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Changes in ant community composition caused by 20 years of experimental warming vs. 13 years of natural climate shift

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Abstract. Predicting the effects of climate change on community composition is hampered by the lack of integration between long term data sets tracking the effects of natural climate change and the results of experimental climate manipulations. Here we compare the effects of change in climate through time to experimental warming on the composition of high elevation ant communities at the Rocky Mountain Biological Station in Gothic Colorado. We take advantage of a 20-year continuously running warming experiment which has increased soil temperature by 1.5°C and advanced snowmelt by 10 days and compare the effects of this experimental warming to natural changes in climate over the past 13 years across three sites spread along a 420-m elevation gradient representing a roughly 1°C difference in average annual soil temperature and average advanced snowmelt of 2 weeks. We compared ant community data collected at all four sites in 1997 to collections made at the same sites in 2010. From 1997 to 2010 there was a community wide shift in ant composition along the natural climate gradient with ant communities shifting to higher elevations. Ant communities in the experimental warming site also changed, but they shifted orthogonally to those along the gradient. Interestingly, after 20 years of experimental warming, there is little discernible effect on ant communities in experimentally warmed plots compared to control plots. This discrepancy between the climate manipulation and elevation gradient is probably an effect of the spatial scale of the experimental warming. Ants respond to experimental warming in complex ways due to the physical location of their nests and their foraging area. This is a concern for warming experiments, but one that is hard to address for species that cover even modest areas in their foraging.

Key words: climate change; community composition; elevation gradient; Formicidae; Rocky Mountain Biological Laboratory; warming experiment.

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INTRODUCTION

Patterns of species distributions along elevation gradients have a long history of study in ecology due to the relatively rapid change in environmental factors (Rosenzweig 1995). Studies in community composition along elevation gradients are making a resurgence in part because global temperatures are increasing at an alarming rate, with an increase ranging from 2–7°C predicted over this century (IPCC 2007). While the global mean land-surface temperature has increased by 0.74°C over the past 100 years, the greatest shifts have been at higher latitudes and elevations (IPCC 2007). Using meta-analyses, this global temperature increase has been

correlated with shifts in phenology and range boundaries for a variety of organisms in a variety of biomes (Walther et al. 2002, Parmesan 2006, Diez et al. 2012). Studying responses of communities along an elevation gradient provides several benefits, including the ability to document differences along a natural climate gradient and see shifts in species responses at both the lower and upper range limit of a community (Wilson et al. 2005, Kelly and Goulden 2008, Warren and Chick 2013).

In addition to the direct role climate plays, recent experiments have demonstrated that species interactions may also directly influence how individual species respond to global warming, and that the responses of the same species in different communities can be idiosyncratic (Suttle et al. 2007, Pelini et al. 2012, Stuble et al. 2013). Projecting the responses of communities to future climate change is further complicated by the potential for non-analog climate space, environments for which we have no modern equivalent (Williams and Jackson 2007). Due to the difficulties in predicting shifts in non-analog climates combined with variable responses of species in the same communities, there has been an increasing focus on documenting empirical range shifts (Parmesan and Yohe 2003, Doak and Morris 2010). Arguably, the dynamics of such observed shifts are best understood in combination with experiments artificially manipulating climate (Walker et al. 2006, Leuzinger et al. 2011).

Work by Dunne et al. (2004) has highlighted the importance of studying the effects of climate change using a combination of long term datasets combined with experimental manipulations. One of the difficulties with combining multiple approaches to studying the effects of climate change is the lack of comparable data sets for the same communities. Short term experimental manipulations are often limited in the number of environmental variables they can manipulate and their spatial extent, therefore their focus is often on plants and microbes (Rustad et al. 2001, Leuzinger et al. 2011), but see Pelini et al. (2011*a*). While the best large scale long term datasets have been studies of phenology and range limits, usually of plants, birds, and butterflies (Parmesan and Yohe 2003). An additional limitation for studying the effects of climate change on community dynamics is the lack of data on species that play important roles as ecosystem engineers. Ants are an ideal system to study and model the effects of climate change because they are ubiquitous (Dunn et al. 2007), play essential roles in almost all terrestrial ecosystems (Hölldobler and Wilson 1990), and their distributions are strongly constrained by local and regional climate (Sanders 2002, Dunn et al. 2009, Jenkins et al. 2011, Warren and Chick 2013).

Here we compare the effects of change in climate through time to experimental warming on the composition of high elevation ant communities. We take advantage of a 20-year continuously running long term warming experiment to compare the effects of artificial warming to natural changes in climate over the past 13 years along an elevation gradient. Since 1973, these sites have experienced a net change in summer temperature of >2°C (Miller-Rushing and Inouye 2009, Lambert et al. 2010) and a snowmelt date occurring 4.5–5 days earlier per decade (Miller-Rushing and Inouye 2009, Lambert et al. 2010; J. Harte, *unpublished data*). The experimental warming manipulation has increased soil temperature by 1.5°C and advanced snowmelt by 10 days in heated vs. control plots (Saleska et al. 1999, Roy et al. 2004; J. Harte, *unpublished data*). We predict that ant communities along both the elevation gradient and in the experimental warming manipulation should shift, and that that shift should lead to (1) higher elevation ant communities coming to resemble those at lower elevations and (2) communities in experimental warming plots to resemble those found in lower elevation sites. We compare both patterns in species richness and community composition.

Methods

Study site

The study took place in four subalpine montane meadows spanning an approximately 420-m elevation gradient (High = N 38.95655°, W 106.97111°, 3190 m; Mid = N 38.96163°, W 106.99044°, 2940 m; Low = N 38.87229°, W 106.91019°, 2770 m) near the Rocky Mountain Biological Laboratory (RMBL) Colorado; see Dunne et al. (2003) for more detailed site descriptions. At these sites, *Artemisia tridentata* var. *vaseyana* is the dominant shrub and *Festuca*

thurberi is the dominant graminoid. The highest elevation site was established close to the elevation limit of *Artemisia* (Dunne et al. 2003). In 1990, at the mid-elevation, the artificial warming experiment was established at a site roughly 500 m south of the mid-elevation control site to study the effects of climate change on vegetation and the soil mesofauna (Harte et al. 1995). The warming meadow consisted of 10 experimental plots (3 × 10 m), treatment and control plots were separated by 5 m, with the five treatment plots receiving radiant heat from heaters suspended 2 m above the ground producing 15 W/m^2 year round additional heat flux from 1991–1992 and 22 W/m^2 from May 1993 to present (Harte et al. 1995).

Sampling

All four sites were sampled in 1997 and again 13 years later in 2010. In 1997, each of the three sites along the elevation gradient was divided into 10 plots (4 × 4 m). Each plot was sampled with three randomly placed pitfall traps. The fourth site, the experimental warming meadow, was divided into 10 plots (3 × 10 m), five treatment and five control plots. Pitfall trapping occurred at all sites for four days (3–6 July) and consisted of Dixie cups filled with a water/alcohol/glycerol solution. Ants were removed from the pitfall traps every 24 hrs and identified to morpho-species. In 2010, each of the 10 plots in the warming meadow was sampled with six pitfall traps for 4 days (23–28 July). Each of the three elevation gradient sites were sampled with 10 pitfall traps per plot spread across 5 plots (4 × 8 m) due to our inability to find the exact placement of the original 10 plots within the sites from 1997. Sampling occurred for 4 days (3–7 July). Pitfall traps in 2010 consisted of 50-mL centrifuge tubes filled with a water/alcohol/glycerol solution. All ants from the 2010 sampling were identified to the same morpho-species classes used in 1997 and to species level. Voucher specimens are deposited at the Chicago Field Museum and the reference collection at RMBL.

Species richness and abundance along an elevation gradient

Species richness and abundance were quantified for each plot in each site. Richness was the total number of species found in all pitfall traps in the plot. Two different measures of ant species abundance were used; a log transform of the average numbers of workers captured per pitfall trap (hereafter referred to as abundance), and the proportion of pitfall traps in which each species was captured (hereafter referred to as occurrence). We used a one-way ANOVA to test how all 4 sites differed in species richness, abundance, and occurrence; all pair-wise comparisons were made with Tukey's multiple comparisons procedure. Due to differences in the type of pitfall traps used in 1997 and 2010, we were unable to directly compare changes between 1997 and 2010. All statistics were performed using JMP 8.0 (SAS Institute, Cary, North Carolina, USA).

Prediction 1: Shifts in ant assemblage composition through time

We performed permutational multivariate analysis of variance (PERMANOVA) (McArdle and Anderson 2001) to test for differences in ant morpho-species log abundances and occurrences between elevations, year, and their interaction. PERMANOVA is a permutational ANOVA, developed to test simultaneous responses of multiple variables to multiple factors. Analyses were based on Bray-Curtis dissimilarity with 999 permutations for each test and pair-wise comparisons. We then used principal coordinates analysis (PCoA) to visualize the distinctiveness of the ant assemblages in each elevation through time. Due to differences in trapping methods between 1997 and 2010, all log abundances were standardized for each plot. We also performed individual PCoA's on the 1997 and 2010 morpho-species log abundance data, occurrence data, and the 2010 species log abundance data and occurrence data without standardizing for each plot. Results from occurrence and log abundance were equivalent so we will only present the results from the analyses on log abundance. We evaluated which ant species were most responsible for differentiating communities using similarity percentage (SIMPER) analysis. SIMPER evaluates the contributions of each species to the Bray-Curtis dissimilarity of all pairs of samples between groups. All statistics were performed in PRIMER v6 (Clarke and Gorley 2006).

Prediction 2: Effects of experimental warming manipulation on ant communities

Species richness, abundance, and occurrence were compared between heated and control plots using paired t-tests. All statistics were performed using JMP 8.0 (SAS Institute, Cary, North Carolina, USA).

Results

In 1997 we captured 13,585 ants of 9 distinct morpho-species representing six genera. Morpho-species richness in a plot ranged from 3–7 (Appendix A). The plots with the most morpho-species were in the experimental warming site and the low elevation site, while the plot with the fewest morpho-species was found in the mid elevation control site. Three of the morpho-species were found in every plot (small-black *Formica*, *Myrmica*, and *Tapinoma sessile*). *Lasius neoniger* was only found in one plot, and *Camponotus* in only 3 plots. In 2010 we captured 15,002 ants comprising 24 species that were lumped into 10 morpho-species (for comparability with the data from 1997) representing seven genera. The one morpho-species that was added was *Polyergus*, an obligate parasite for *Formica*. Species richness in a plot ranged from 5–12 species (Appendices B and C) and morpho-species richness ranged from 5–7 (Appendix A). The most species rich plots with 12 species were found in the warming meadow, in both a treatment and a control plot. Collectively, the five high elevation plots only captured five species. *Camponotus herculeanus*, *C. modoc*, *Formica aserva, F. neorufibarbis*, and *Leptothorax crassipilis* were only captured in one plot, while *F. lasioides*, *Myrmica tahoensis*, and *T. sessile* were captured in at least 24 of the 25 plots.

Species richness and abundance along an elevation gradient

There was a significant effect of site elevation on morpho-species richness in both 1997 ($F_{3,36} = 5.50$, $p = 0.0032$) and 2010 ($F_{3,21} = 5.74$, $p < 0.005$) and in species richness in 2010 ($F_{3,21} = 15.50$, $p < 0.0001$). In pair-wise comparisons, the highest elevation site consistently had the fewest species and the low elevation and warming sites consistently had the greatest number of species (Fig. 1). Both worker abundance (1997: $F_{3,36} = 32.75$, $p < 0.0001$; 2010: $F_{3,21} = 85.38$, $p < 0.0001$) and occurrence (1997: $F_{3,36} = 13.03$, $p < 0.0001$; 2010 morpho-species: $F_{3,21} = 19.07$, $p < 0.0001$, 2010 species: $F_{3,21} = 18.21$, $p < 0.0001$) followed a similar pattern with decreasing ant abundance and occurrence as elevation increases. In the pairwise comparisons there is some indication that the mid-elevation experimental warming site is more similar in patterns of richness and abundance to the low elevation site than to the mid-elevation control site in 2010 (Fig. 1).

Prediction 1: Shifts in ant assemblage composition through time

Morpho-species community composition differed by site and year with a significant interaction (PERMANOVA; Site: $p < 0.001$; Year: $p < 0.001$; Site × Year: $p < 0.001$; Fig. 2A). Sites in both 1997 and 2010 are spaced out on the x-axis from high elevation on the left to low elevation on the right. The PCoA demonstrates large shifts in community structure through time. Shifts through time were consistent in their directionality in that all sites in 2010, except for the High elevation site, shift toward the right (lower elevation), to increased similarity with lower elevation sites from 1997 (Fig. 2A). The PCoA performed on only the 1997 morpho-species data revealed three distinct communities, the Low elevation plots which were widely distant from a mixture of Mid, Warming, and High elevation plots and small cluster of 4 High elevation plots (Fig. 2B). Independent PCoA's of the 2010 morpho-species and species level data reveal four distinct communities, one for each site (Fig. 2C–D).

An analysis of the rank order of change based on calculated similarities from the PERMANOVA revealed that both mid-elevation sites (Warming and Mid-Control) changed the most, followed by Low then High (Table 1). Five different pairs of sites share a similarity 80–82% (from most similar to least similar, 1998 Warm–1998 Mid, 2010 Low–2010 Mid, 2010 Mid–1998 Low, 2010 High–1998 Mid, 1998 Warm–1998 High). The warming meadow site at the mid-elevation shows both low similarity with itself through time (65.96%) and the least similarity between plots within a site in 2010 (76.39%) (Table 1).

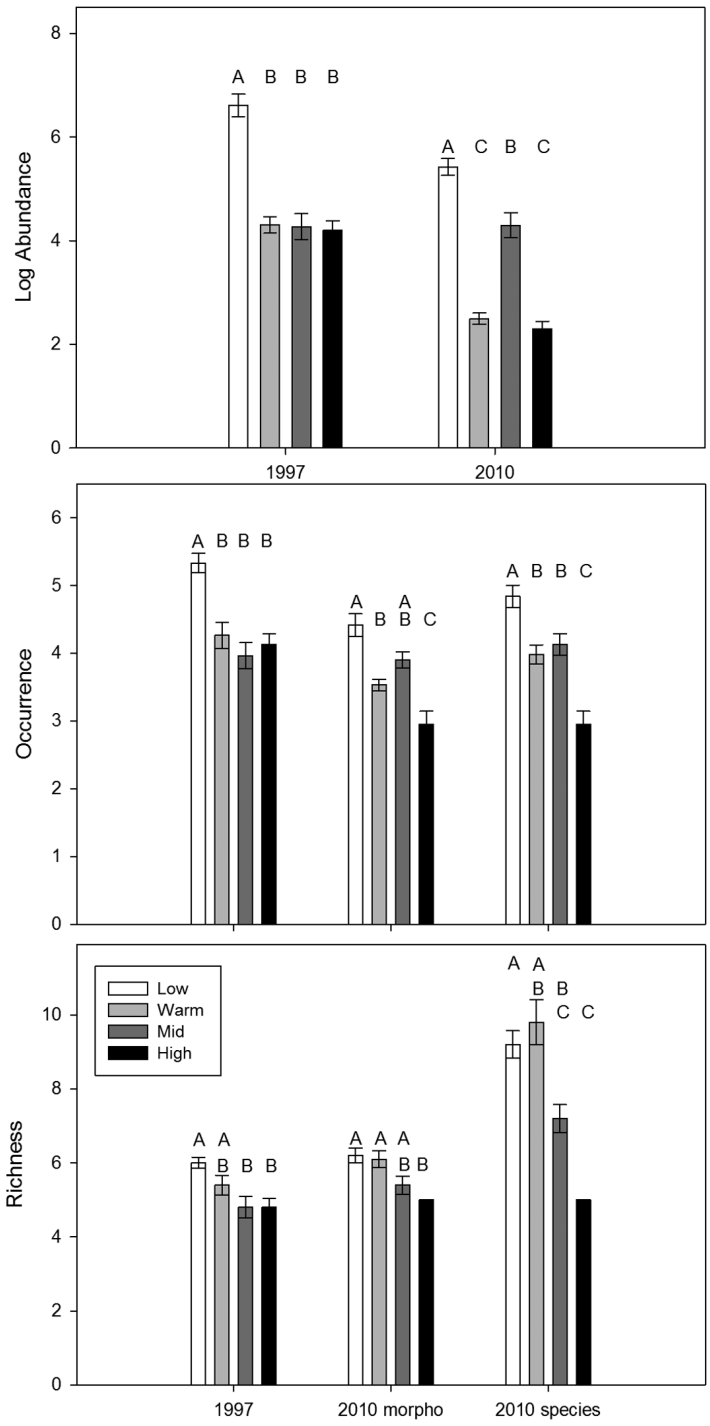

Fig. 1. Patterns in total species richness, occurrence, and abundance across all four elevation sites. Warm refers to the mid-elevation site that has been treated with experimental warming. Letters above the bars represent statistically similar groups.

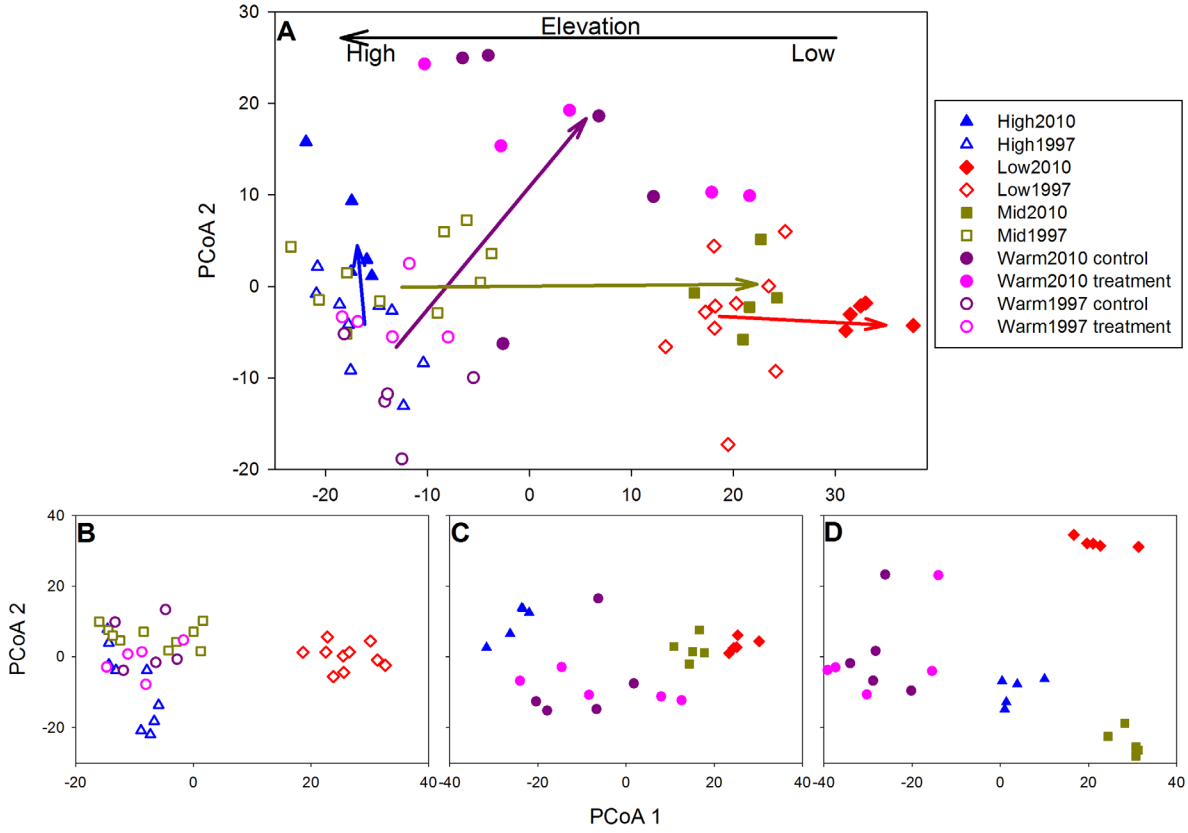

Fig. 2. Two-dimensional PCoA (principal coordinates analysis) plots based on log abundance of ant community composition. (A) All plots sampled in 1997 and 2010 based on morpho-species composition with standardized total abundance in each plot (PCO1 = 61.7%, PCO2 = 17.9% of variation). (B) All plots sampled in 1997 based on morpho-species composition (PCO1 = 64%, PCO2 = 16.1% of variation). (C) All plots sampled in 2010 based on morpho-species composition (PCO1 = 72%, PCO2 = 15.8% of variation). (D) All plots sampled in 2010 based on species composition (PCO1 = 43.4%, PCO2 = 28.9% of variation). Symbols correspond to sites along the elevation gradient. Color of the symbols represent year of sampling with filled symbols representing 2010 and hollow symbols showing samples from 1997. Arrows represent magnitude of change within a site over a 13-year period.

Based on the SIMPER analysis, changes in morpho-species composition through time were strongly driven by an increase in Red/Black *Formica* and a decrease in the Small Black *Formica* in the mid and low elevation sites (Table 2). Changes in high elevation sites were driven by an increase in *Tapinoma sessile*, and decreases in Big Black and Small Black *Formica* (Table 2). Within both 1997 and 2010, the morpho-species driving differences between sites along the elevation gradient were Red/Black *Formica* decreasing in abundance with increasing elevation, and *Tapinoma sessile* and *Myrmica* which increase in abundance with increasing elevation. The SIMPER analysis of species differences in 2010, reveals that the Red/Black *Formica* morpho-species is comprised mostly of *Formica obscuripes*, *F. puberula*, and *F. oreas*, which are each numer-

Table 1. Average percent similarity between and within sites calculated in PERMANOVA.

Site	Percentage similarity		
	Between 1997 and 2010	Within a site in 1997	Within a site in 2010
High	78.977	81.289	88.515
Mid	63.603	85.658	88.160
Warm	65.962	84.434	76.390
Low	77.391	86.806	91.794

Table 2. Ant morpho-species responsible for differentiating elevation sites over a 13-year time period (SIMPER analysis).

Ant species	Average abundance		Average dissimilarity	Contribution (%)
	Site 1, 1997	Site 2, 2010		
Low				
Red/Black *Formica*	0.31	0.49	9.03	39.96
Leptothorax	0.10	0.04	3.17	14.00
Small Black *Formica*	0.22	0.16	3.10	13.72
Myrmica	0.07	0.13	2.83	12.51
Tapinoma sessile	0.17	0.21	2.47	10.91
Warm				
Red/Black *Formica*	0.03	0.23	10.19	29.93
Small Black *Formica*	0.30	0.12	9.26	27.21
Myrmica	0.17	0.21	4.26	12.51
Big Black *Formica*	0.10	0.04	3.49	10.26
Tapinoma sessile	0.36	0.36	3.49	10.25
Mid				
Red/Black *Formica*	0.07	0.38	15.29	42.00
Tapinoma sessile	0.35	0.18	8.55	23.50
Small Black *Formica*	0.30	0.19	5.49	15.09
Myrmica	0.24	0.17	3.57	9.80
High				
Tapinoma sessile	0.30	0.43	6.65	31.63
Big Black *Formica*	0.15	0.06	5.13	24.41
Small Black *Formica*	0.26	0.19	3.97	18.90
Myrmica	0.26	0.27	3.26	15.52

ically dominant at a different site (Low, Warm, and Mid, respectively) (Table 3). *Formica lasioides* and *F. neogagates* are the two numerically dominant species in the Small Black Formica morpho-species (Table 3).

Prediction 2: Effects of experimental warming manipulation on ant communities

In 1997, after 7 years of experimental warming, 2,362 ant workers were captured in the warming meadow. There were no significant differences between heated and control plots in morpho-species richness, average ant worker abundance, or ant species occurrence (Fig. 3). In 2010, after 20 years of experimental warming, 1,659 ant workers were captured. There were no significant differences between treatment and control plots in species richness, average ant worker abundance, or ant species occurrence (Fig. 3). However, there was a higher morpho-species richness (paired t-test; $t_4 = -3.16$, $p = 0.034$) and morpho-species occurrence (paired t-test; $t_4 = -3.14$, $p = 0.035$) in control plots (Fig. 3). There were also no significant effects of experimental warming on ant community composition (Fig. 2B–D).

Discussion

Summary

In this study, we address two predictions about how changing climate affects ant community structure; (1) that modern high elevation ant communities have shifted to resemble the ant community structure that was historically found at lower elevations due to natural climate change over the past 13 years, and (2) ant communities experiencing 20 years of experimental climate warming will shift to resemble ant communities that are found at lower elevations with naturally warmer temperatures. We demonstrated that in subalpine montane meadows ant richness and abundance decreases with increasing elevation, and that the differences between sites are greater in 2010 than those found in 1997 (Fig. 1). Ant communities have shifted upward in elevation over the last 13 years such that modern high elevation communities resemble historic low elevation communities (Fig. 2). Experimental warming also led to changes in composition, but these changes were distinct from those associated with large-scale temporal trends (Fig. 2A–D).

Simple models of range shift with climate change suggest species will move uphill as

Table 3. Ant species responsible for differentiating the different elevations sites in 2010 (SIMPER analysis).

Ant species	Average abundance		Average dissimilarity	Contribution (%)
	Site 1	Site 2		
Site 1, Low; Site 2, Warm				
Formica obscuripes	2.43	0.18	28.85	44.56
Formica lasioides	0.66	0.17	6.46	9.98
Formica puberula	0.00	0.37	4.81	7.43
Formica neogagates	0.31	0.00	3.93	6.07
Myrmica brevispinosa	0.00	0.29	3.73	5.76
Formica podzolica	0.31	0.06	3.36	5.19
Myrmica tahoensis	0.37	0.16	2.85	4.40
Tapinoma sessile	0.85	0.84	2.47	3.81
Leptothorax muscorum	0.20	0.01	2.47	3.81
Site 1, Low; Site 2, Mid				
Formica obscuripes	2.43	0.02	24.89	41.61
Formica oreas	0.00	1.46	15.11	25.26
Formica neogagates	0.31	0.50	3.24	5.41
Myrmica tahoensis	0.37	0.64	2.80	4.68
Formica lasioides	0.66	0.43	2.79	4.66
Tapinoma sessile	0.85	0.69	2.53	4.22
Formica podzolica	0.31	0.34	2.29	3.83
Site 1, Warm; Site 2, Mid				
Formica oreas	0.01	1.46	21.67	31.59
Formica neogagates	0.00	0.50	7.31	10.66
Myrmica tahoensis	0.16	0.64	7.20	10.49
Formica puberula	0.37	0.02	5.39	7.86
Formica lasioides	0.17	0.43	4.77	6.96
Formica podzolica	0.06	0.34	4.47	6.52
Myrmica brevispinosa	0.29	0.00	4.34	6.33
Tapinoma sessile	0.84	0.69	3.04	4.43
Formica obscuripes	0.18	0.02	2.57	3.75
Formica canadensis	0.02	0.16	2.36	3.44
Site 1, Warm; Site 2, High				
Myrmica tahoensis	0.16	0.63	9.92	20.00
Formica puberula	0.37	0.00	8.03	16.19
Formica lasioides	0.17	0.44	6.78	13.67
Myrmica brevispinosa	0.29	0.00	6.17	12.43
Tapinoma sessile	0.84	0.99	3.48	7.02
Formica obscuripes	0.18	0.00	3.47	7.00
Formica podzolica	0.06	0.15	2.65	5.34
Formica altipetens	0.12	0.00	2.36	4.78
Myrmica incomplete	0.07	0.00	1.39	2.80
Leptothorax muscorum	0.01	0.06	1.13	2.27
Formica canadensis	0.02	0.16	2.36	3.44
Site 1, Mid; Site 2, High				
Formica oreas	1.46	0.00	22.34	48.19
Formica neogagates	0.50	0.00	7.51	16.19
Tapinoma sessile	0.69	0.99	4.59	9.89
Formica podzolica	0.34	0.15	3.57	7.69
Formica lasioides	0.43	0.44	2.49	5.38
Formica canadensis	0.16	0.00	2.36	5.08

climate warms. Such models are at the heart of recent predictions of low and high elevation extinctions. However, the few studies of the response in species along elevation gradients to warming suggest responses may be more stochastic, or, if deterministic, dependent on species by species responses to many variables in addition to temperature (Suttle et al. 2007, Pelini et al. 2012, Stuble et al. 2013, Warren and Chick 2013). Here we found that changes through time in composition were in line with (we would have thought, overly) simplistic predictions of uphill shifts of entire assemblages, although there were a number of complexities. First, the shifts in composition were uneven in magnitude along the elevation gradient. From 1997 to 2010, the smallest observed changes in community structure were at the high and low elevation sites and the largest changes in community structure were observed at the two mid elevation sites (Table 1, Fig. 2A). Pelini et al. (2011*a*) in a six-month experimental climate manipulation found that

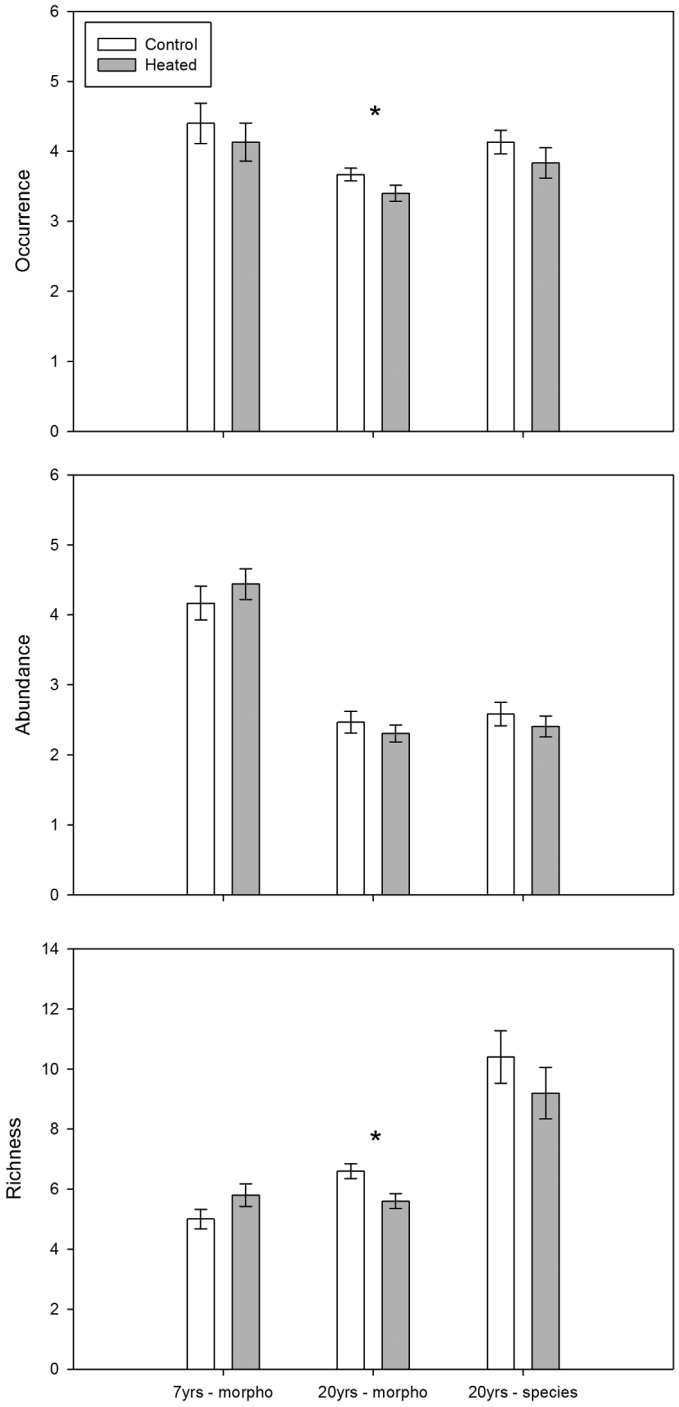

Fig. 3. Average ant species richness, worker abundance, and worker occurrence in pitfall traps calculated for morpho-species in 1997 (7 years after the start of the warming experiment) and for both species and morpho-species in 2010 (20 years after the start of the warming experiment). An asterisk represents significant differences ($p < 0.05$).

community responses in ants were weakest at their high latitude site compared to their low latitude site. Their low latitude site is near the northern extent of southern species, while our mid-elevation sites have historically been just beyond the elevational extent of *Formica obscuripes*, a behaviorally dominant ant species (I. Billick, *personal communication*), which were becoming abundant in the 2010 sampling period. Shifts in community composition within the mid elevation sites resulted in their reduced similarity with each other, as well as reduced similarity to the high elevation site that was observed in 1997 (Fig. 2B). While in 2010, the mid elevation sites demonstrated increased similarity with the low elevation site from 1997 (Fig. 2A). Second, at the site level, the mid elevation experimental warming site (including control and experimental plots) and mid elevation control site diverged from each other over the 13 year time span. A-priori we hypothesized that experimental warming would affect ant communities in ways similar to that due to temporal warming. Experimental warming (at the site scale) was associated with a change in the ant community, but this change was distinct from that due to natural warming.

One limitation of our study is that the community comparisons between 1997 and 2010 took place at the morpho-species taxonomic level which prevents us from completely assessing how much of the community shift is driven by normal population dynamics versus climate change. Even though the use of morpho-species taxonomy obscures some potentially important species level differences (Warren and Chick 2013), the community trends are general through time and across elevation, and they correspond well to the results from the species level data along the elevation gradient from 2010. For instance, changes in both mid elevation sites through time were driven in large part by an increase in abundance of Red/Black *Formica* (Table 2), which is the most abundant morpho-species at the low elevation site and is absent from the high elevation site (Appendix A). However, the sites may have changed through time more than is apparent on the basis of the morpho-species level data. Within the Red/Black *Formica* morpho-species group, there are important species level differences. At the experimental warming site, the most common species were *F. obscuripes* and *F. puberula*, while at the control site *F. oreas* was the only member of the Red/Black *Formica* morpho-species found and it was not present at any other site (Appendices B and C). *Formica obscuripes* is the most abundant ant at the low elevation site, is a behaviorally dominant ant known for building large thatch mounds, occurring at high densities, and suppressing the local abundance of other ant species (Gregg 1963) while *F. puberula* is a facultative parasite conducting slave-raids on other species of *Formica* (Gregg 1963). Another Red/Black *Formica*, *F. oreas*, is a nesting generalist forming nests under rocks or building small thatch mounds and is not as behaviorally dominant as the other two species (Gregg 1963).

While the entire experimental warming site, including treatment and controls, changed in morpho-species composition, it changed in a way distinct from the uphill shift seen more generally in the other sites. We hypothesize that this orthogonal shift has to do with differences between the real climate change and climate change caused by experimental warming. The orthogonal shift in community composition in the experimental warming site compared to the control mid-elevation site contrasts with the lack of differences in community composition between warming and control plots within the experimental warming site. A-priori one might predict that warming would increase the abundance of ants, both due to an increase in food availability and an increased number of days during which foraging can occur. Therefore it was surprising to find decreased ant abundance at both the plot level (Fig. 3) and site level (Fig. 1). While species richness was higher in the experimental warming meadow site relative to the control site (Fig. 1), within the warming site richness was reduced in treatment plots relative to control plots (Fig. 3). The simplest explanation is that the warming experiment, while at a spatial scale appropriate for many questions is at a scale too small for large-bodied ants with large foraging distances. Most species of ants in subalpine meadows have foraging ranges >10 m (Gregg 1963; *personal observation*) while the experimental warming plots were only 3×10 m. Ants may, as a result, respond to the warming manipulation in complex ways as a function of their foraging area. Some ants, in effect, receive

the treatment on the nest, while others receive half of the treatment effect due to foraging, but the nest itself would experience the climate of the control plot.

Alternatively, changes in foraging resources or the effect of patchy microenvironments, and novel microenvironments could also explain the lack of differences in community composition between control and warming plots. Numerous studies have demonstrated the importance of microclimate on ant richness, abundance, and foraging (Wehner et al. 1992, Cerda et al. 1997, McCaffrey and Galen 2011, Stuble et al. 2013). The differences between warming plots and control plots roughly match the differences across the entire 420-m elevation gradient of 1°C difference in average annual soil temperature and a difference in average snow melt date of 2 weeks (Dunne et al. 2003). These differences in soil temperature and snowmelt dates can have a profound direct effect on ant demography (Billick 2001, McCaffrey and Galen 2011) and an indirect effect by changing the timing of plant growth and foraging resources (Saavedra et al. 2003). For instance Adler et al. (2007) demonstrated a reduced population of aphids in the experimental warming plots relative to the control plots while Aldridge et al. (2011) showed that there was a change in timing of peak nectar resources. Potentially, the overall food availability may have decreased due to change in the plant community to favor sagebrush growth over other forbs, resulting in a change in the quality of plant based resources (Price and Waser 1998, Shaw and Harte 2001, Saleska et al. 2002, Perfors et al. 2003). In addition, the variety of microclimates may have increased due to the local effects of warming (Harte et al. 1995). These changes could potentially have opened up new or even novel niches for a greater variety of species, especially those in the Red/Black *Formica* morpho-species. It is possible that our sampling took place in a period of demographic changeover before the behaviorally dominant species were able to eliminate others from the site. The greatest change in species composition in the warming meadow over the 13-year period was the increase in *Formica obscuripes* which is a dominant and aggressive thatch building ant which defends its territories from other species (Gregg 1963).

Conclusions

By integrating the results from experimental climate manipulations with data collected along natural climate gradients incorporating long term community datasets, we were able to demonstrate that at course taxonomic scales communities within a single environment respond in a predictable manner by shifting upward in elevation. Singly, all of these approaches have limitations, but when combined, the generality of the pattern is more believable (Dunne et al. 2004). Individual species responses to climate change may vary, but overall ecosystem functions are maintained by taxonomically related species. Climate change manipulations at course scales do mimic natural community shifts, but it is important to match the spatial scale of the experimental manipulation to that of the study organism. With the increasing number of climate manipulation studies (Rustad et al. 2001, Ainsworth and Long 2005, Pelini et al. 2011*b*) it will be important to see how predictions change and can be made across shifting environments rather than within a single habitat. While most climate manipulation studies are focused on one or a few focal species, our study demonstrates the utility of collecting samples from a variety of non-focal taxa. Our results also highlight the dangers of only preserving voucher specimens rather than keeping all specimens collected. In addition, a protocol of regular collections rather than endpoint data collections permit a more thorough investigation of relative importance of natural community dynamics and shifts caused by environmental change.

Future climate change will result in the creation of environments that have no modern analog (Williams and Jackson 2007, Jenkins et al. 2011). Many of these non-analog communities will be occurring at the lower latitudinal boundary (warm temperature) for temperate species (Jenkins et al. 2011). Most studies have focused on the upper latitudinal boundary for the effects of climate change (cold temperature) because these are where the fastest and strongest responses are observed (Diamond et al. 2012). We demonstrate that communities found at the two elevation extremes of the subalpine meadows changed the least through time, and that the lower elevation community increased the abundance of the dominant species, similar to that

found in the short term experiment conducted by Pelini et al. (2011*a*) and Doak and Morris (2010). Climate manipulation experiments may prove to be the best way we have for making predictions about how communities will respond to these non-analog environments, despite the risks associated with the interpretation of results from these experiments (Leuzinger et al. 2011). These limitations can be somewhat ameliorated when combined with long term datasets from the same environments (Dunne et al. 2004).

The consistency of community change demonstrated here at the morpho-species level overlays potentially important effects of trophic cascades driven by species level shifts. In these subalpine meadows, previous research has already demonstrated how a shift in phenology can disrupt several important mutualisms (Saavedra et al. 2003, Diez et al. 2012, McKinney et al. 2012). Due to the important role ants play in this specific system as well as most terrestrial ecosystems as mutualists, predators, and nutrient distribution (Hölldobler and Wilson 1990), shifts in individual species' distributions can play an important role (Fraser et al. 2001). A changing climate selects for success of different genotypes within a given species (Rank and Dahlhoff 2002, Skelly et al. 2007). Differences in abundance of selected genotypes can cause trophic cascades throughout the system on associated mutualists, parasites, predators, and parasitoids (Moreira and Mooney 2013).

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Supplemental Material

Appendix A

Table A1. Average number of ant workers captured in pitfall traps in 1997 and 2010 in each plot. Ant workers were identified to morpho-species.

Site	Year	Plot	Sp. rich	*Ca*	RB *Fo*	SB *Fo*	LB *Fo*	*Lafa*	*Lane*	*Le*	*My*	*Po*	*Tase*
Warming	1997	1	6	0.0	1.7	27.7	2.0	0.0	0.0	0.7	2.0	0.0	35.7
Warming	1997	2	5	0.0	0.7	39.7	0.0	0.0	0.0	1.3	4.3	0.0	50.0
Warming	1997	3	5	0.0	0.0	43.7	12.7	0.0	0.0	1.0	5.3	0.0	34.3
Warming	1997	4	5	0.3	0.0	33.7	1.0	0.0	0.0	0.0	7.7	0.0	81.7
Warming	1997	5	5	0.0	0.0	13.7	2.0	0.0	0.0	0.7	2.0	0.0	28.7
Warming	1997	6	6	0.0	1.7	11.0	1.7	0.0	0.0	0.7	5.7	0.0	41.3
Warming	1997	7	5	0.0	0.3	28.3	3.0	0.0	0.0	0.0	6.3	0.0	19.7
Warming	1997	8	6	0.0	0.0	24.3	2.3	1.0	0.0	0.3	37.0	0.0	39.7
Warming	1997	9	4	0.0	0.0	13.0	6.0	0.0	0.0	0.0	7.3	0.0	28.0
Warming	1997	10	7	0.0	1.0	9.0	1.3	0.3	0.0	0.7	19.0	0.0	43.3
Low	1997	1	7	0.00	55.00	83.67	2.33	0.00	0.33	1.67	2.67	0.00	16.00
Low	1997	2	6	0.00	49.00	44.33	1.33	0.00	0.00	1.33	7.33	0.00	24.33
Low	1997	3	6	0.00	92.00	25.67	0.67	0.00	0.00	8.33	10.33	0.00	23.67
Low	1997	4	6	0.00	114.00	13.33	1.00	0.00	0.00	7.33	31.00	0.00	29.00
Low	1997	5	6	0.00	236.67	39.00	1.00	0.00	0.00	1.33	5.33	0.00	72.67
Low	1997	6	6	0.00	153.67	28.67	2.33	0.00	0.00	7.00	5.67	0.00	91.00
Low	1997	7	6	0.00	163.67	19.67	0.33	0.00	0.00	18.00	11.00	0.00	27.67
Low	1997	8	6	0.00	336.00	10.00	0.33	0.00	0.00	14.00	16.67	0.00	46.67
Low	1997	9	5	0.00	157.00	20.33	0.00	0.00	0.00	5.67	5.33	0.00	41.67
Low	1997	10	6	0.00	84.67	23.33	0.67	0.00	0.00	5.67	4.00	0.00	8.00
Mid	1997	1	5	0.0	3.3	15.3	0.7	0.0	0.0	0.0	12.7	0.0	34.0
Mid	1997	2	5	0.0	0.3	24.0	1.0	0.0	0.0	0.0	18.0	0.0	64.7
Mid	1997	3	6	0.0	6.0	23.7	1.3	0.3	0.0	0.0	19.0	0.0	55.3
Mid	1997	4	4	0.0	0.0	22.7	0.3	0.0	0.0	0.0	6.7	0.0	22.0
Mid	1997	5	5	0.3	3.3	22.0	0.0	0.0	0.0	0.0	11.0	0.0	8.7
Mid	1997	6	5	0.0	0.7	29.7	0.3	0.0	0.0	0.0	12.0	0.0	15.0
Mid	1997	7	5	0.0	12.0	15.3	0.3	0.0	0.0	0.0	16.7	0.0	77.0
Mid	1997	8	3	0.0	0.0	8.3	0.0	0.0	0.0	0.0	5.3	0.0	32.3
Mid	1997	9	6	0.0	4.7	28.3	2.0	0.0	0.0	0.3	10.7	0.0	41.0
Mid	1997	10	4	0.0	0.0	14.7	1.3	0.0	0.0	0.0	4.7	0.0	33.3
High	1997	1	4	0.0	0.0	9.7	1.3	0.0	0.0	0.0	43.0	0.0	26.0
High	1997	2	6	0.0	0.0	9.0	16.0	0.3	0.0	1.3	23.7	0.0	28.3
High	1997	3	4	0.0	0.0	16.0	1.7	0.0	0.0	0.0	45.3	0.0	30.3
High	1997	4	5	0.3	0.0	14.7	0.3	0.0	0.0	0.0	24.7	0.0	19.0
High	1997	5	4	0.0	0.0	13.0	2.3	0.0	0.0	0.0	4.7	0.0	12.7
High	1997	6	4	0.0	0.0	26.3	0.3	0.0	0.0	0.0	8.3	0.0	18.7
High	1997	7	5	0.0	0.0	11.3	1.7	0.0	0.0	1.3	16.0	0.0	45.3
High	1997	8	5	0.0	0.0	15.3	14.0	0.0	0.0	1.3	51.0	0.0	17.3
High	1997	9	6	0.0	0.3	8.0	28.7	0.0	0.0	0.3	14.3	0.0	21.0
High	1997	10	5	0.0	0.0	7.3	19.7	0.0	0.0	0.3	3.7	0.0	12.3
Warming	2010	1	6	0.0	4.3	11.5	1.5	0.0	0.0	0.2	4.0	0.0	4.3
Warming	2010	2	5	0.0	1.7	1.3	0.3	0.0	0.0	0.0	2.0	0.0	13.3
Warming	2010	3	6	0.0	5.3	0.7	0.2	0.0	0.7	0.0	9.2	0.0	7.0
Warming	2010	4	6	0.0	56.5	1.0	1.0	0.2	0.0	0.0	0.8	0.0	8.5
Warming	2010	5	7	0.0	33.7	3.8	0.2	0.0	0.3	0.2	2.2	0.0	7.5
Warming	2010	6	6	0.2	21.7	1.8	0.0	0.0	0.2	0.0	1.0	0.0	5.0
Warming	2010	7	7	0.0	2.2	0.7	0.2	0.2	0.3	0.0	5.8	0.0	8.3
Warming	2010	8	6	0.0	4.8	1.2	0.2	0.0	0.2	0.0	5.3	0.0	6.7
Warming	2010	9	7	0.3	5.5	0.7	0.3	0.0	0.2	0.0	2.0	0.0	5.3
Warming	2010	10	5	0.0	1.3	0.3	0.3	0.0	0.0	0.0	3.3	0.0	7.7
Low	2010	1	7	0.0	253.0	4.2	1.2	0.0	0.0	0.5	1.5	0.3	2.0
Low	2010	2	6	0.0	289.4	5.5	1.0	0.0	0.0	0.5	1.6	0.0	5.8
Low	2010	3	6	0.0	286.9	11.5	0.4	0.0	0.0	0.6	1.4	0.0	6.8
Low	2010	4	6	0.0	227.4	4.6	1.3	0.0	0.0	0.6	0.9	0.0	8.4
Low	2010	5	6	0.0	277.9	4.1	2.4	0.0	0.0	0.8	1.5	0.0	10.6
Mid	2010	1	6	0.0	42.4	9.1	1.1	0.0	0.0	0.1	3.6	0.0	3.8
Mid	2010	2	5	0.0	25.0	2.6	1.9	0.0	0.0	0.0	3.0	0.0	2.5
Mid	2010	3	6	0.0	27.5	3.0	4.1	0.1	0.0	0.0	3.1	0.0	6.4
Mid	2010	4	5	0.0	22.1	8.3	0.3	0.0	0.0	0.0	3.8	0.0	5.5
Mid	2010	5	5	0.0	26.8	3.4	0.3	0.0	0.0	0.0	3.6	0.0	2.7
High	2010	1	5	0.0	0.0	1.0	0.4	0.0	0.0	0.3	3.5	0.0	6.7

Table A1. Continued.

Site	Year	Plot	Sp. rich	*Ca*	RB *Fo*	SB *Fo*	LB *Fo*	*Lafa*	*Lane*	*Le*	*My*	*Po*	*Tase*
High	2010	2	5	0.0	0.0	2.3	0.4	0.0	0.0	0.1	2.3	0.0	8.4
High	2010	3	5	0.0	0.0	1.5	0.1	0.1	0.0	0.0	5.1	0.0	9.9
High	2010	4	5	0.0	0.0	1.7	0.3	0.0	0.0	0.2	1.7	0.0	8.5
High	2010	5	5	0.0	0.0	2.7	0.9	0.0	0.0	0.4	4.9	0.0	10.8

Note: Abbreviations are: Sp. rich = species richness; *Ca* = *Camponotus*; RB *Fo* = Red/Black *Formica*; SB *Fo* = Small/Black *Formica*; LB *Fo* = Large/Black *Formica*; *Lafa* = *Lasius fallax*; *Lane* = *Lasius neoniger*; *Le* = *Leptothorax*; *My* = *Myrmica*; *Po* = *Polyergus*; *Tase* = *Tapinoma sessile*.

Appendix B

Table B1. Average number of 12 of the 24 ant workers captured in pitfall traps in 2010 in each plot. All workers are identified to species.

			Morpho-species											
			Ca	*Ca*	RB *Fo*	RB *Fo*	RB *Fo*	RB *Fo*	RB *Fo*	RB *Fo*	SB *Fo*	SB *Fo*	SB *Fo*	SB *Fo*
			Species											
Site	Sp. rich	Plot	Cahe	Camo	Foad	Foas	Fone	Foob	Foor	Fopu	Foal	Foca	Fola	Foneo
Warm	7	1	0.0	0.0	0.0	0.0	0.0	0.0	0.0	4.3	0.0	0.0	11.5	0.0
Warm	8	2	0.0	0.0	0.0	0.0	0.0	0.0	0.0	1.7	0.5	0.0	0.8	0.0
Warm	11	3	0.0	0.0	0.0	0.0	0.0	0.2	0.0	5.2	0.3	0.0	0.3	0.0
Warm	9	4	0.0	0.0	0.0	0.0	0.0	54.5	0.0	2.0	0.8	0.0	0.2	0.0
Warm	11	5	0.0	0.0	0.0	0.0	0.0	33.2	0.0	0.5	3.7	0.0	0.2	0.0
Warm	12	6	0.0	0.2	0.0	0.0	0.2	1.3	0.0	20.2	1.2	0.2	0.5	0.0
Warm	12	7	0.0	0.0	0.8	0.0	0.0	0.0	0.0	1.3	0.3	0.3	0.0	0.0
Warm	10	8	0.0	0.0	1.0	0.7	0.0	0.2	0.0	3.0	0.0	0.0	1.2	0.0
Warm	11	9	0.3	0.0	0.2	0.0	0.0	0.0	0.2	5.2	0.0	0.0	0.7	0.0
Warm	7	10	0.0	0.0	0.0	0.0	0.0	0.0	0.0	1.3	0.0	0.2	0.2	0.0
Low	9	1	0.0	0.0	0.0	0.0	0.0	253.0	0.0	0.0	0.0	0.2	3.0	1.0
Low	8	2	0.0	0.0	0.0	0.0	0.0	289.4	0.0	0.0	0.9	0.0	4.1	0.5
Low	10	3	0.0	0.0	0.0	0.0	0.0	286.9	0.0	0.0	0.1	0.1	5.9	5.4
Low	10	4	0.0	0.0	0.0	0.0	0.0	227.4	0.0	0.0	1.4	0.4	2.5	0.4
Low	9	5	0.0	0.0	0.0	0.0	0.0	277.9	0.0	0.0	0.5	0.0	3.3	0.4
Mid	8	1	0.0	0.0	0.0	0.0	0.0	0.0	42.4	0.0	0.0	2.8	0.6	5.8
Mid	7	2	0.0	0.0	0.0	0.0	0.0	0.0	25.0	0.0	0.0	0.7	1.2	0.7
Mid	8	3	0.0	0.0	0.0	0.0	0.0	0.0	27.3	0.2	0.0	0.0	1.6	1.4
Mid	7	4	0.0	0.0	0.0	0.0	0.0	0.3	21.8	0.0	0.0	0.0	4.6	3.7
Mid	6	5	0.0	0.0	0.0	0.0	0.0	0.0	26.8	0.0	0.0	0.0	1.9	1.5
High	5	1	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	1.0	0.0
High	5	2	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	2.3	0.0
High	5	3	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	1.5	0.0
High	5	4	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	1.7	0.0
High	5	5	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	2.7	0.0

Note: Abbreviations are: Sp. rich = species richness; *Ca* = *Camponotus*; RB *Fo* = Red/Black *Formica*; SB *Fo* = Small/Black *Formica*; Cahe = *Camponotus herculeanus*; Camo = *Camponotus modoc*; Foad = *Formica adamsi*; Foas = *Formica aserva*; Fone = *Formica neorufibarbi*; Foob = *Formica obscuripes*; Foor = *Formica oreas*; Fopu = *Formica puberula*; Foal = *Formica altipetens*; Foca = *Formica canadensis*; Fola = *Formica lasioides*; Foneo = *Formica neogagates*.

APPENDIX C

Table C1. Average number of the remaining 12 of the 24 ant workers captured in pitfall traps in 2010 in each plot. All workers are identified to species.

			Morpho-species											
			LB *Fo*	LB *Fo*	*Lafa*	*Lane*	*Le*	*Le*	*My*	*My*	*My*	*My*	*Pobr*	*Tase*
			Species											
Site	Sp. rich	Plot	*Fofu*	*Fopo*	*Lafa*	*Lane*	*Lecr*	*Lemu*	*Mybr*	*Myin*	*Mylo*	*Myta*	*Pobr*	*Tase*
Warm	7	1	0.0	1.5	0.0	0.0	0.0	0.2	3.2	0.8	0.0	0.0	0.0	4.3
Warm	8	2	0.3	0.0	0.0	0.0	0.0	0.0	1.2	0.7	0.0	0.2	0.0	13.3
Warm	11	3	0.0	0.2	0.0	0.7	0.0	0.0	8.0	0.2	0.5	0.5	0.0	7.0
Warm	9	4	1.0	0.0	0.2	0.0	0.0	0.0	0.0	0.7	0.0	0.2	0.0	8.5
Warm	11	5	0.2	0.0	0.0	0.3	0.0	0.2	0.7	0.0	0.2	1.3	0.0	7.5
Warm	12	6	0.0	0.0	0.0	0.2	0.0	0.0	0.2	0.0	0.2	0.7	0.0	5.0
Warm	12	7	0.0	0.2	0.2	0.3	0.0	0.0	4.7	0.3	0.5	0.3	0.0	8.3
Warm	10	8	0.2	0.0	0.0	0.2	0.0	0.0	3.2	0.0	0.0	2.2	0.0	6.7
Warm	11	9	0.2	0.2	0.0	0.2	0.0	0.0	1.5	0.0	0.0	0.5	0.0	5.3
Warm	7	10	0.0	0.3	0.0	0.0	0.0	0.0	0.8	0.0	0.0	2.5	0.0	7.7
Low	5	1	0.0	1.2	0.0	0.0	0.0	0.5	0.0	0.0	0.0	1.5	0.3	2.0
Low	4	2	0.0	1.0	0.0	0.0	0.0	0.5	0.0	0.0	0.0	1.6	0.0	5.8
Low	5	3	0.3	0.1	0.0	0.0	0.0	0.6	0.0	0.0	0.0	1.4	0.0	6.8
Low	5	4	0.1	1.1	0.0	0.0	0.0	0.6	0.0	0.0	0.0	0.9	0.0	8.4
Low	5	5	0.1	2.3	0.0	0.0	0.0	0.8	0.0	0.0	0.0	1.5	0.0	10.6
Mid	4	1	0.0	1.1	0.0	0.0	0.0	0.1	0.0	0.0	0.0	3.6	0.0	3.8
Mid	3	2	0.0	1.9	0.0	0.0	0.0	0.0	0.0	0.0	0.0	3.0	0.0	2.5
Mid	4	3	0.0	4.1	0.1	0.0	0.0	0.0	0.0	0.0	0.0	3.1	0.0	6.4
Mid	3	4	0.0	0.3	0.0	0.0	0.0	0.0	0.0	0.0	0.0	3.8	0.0	5.5
Mid	3	5	0.0	0.3	0.0	0.0	0.0	0.0	0.0	0.0	0.0	3.6	0.0	2.7
High	4	1	0.0	0.4	0.0	0.0	0.3	0.0	0.0	0.0	0.0	3.5	0.0	6.7
High	4	2	0.0	0.4	0.0	0.0	0.0	0.1	0.0	0.0	0.0	2.3	0.0	8.4
High	4	3	0.0	0.1	0.1	0.0	0.0	0.0	0.0	0.0	0.0	5.1	0.0	9.9
High	4	4	0.0	0.3	0.0	0.0	0.0	0.2	0.0	0.0	0.0	1.7	0.0	8.5
High	4	5	0.0	0.9	0.0	0.0	0.0	0.4	0.0	0.0	0.0	4.9	0.0	10.8

Note: Abbreviations are: Sp. rich = species richness; LB *Fo* = Large/Black *Formica*; *Lafa* = *Lasius fallax*; *Lane* = *Lasius neoniger*; *Le* = *Leptothorax*; *My* = *Myrmica*; *Pobr* = *Polyergus breviceps*; *Tase* = *Tapinoma sessile*; *Fofu* = *Formica fusca*; *Fopo* = *Formica podzolica*; *Lecr* = *Leptothorax crassipilis*; *Lemu* = *Leptothorax muscorum*; *Mybr* = *Myrmica brevispinosa*; *Myin* = *Myrmica incomplete*; *Mylo* = *Myrmica lobicornis*; *Myta* = *Myrmica tahoensis*.