush with the soil surface and partially filled with propylene glycol. The traps were collected every 2 weeks from January 2001 until January 2002 for a total of approximately 40 150 trap days (ten traps per site  $\times$  11 sites  $\times$  365 days). Pitfall traps effectively capture ground-foraging ants (Bestelmeyer *et al.*, 2000), whereas they do not capture the exclusively litter-dwelling species unlikely to directly compete with the group of ants we are interested in. Our within-site sampling effort is similar to, and in many cases greater than, that used in other studies of ant assemblages (Porter & Savignano, 1990; Human & Gordon, 1996; Andersen, 1997; Suarez *et al.*, 1998; Gibb, 2003; Lassau & Hochuli, 2004). For the purposes of the current study, pitfall trap results are combined within each elevational site (except when estimating the total number of species at each site).

Voucher specimens are deposited in the authors' collections at the University of Tennessee, North Carolina State University, and in the collection at GSMNP. A single HOBO datalogger was installed at each site and monitored for the entire year to measure temperature at each site over time.

#### ESTIMATING DIVERSITY

We estimated ant diversity in several ways. Estimated diversity and species accumulation curves were used only to compare patterns in diversity among sites and to judge the completeness of sampling. To estimate diversity for these comparisons, we used the program EstimateS (Colwell, 2005) to estimate the total number of species at each site based on Chao2. As a separate measure of the completeness of our sampling, we compared the number of species collected at each site with the number collected including both the results from the present study and results from an additional 2 years of sampling at the same sites (e.g. approximately 80 000 additional pitfall trap days). The additional sampling yielded no additional species at Cades Cove, Brushy Mountain, Clingman's Dome, Albright Grove, or Indian Gap; only one species at Andrew's Bald and Snakeden Ridge; two more species at Twin Creeks and Cataloochee; and three more species at Goshen Prong. At Purchase Knob, five additional species were added with further sampling. The correlation between the diversity sampled after 1 year (data used in this study) and that sampled after 3 years was strong ( $r^2 = 0.99$ ) and positive. As a final check on sam-

pling completeness, we examined the relationship between the maximum number of individuals sampled of a species in a given month and the number of months that the species was active. At no site were these two variables well correlated ( $P > 0.1$  in all cases). We are confident that our sampling at each site represents an unbiased view of the epigeic ant assemblage over time.

As a measure of diversity within sites at a single time period, we used the number of species phenological ranges that overlapped on a given day or sampling period as an estimate of the diversity of species active during that sampling period. We assumed that a species was active during a focal time period if it was active in any time period before or after that time period. Although this method of interpolation obscures interesting variation within ranges (Dunn, Colwell & Nilsson, 2006), it has the advantage of partly correcting for weeks in which ants were not collected due to sampling effects.

#### DO PATTERNS OF SPECIES DIVERSITY OVER TIME DIFFER FROM NULL MODEL EXPECTATIONS AND ARE THOSE DIFFERENCES MORE RECONCILABLE WITH COMPETITION OR ENVIRONMENTAL CONSTRAINTS?

For the analyses of seasonal patterns of diversity, we defined the beginning of the activity season at each elevation as the first 2-week period during the year in which ants were collected in the traps, and the end of the season as the last 2-week period in which ants were collected (Pleasants, 1990; Morales *et al.*, 2005). Each species at each elevation therefore had a phenological range and a phenological midpoint (the date half-way between the first and last activity dates). We generated null models of species diversity at each elevation by randomizing the midpoints of the empirical phenological ranges with replacement using RangeModel (Colwell, 2000). We used a one-dimensional adaptation of the 'spreading dye' model of Jetz & Rahbek (2001, 2002) akin to model 3 of Ashton, Givinish & Appanah (1988). In this algorithm, empirical phenological ranges are selected at random, one at a time, without replacement, then placed at random on the domain by choosing a midpoint from the uniform random distribution spanning the domain. If the range then lies fully within the domain, it is kept in that position and the algorithm repeats. If a range extends beyond the domain limit, its initial random midpoint is simply shifted into the domain, the minimum distance necessary, so that its endpoint coincides with the domain limit. We compared the empirical patterns of diversity with the simulated patterns of diversity (based on 50 000 simulations) and temperature by using stepwise linear regression with the probability for a predictor variable to enter set at 0.15 and probability to

exclude set at 0.10. Temperature was measured for each site  $\times$  sampling period combination as the mean temperature during each 2-week sampling period.

DO PATTERNS IN PHENOLOGICAL RANGES OVER TIME DIFFER FROM NULL MODEL EXPECTATIONS AND ARE THOSE DIFFERENCES MORE RECONCILABLE WITH COMPETITION OR ENVIRONMENTAL CONSTRAINTS?

To test whether environmental tolerances of species and consequent phenological ranges have evolved in such a way as to minimize temporal overlap and competition, we compared the mean overlap in phenological ranges of species in the empirical dataset at each elevation with those generated in the simulations for the models discussed in the section 'seasonal patterns of diversity' above (i.e. similar to related tests; Inger & Colwell, 1977; Pleasants, 1990). Whereas Pleasants (1990) uses an index of overlap that weights the overlap of species ranges by their relative abundance at different points along their range, we compare just the linear number of days that the ranges of species overlap one another, as in Ashton *et al.* (1988). For the simulated datasets, we used the results of 500 simulations of the spreading dye model for each elevation. If the mean empirical overlap fell within the 5% most extreme of the values for the simulated communities, the difference between the simulated and empirical communities was considered to be significantly different from random. If the empirical overlap was greater than the simulated overlap, it was considered to be evidence of the effects of environmental drivers. If the empirical overlap was less than the simulated overlap, it was considered to be evidence of the effects of competition.

In the first two sets of analyses, the null models we used are null for the evolutionary patterns in the seasonal ranges of species. Both of the evolutionary models address whether the phenological ranges of species overlap more or less than would be expected were those ranges to evolve by chance relative to one and other. Even if the phenological ranges of ants do not deviate from the expectations of null evolutionary models, ants may respond to competitors or the environment in ecological time by moderating their activity patterns within those days on which they can be active (Sanders & Gordon, 2000). If ants responded to competition by moderating their activity patterns, species activity patterns in a given assemblage would be more staggered than expected by chance, even when phenological ranges are held constant (Albrecht & Gotelli, 2001). For example, even though *Aphaenogaster rudis* might be active the entire season, its activity levels might be reduced in the portion of the season during which *Formica subsericea* is particularly abundant. We test for such nonrandom activity

patterns by holding the period over which each species is active constant, but randomizing the number of captures among those days, and comparing the patterns of overlap of the simulated communities with the empirical communities. This randomization is identical to RA4 randomizations in Gotelli & Graves (1996).

For all RA4 analyses we compared simulated communities with empirical communities based on the mean Czechanowski index for each site. As used here, the Czechanowski index (Feinsinger, Spears & Poole, 1981) is a measure of the overlap in activity between pairs of species. Interspecific competition should cause overlap to be less than expected by chance (and hence the Czechanowski index to be lower than expected) and variance in overlap to be greater than expected by chance (Inger & Colwell, 1977; Albrecht & Gotelli, 2001). Abiotic environmental constraints, on the other hand, should cause overlap to be more than expected (Albrecht & Gotelli, 2001) and the variance in niche overlap to be less than expected (Inger & Colwell, 1977). We compared the mean (for all pairwise comparisons) and variance of the Czechanowski indices for empirical communities with simulated communities generated according to the algorithm RA4. In this algorithm, the abundance of species in particular time periods is randomly reshuffled but with the constraint that a species cannot occur on a day on which it was not found. Thus, the abundance of each species is randomized but only among the time windows in which it was active. Each empirical matrix was randomized 1000 times to create a thousand simulated communities, from which we calculated mean and variance of the Czechanowski index (using Ecosim version 7; Gotelli & Entsminger, 2004). The mean empirical Czechanowski index and the empirical variance in the index were then compared with the histogram of the simulated indices and their variance. We calculated the two-tailed probability that the Czechanowski index or its variance was higher or lower than the simulated measures. When empirical indices were higher than the simulated indices at  $P < 0.05$ , this was judged to be evidence of competition. When the converse was true, this was judged to be evidence of environmental conditions driving patterns of activity.

DO THE RELATIVE INFLUENCES OF ENVIRONMENTAL CONSTRAINTS AND COMPETITION ON PHENOLOGICAL PATTERNS VARY WITH ELEVATION?

The work of Fischer (1960) predicts that, where environmental conditions are more extreme, such as at high latitudes and elevations, environmental constraints should structure ecological communities. Conversely, where environmental conditions are more permissive, biotic interactions and in particular competition should structure ecological communities. We



group our sites into low-elevation, intermediate-elevation, and high-elevation sites to compare the relative influence of competition and environmental constraints on patterns of phenological ranges and diversity over time.

## RESULTS

### OVERALL PATTERNS

Over the course of 1 year of sampling and 40 150 trap-days, ants of 43 species were collected. The number of species collected was close to the number of species known to be collectable using pitfall traps from forest plots based on more extensive surveys over 3 years and the number of ant species collected at the same sites using malaise traps (Dunn *et al.* 2007). In addition, species diversity for the plots overall based on the 2001 data was close to the Chao2 estimate of species diversity of the ant species that are potentially sampled by pitfall traps in the plot (56 species). The length of activity season decreased with elevation. Maximum July temperatures decreased and minimum January temperatures decreased with elevation (Table 1). At the high-elevation sites, such as Clingman's Dome, few days were above 15 °C, the minimum temperature necessary for development (Southerland, 1988) in one of the most elevationally widespread ants considered here, *A. rudis* (Fig. 1). At lower elevation sites, such as

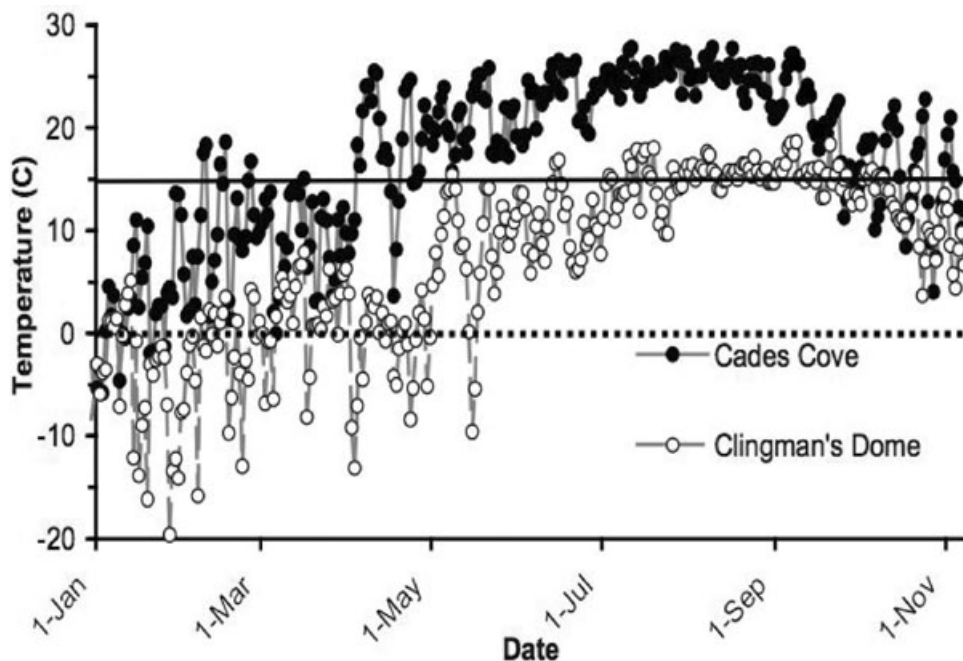
Cades Cove, most days had mean temperatures above 15 °C (Fig. 1).

DO PATTERNS OF SPECIES DIVERSITY OVER TIME DIFFER FROM NULL MODEL EXPECTATIONS AND ARE THOSE DIFFERENCES MORE RECONCILABLE WITH COMPETITION OR ENVIRONMENTAL CONSTRAINTS?

At all elevations, diversity peaked toward the end of summer and, not surprisingly, declined in winter months. When both temperature and the evolutionary null model predictions were included in stepwise regression analyses, temperature alone stayed in the model at the lowest elevation and, as elevation increased, the contribution of temperature decreased. The contribution of the evolutionary null models to the final model of diversity was greatest at mid elevations (Table 2). At the highest elevations, where diversity was low, none of the variables considered explained significant variation in diversity.

DO PATTERNS IN PHENOLOGICAL RANGES OVER TIME DIFFER FROM NULL MODEL EXPECTATIONS AND ARE THOSE DIFFERENCES MORE RECONCILABLE WITH COMPETITION OR ENVIRONMENTAL CONSTRAINTS?

When phenological ranges were randomized with the evolutionary null models, patterns of range overlap



**Figure 1.** Mean daily temperature at the lowest (Cades Cove) and highest (Clingman's Dome) of the 11 sites in Great Smoky Mountains National Park. Cades Cove and Clingman's Dome have the warmest and coldest mean annual temperatures, respectively. Solid black line denotes 15 °C, the temperature below which *Aphaenogaster rudis* workers cannot develop in the laboratory (Southerland, 1988). A dashed line indicates freezing.

**Table 2.** Stepwise regression results at each of the nine sites with ant activity

Site	Parameter	Partial $r^2$	$F$	$P$
Low elevation				
Cades Cove	Temperature	0.91	36.2	< 0.00001*
Twin Creeks	Temperature	0.80	83.4	< 0.00001*
Goshen Prong	Temperature	0.56	17.1	0.0001*
	MDE	0.05	2.2	0.15
Snakeden Ridge	Temperature	0.29	3.7	0.09
Mid elevation				
Albright Grove	MDE	0.64	26.3	0.0001*
Cataloochee	MDE	0.56	12.6	0.005*
Brushy Mountain	MDE	0.71	8.9	0.007*
	Temperature	0.02	1.9	0.18
High elevation				
Purchase Knob	No significant model			
Indian Gap	No significant model			

Results show final models, with temperature and mid-domain effect (MDE) null models as the potential independent variables and species diversity as the dependent variable. Results that were significant after adjusting alpha to 0.0045 for the number of tests ( $N = 11$ ) using the Bonferroni adjustment are indicated by an asterisk\*.

**Table 3.** Results of phenological range randomizations using mid-domain effect null models

Sites (sorted by elevation)	Empirical overlap	Simulation overlap	Empirical < simulated	Simulated < empirical
Cades Cove	0.14	0.15	0.54	0.45
Twin Creeks	0.08	0.07	0.63	0.37
Goshen Prong	0.14	0.1	0.28	0.72
Snakeden Ridge	0.09	0.056	0.29	0.71
Albright Grove	0.152	0.25	0.19	0.81
Cataloochee	0.14	0.25	0.02	0.88
Brushy Mountain	0.067	0.048	0.25	0.75
Purchase Knob	0.08	0.06	0.34	0.66
Indian Gap	0.049	0.056	0.32	0.68

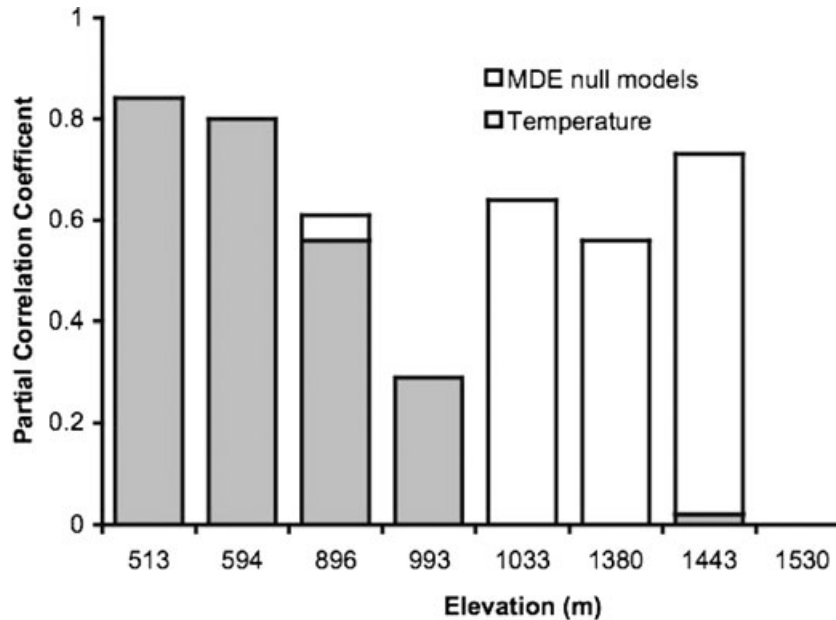
After adjusting alpha for the number of tests ( $N = 9$ ) using the Bonferroni adjustment, no tests were significant at the critical value (0.005). In no case did the empirical and simulated overlap of phenological ranges differ from one another.

did not generally differ from null model predictions. In other words, the amount of overlap among species ranges was similar to that expected were phenological ranges to evolve independent of one another. At no sites was the empirical overlap different from the overlap of the randomized communities (Table 3).

At all but one elevation, activity patterns within phenological ranges did not differ from random. Ant activity patterns within phenological ranges were more clumped in time than expected by chance at one site, Twin Creeks ( $P < 0.00001$  for both the Czechowski index and its variance).

#### DO THE RELATIVE INFLUENCES OF ENVIRONMENTAL CONSTRAINTS AND COMPETITION ON PHENOLOGICAL PATTERNS VARY WITH ELEVATION?

At low elevations, empirical diversity patterns deviated from null model predictions due to the effects of temperature. At mid elevations, patterns of diversity did not appear to differ from null model expectations and, at low-diversity, high-elevation sites, none of the variables considered appeared to be important (Table 2, Fig. 2). Comparisons of low and mid-elevation sites (Fig. 3) show that, at both sites, nearly all species had patterns of activity that peaked in



**Figure 2.** Variation in explanatory power (partial  $r^2$ ) of mid-domain effect (MDE) null models and temperature as a function of elevation. The total height of each bar represents the total  $r^2$  (MDE + temperature) for the model, where the overall model explained significant variation. The filled portion indicates the contribution of temperature and the unfilled portion represents the contribution of the null models. Each bar corresponds to a single site and elevation.

warm months such that the diversity of small-ranged species also peaked in the middle of the summer. In other words, the greatest difference among species was in the length of their phenological range, rather than the midpoint of their phenological range. Only one species, *Prenolepis imparis*, deviated from this pattern. *Prenolepis imparis* was inactive during the warmest periods of the year and active in those cooler months when few other species were foraging (Fig. 3).

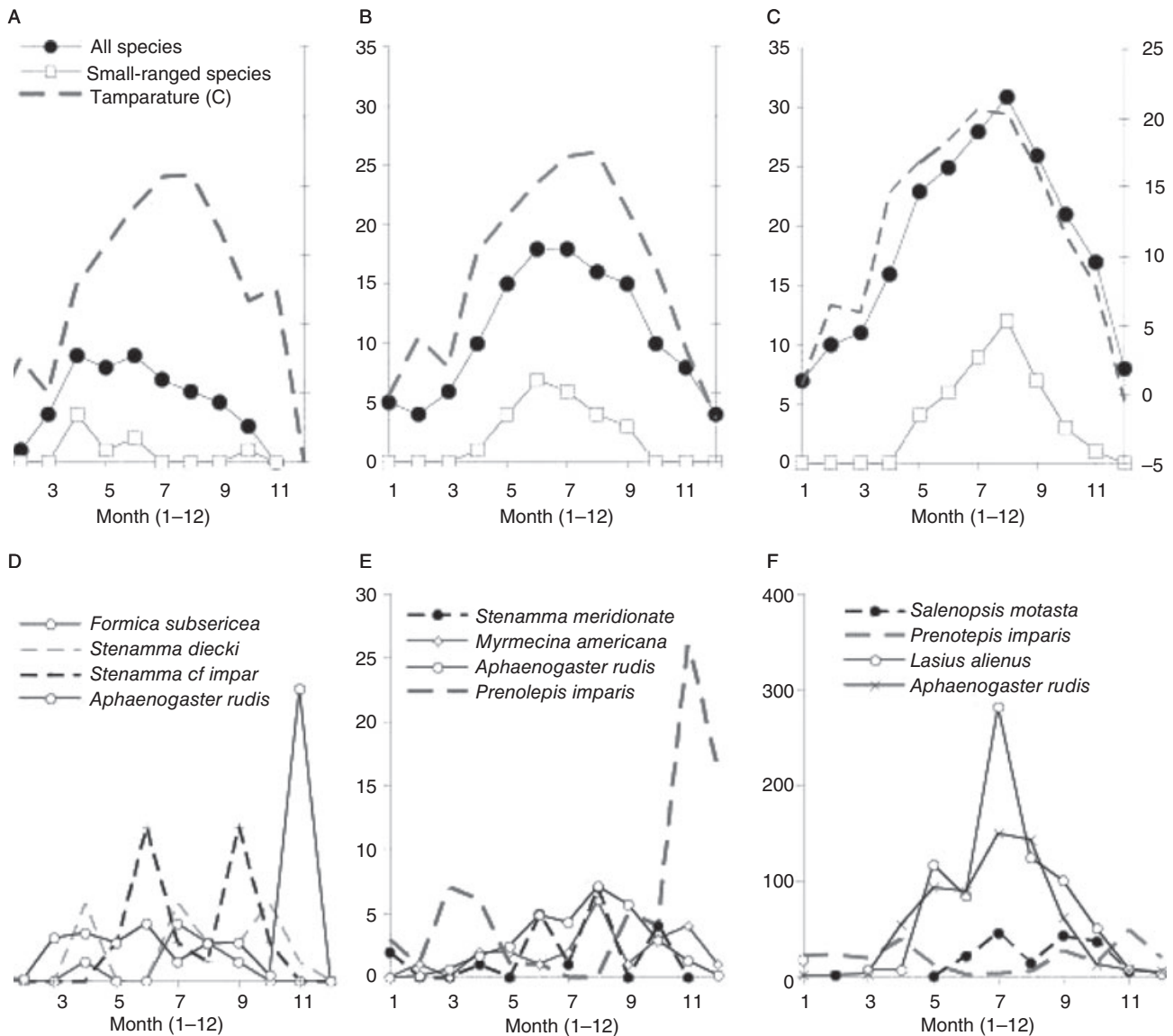
## DISCUSSION

Work at single sites has long emphasized the effects of interspecific competition on ant community structure (Fellers, 1987; Savolainen & Vepsäläinen, 1988; Savolainen, Vepsäläinen & Wuorenrinne, 1989) and species diversity (Andersen, 1992; Andersen & Patel, 1994). Other studies have implicated interspecific competition as a leading cause of temporal activity patterns (Suarez *et al.*, 1998). However, along an elevational gradient in the southern Appalachians, we found little evidence of competition in structuring seasonal patterns in ant activity. At all but the highest elevations, a model including evolutionary null models and/or temperature explained much of the seasonal variation in species diversity. Although other studies, in ants and other taxa, implicate competition as a key force in structuring patterns of diversity in both space and time, our broad-scale examination of multiple communities along an environmental gradient suggests that

seasonal patterns in southern Appalachian ant communities are not driven by competition. When seasonal patterns in ant diversity or activity differed from null models, temperature, not competition, appeared to explain that deviation. The extent to which observed patterns of diversity differed from null model predictions varied with elevation. At the lowest sites (Cades Cove, Twin Creeks, and Goshen Prong), seasonal diversity patterns were nearly entirely explained by temperature. By contrast, at the very highest elevations, seasonal diversity patterns were idiosyncratic within a narrower window of ant activity and were poorly predicted by either the phenological null models or temperature. At mid elevations, seasonal diversity patterns were best explained by null model predictions but, at these elevations, temperature appears to set the boundaries that define the beginning and end of the activity season.

Why might species diversity in time track temperature, and why does the importance of temperature vary spatially along the elevational gradient? Work along spatial gradients suggests several mechanisms by which ant diversity might be positively correlated with temperature. Temperature may indirectly affect ants via its effects on primary productivity, which can influence diversity through a variety of mechanisms (Kaspari *et al.*, 2000).

Alternatively, because ants are thermophilic, higher temperatures may allow more ants to be active. This could affect seasonal patterns of diversity in two ways.



**Figure 3.** Seasonal patterns of diversity pooled from high- (A), medium- (B), and low- (C) elevation sites along with activity patterns for the four most abundant species at the same high- (D), medium- (E), and low- (F) elevation sites. *N* for the sites = 2, 3 and 4, respectively. Grey lines in the upper panels show temperature from a representative site from each elevational grouping. Patterns of diversity show the diversity pattern of all species and, as a separate line, the pattern of diversity of the half of all species with the smallest phenological ranges.

First, higher temperature might meet the minimum foraging temperature necessary for a higher percentage of species. Higher temperatures might also increase the activity of individuals within colonies and, because there are more individuals out foraging, more individuals are likely to cross a given patch of soil and hence fall into a pitfall trap or find a food resource. Because more individuals cross a given point in space per unit time, the probability of detecting new species increases.

We found that the effects of temperature at mid elevations were reduced relative to low elevations, but

this result must be interpreted with caution. Patterns of diversity predicted by null models and patterns of variation in temperature over time were similar such that our ability to distinguish the relative importance of temperature and null model predictions is limited, particularly at mid-elevation sites (Fig. 3). Furthermore, even though the geometric constraints of null models are not expected to strongly influence the diversity patterns of diversity of small-ranged species (Dunn *et al.*, 2006), seasonally rare small-ranged species in both the high- and low-elevation sites tended to be clustered near the middle of the year (Fig. 3). Such



clustering can only be due to temperature or some other abiotic driver.

As would be expected given that patterns of species diversity did not deviate strongly from null model expectations, we found no deviations in phenological range overlap from null models that might be reconcilable with either temperature or competition. Instead, the differences between empirical patterns of diversity and null models of diversity were apparently due to more complex (and not statistically significant) differences between the spatial arrangements of phenological ranges empirically and in the null models. Peaks in diversity at high temperatures were often due to the occurrence of seasonally and spatially rare species. Thus, the few deviations of empirical diversity patterns from null models appeared to be due to the seasonal aggregation of temporally rare species during warm periods.

Phenological ranges could evolve nonrandomly with respect to each other, although, as we show above, this is apparently not the case for southern Appalachian ants. Activity patterns within the period of ant activity could, however, also differ from random due to individual decisions about when, and when not, to forage within phenological ranges. For example, *A. rudis*, which is competitively subordinate (Fellers, 1989) but abundant, might forage in those weeks when the competitively dominant *F. subsericea* or *P. imparis* are rare. In general, we found more, not less, overlap in activity patterns (within phenological ranges) than expected by chance, but this difference was significant at only one site. This suggests that environmental variation in general, and temperature in particular, drives not only seasonal patterns of diversity and phenological ranges in ants, but also can shape the activity periods of ants within those ranges.

Overall, we believe that our results are most reconcilable with the following model. At the highest elevations, the activity of individuals is idiosyncratic and represents the occasional foraging of colonies from what we suspect are sink populations with low to non-existent yearly reproduction (Dunn *et al.*, 2007). At low and mid elevations, the ends of the activity season are determined by temperature. Within the activity season, many species take advantage of almost the entire year and the overlapping of these species' ranges generates a diversity pattern close to null model predictions. Deviations from these null model predictions for mid elevations come from the occurrence of temporally rare species during the warmest months of the year.

Our results stand in contrast to local studies typically emphasizing the role of competition in structuring ant communities and more broad-scale studies that show how competition by a particular species might affect species diversity (Gotelli & Arnett, 2000).

However, just because we did not find strong evidence that competition structured patterns of seasonal diversity, phenological range overlap, or activity for entire ant assemblages does not mean that competition has no effects on seasonal patterns of activity. Competition may structure seasonal patterns of activity for particular pairs of competing species. For example, *P. imparis* has a peak in activity in the early spring and late fall (Fig. 3), a pattern long thought to result in reduced competition between *P. imparis* and other ant species (Ward, 1987; Suarez *et al.*, 1998). In our analysis, *P. imparis* was the only species that was not most active during the warm summer months.

If competition is the 'hallmark of ecology' (Hölldobler & Wilson, 1990) and mediates so many patterns in space and time, why are its effects not observed on seasonal patterns in ant communities in the southern Appalachians? Three phenomena might preclude the evolution of non-overlapping phenological ranges and activity patterns. First, the constraints imposed by temperature on foraging may be so great that they outweigh the potential costs of competition. That only one ant species in our analyses, *P. imparis*, was inactive in the warmest months suggests that the advantages of foraging in the warmest months are great. Second, and not mutually exclusive, coexistence may be facilitated by other mechanisms such as daily temporal patterns of non-overlap (Albrecht & Gotelli, 2001) and dietary specialization (Davidson *et al.*, 2003). Third, because local assemblage membership differs from site to site, the phenological ranges of ants might be exposed to very different selective pressures in different sites and, on average, these selective forces might balance one and other out.

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