

# Effects of tree mortality caused by a bark beetle outbreak on the ant community in the San Bernardino National Forest

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**Abstract.** 1. A severe bark beetle outbreak caused very high levels of tree mortality in the San Bernardino National Forest in southern California in 2003.

2. In 2009, the impact of the outbreak on the ant community was examined by pitfall-trapping ants in 15 sites that saw high tree mortality ('red' sites) and 15 sites that suffered little or no tree mortality ('green' sites) during the outbreak.

3. Ant species turnover between green and red sites was low, and no invasive species were observed.

4. However, changes in the abundances of various species resulted in a significant alteration of the ant community.

5. If the ant community is an accurate bioindicator of other taxa in this forest, the effects of the bark beetle outbreak may be described as dramatic but not catastrophic or irreversible.

6. The changes in the ant community are consistent with the hypothesis that this community is structured by nest site limitation rather than inter-specific competition or thermal limitation.

**Key words.** Ants, bark beetles, community structure, nest-site limitation, outbreak, tree mortality.

## Introduction

Outbreaks of bark beetles (Curculionidae: Scolytinae) have decimated forests across the western United States and Canada in the past few decades. While much work has been done to monitor the tree mortality caused by these outbreaks, little is known about the impact on other organisms. Because of the obvious difficulties in surveying all of the taxa that might be affected, assessing changes in a relevant indicator taxon is an attractive approach to studying the broader impacts of such disturbances.

Ants are used as bioindicators of the effects of disturbance on ecosystems for several reasons. First, ants are generally responsive to alteration of the biomass and diversity of the local plant community (Kalif *et al.*, 2001) and other environmental variables (Underwood & Fisher, 2006). Second, because they occupy fixed nest locations, ants are affected by conditions on

a very small scale, so that their presence and abundance are a better indicator of local conditions than are the presence or abundance of more mobile animals (Stephens & Wagner, 2006; Underwood & Fisher, 2006). Ants play important ecosystem roles and are therefore often a relevant choice for monitoring (Hölldobler & Wilson, 1990). They make up a significant percentage of the animal biomass in many ecosystems, they can be crucial to processes such as soil mixing and nutrient transport (Gentry & Stiritz, 1972), and they are important players in nutrient cycling and energy flow. Ants can also strongly influence the plant community via seed dispersal and granivory (Christian, 2001; Barrow *et al.*, 2007). While the diversity of a given taxon is often not a reliable indicator of the diversity of other groups (Lawton *et al.*, 1998; Bennett *et al.*, 2009; Maleque *et al.*, 2009; Wike *et al.*, 2010), ant diversity is known to reflect the diversity of other invertebrates in ecosystems recovering from a disturbance in some cases (Andersen & Majer, 2004).

The use of ants as bioindicators must be undertaken with caution (Underwood & Fisher, 2006). Different ant communities do not always respond to a disturbance in the

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same way (Arnan *et al.*, 2009). In addition, broad measures of a bioindicator taxon, such as species richness or abundance, are potentially misleading. For instance, while it is popular to measure the species richness of bioindicator groups, the ant species richness of different habitats has been observed to respond differently to similar disturbances (Farji-Brener *et al.*, 2002; Ratchford *et al.*, 2005; Barrow *et al.*, 2007), and ant species richness often does not respond at all unless disturbances are extreme (Andersen & Majer, 2004).

Nonetheless, changes in the ant community can provide useful information about the responses of the ecosystem as a whole. Various studies have examined the responses of ant communities to anthropogenic disturbances, such as clear-cutting (Punttila *et al.*, 1991; Vasconcelos, 1999; Zettler *et al.*, 2004; Gibb & Hjältén, 2007), selective logging (Kalif *et al.*, 2001; Widodo *et al.*, 2004; Yi & Moldenke, 2005; Gunawardene *et al.*, 2010), and mining (Hoffmann *et al.*, 2000; Andersen *et al.*, 2003). Other studies have examined the effect of natural disturbances such as the formation of tree-fall gaps (Feener & Schupp, 1998) on ants, and many studies have examined the effect of fire (e.g., Parr *et al.*, 2004; Gunawardene & Majer, 2005; Ratchford *et al.*, 2005; Arnan *et al.*, 2006; Lafleur *et al.*, 2006; Gibb & Hjältén, 2007; Kutt, 2009). Perhaps because large-scale biotic disturbances are less common, few studies have investigated the effects of such disturbances on ants, although one study examined the impact of an outbreak of cinnamon fungus (*Phytophthora cinnamomi* Ronds) on ground-dwelling invertebrates (Newell, 1997). Because the response of ant communities to a disturbance has been examined in the context of many habitats and many types of disturbance, there exists a fairly rich database to which the effects of the large-scale tree mortality now occurring in North America may be compared. However, to our knowledge, no studies so far have examined the response of ant communities to bark beetle outbreaks (or to damaging outbreaks of any other insect pest).

Perhaps the most similar type of disturbance that has been frequently studied with respect to ants is logging. The effect of logging on ants has been examined in a handful of forest ecosystems, particularly tropical forests (Vasconcelos *et al.*, 2000; Kalif *et al.*, 2001; Fredericksen & Fredericksen, 2002; Widodo *et al.*, 2004; Gunawardene *et al.*, 2010). While some such studies have been carried out in temperate deciduous forests (Zettler *et al.*, 2004; Andersen *et al.*, 2009), and temperate coniferous forests (Yi & Moldenke, 2005; Palladini *et al.*, 2007; Arnan *et al.*, 2009), temperate forests are relatively understudied with respect to the effects of disturbance on ant communities (Ellison *et al.*, 2007).

No consistent theme emerges from a review of these temperate-zone studies. For example, ant species richness has been observed to decrease (Zettler *et al.*, 2004) and increase (Palladini *et al.*, 2007) after clearing of a forest. While in some systems ant community structure appears to be determined largely by competitive hierarchies (Arnan *et al.*, 2009), this is not universally the case (Kaspari *et al.*, 2000), and other authors suggest that thermal tolerances drive ant abundance and diversity in temperate areas (Palladini *et al.*, 2007; Wittman, 2007). Because there is no general agreement on the main

factors that structure temperate ant communities, we lack a theoretical framework that would allow predictions to be made about the result of a disturbance. In this study, we document changes in the ant community of the San Bernardino Mountains of southern California after severe tree mortality caused by a bark beetle outbreak, and, based on those changes, draw inferences about the impact of this tree mortality on the forest ecosystem as a whole. Additionally, we use our data to evaluate hypotheses about what factors may control the structure of ant communities in the San Bernardino Mountains.

## Methods

### Background

Starting in the winter of 1998–1999, the San Bernardino Mountains experienced an ‘extraordinarily severe drought’ (Keeley *et al.*, 2004) that imposed severe stresses on trees throughout the region. This stress is thought to have been exacerbated by fire-suppression policies that resulted in high densities of young trees (California Forest Pest Council, 2002; Keeley *et al.*, 2004). Although precipitation returned to normal levels in 2002–2003, beetle populations had already reached epidemic levels, and massive tree mortality occurred in 2003. The western pine beetle, *Dendroctonus brevicomis* LeConte, particularly reduced numbers of Coulter and ponderosa pines. The mountain pine beetle, *D. ponderosae* Hopkins, killed large numbers of ponderosa and sugar pines, but attacked the single-leaf pinyon pine as well. Other beetle species, such as the Jeffrey pine beetle, fir engraver, and pine engraver, also contributed to the mortality of various tree species (California Forest Pest Council, 2004). While the mortality caused by the drought and beetles affected a broad range of plants, including hardwoods, conifers were especially harmed, with mortality rates over 90% for pines in some areas (California Forest Pest Council, 2004).

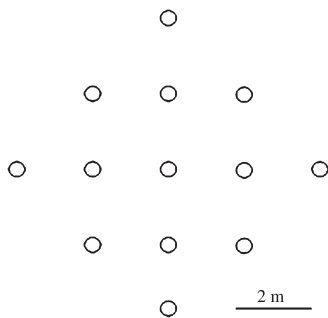
### Methods

To study the effects that this disturbance had on ant communities, we established study sites in July 2009 in an accessible area of the San Bernardino National Forest, centred roughly at 34°09′26″N, 116°57′26″W at roughly 1800 m a.s.l., just east of the town of Angelus Oaks (Fig. 1). This area saw extremely high conifer mortality during the 2003 outbreaks. The year that a tree is killed, its needles turn red (the ‘red dead’ stage), making recently killed trees easy to identify from aerial photography. Aerial photographs taken in 2003 were made available by the San Bernardino National Forest and by Google Earth. From these photographs, we identified patches of red trees (those killed by beetles in 2003) and green trees (those left intact through the beetle outbreak).

We visited candidate sites to verify their suitability. We chose locations to maximise the contrast between ‘red’ sites, where forest modification caused by bark beetles was extreme, and ‘green’ sites, which suffered little or no loss of conifers in 2003. We ruled out areas such as riparian



**Fig. 1.** Map showing the locations of our 30 sample sites. Green sites (with little or no tree mortality) are shown as black circles; red sites (with very high tree mortality) are shown as white circles.



**Fig. 2.** The standard arrangement of the 13 pitfall traps at each site.

areas where environmental factors could have clearly affected tree mortality, and avoided locations with large numbers of hardwoods, which were not subject to attack by bark beetles. In order to control roughly for other environmental factors, we tried to locate sites in pairs, with each green site accompanied by a nearby red site, but this was not possible in all cases.

In total, we set up 15 red and 15 green sites (Fig. 1), and carried out pitfall trapping at each. While pitfall traps do not yield an entirely unbiased sample of an ant community (Lassau & Hochuli, 2004), they have been shown to yield reliable estimates of community composition (Stephens & Wagner, 2006). At each site, we buried 13 pitfall traps flush with the ground, 2 m apart from one another. We set up these traps in a standard pattern (Fig. 2), modifying this pattern to avoid trees or boulders as necessary. Each trap contained approximately 40 ml of propylene glycol mixed with a drop of liquid soap.

Because our sites were widely scattered across steep terrain, it was not possible to place traps at all 30 sites in a single day.

We set out traps between 12 and 19 July 2009, and removed them from the field between 15 and 20 August, 2009. During this period, traps were replaced once, between 30 July and 4 August. We monitored the traps and added more propylene glycol if it appeared that a trap was in danger of drying out as a result of evaporation. No rain occurred during our collecting period. At all but two sites, traps were in place for at least 2 weeks before we began collecting the data reported here; this should ameliorate any 'digging-in' effect (Greenslade, 1973).

During the collecting period, some of our traps experienced disturbances that might have made it difficult for ants to be captured by that trap; that is, they were dug up by animals or filled in with debris, or the liquid in them evaporated completely. When we replaced or removed a trap, we recorded these conditions. If a disturbance interfered with the ability of a trap to collect ants during any of the collecting period, ants from that trap were excluded from our data set for purposes of calculating ant abundances.

We removed all ants to 70% ethanol and sorted them to morphospecies. Species identifications were made by one of us (A.W.) based on a subset of specimens from each morphospecies.

#### Statistical analyses

When analysing ant abundances (including when calculating Shannon and Simpson diversity indices), we applied a fourth-root transformation to reduce the influence of the extremely high numbers that can result when a trap is located close to a nest entrance or foraging trail (Hoffmann & Andersen, 2003; Barrow *et al.*, 2007). For all analyses other than the



diversity indices, we corrected for the fact that some traps were compromised, and therefore excluded from the data set, by dividing the abundance for each species by the number of available trap days for that site. Because, for many species, abundances were zero for a considerable number of the sites, we used a resampling analysis rather than a parametric test to test for species-specific differences in abundance between green sites and red sites. We used the macros JACK and BOOT (SAS Institute Inc., 2001) to take 10 000 resamples for each of the species analysed, and to calculate confidence intervals corrected for bias and skewness (BCa confidence intervals; Efron & Tibshirani, 1993) based on these resamples. We only analysed species-specific abundance data for the 13 ant species that occurred in five or more sites and had total abundances greater than 30. We applied a sequential Bonferroni correction to these 13 analyses to keep the overall confidence level at  $\alpha = 0.05$ .

To compare the overall communities found in red and green sites, we carried out an analysis of similarities (ANOSIM) with 10 000 permutations, using the analysis program PAST. We calculated similarity percentages (SIMPER) to determine which species contributed most to the overall difference between ant communities in red and green sites. We calculated Shannon and Simpson diversity indices for all sites, based on fourth-root-transformed abundances, and performed an ANOVA on these measures using the statistical program NCSS, to test for a difference in diversity between red and green sites.

We constructed species-accumulation curves using EstimateS version 8.2 (Colwell, 2011). In exploratory analyses, for both red and green sites, rarefaction curves calculated from the data from individual traps lay considerably below rarefaction curves calculated from the pooled data for sites, suggesting non-random aggregation of individuals among samples (Colwell & Coddington, 1994; Colwell *et al.*, 2004). We therefore used sample-based estimation, which accounts for such aggregation, for both rarefaction curves and for the estimation of total species richness. However, we rescaled these measures by individuals rather than samples, so that they reflect species richness rather than species density (Gotelli & Colwell, 2001). We performed 500 randomisations in EstimateS 8.2 to calculate the first-order jackknife estimator for the total species richness of the red and green habitats (Walther & Morand, 1998; Walther & Moore, 2005). So that we could rescale our estimates by the number of individuals, we used untransformed abundances, which made it unnecessary to correct these numbers by trap days.

In order to represent the differences among our sites visually, we calculated Bray–Curtis dissimilarities based on the untransformed abundances for all ant species, corrected for the number of trap days. Based on this dissimilarity matrix, we used non-metric multidimensional scaling (NMDS) in the statistical program NCSS to generate a two-dimensional plot mapping the similarities and differences among sites.

To examine patterns of co-occurrence among species, we implemented a C-score test using EcoSim 1.1 (Gotelli & Entsminger, 2012). This metric of co-occurrence is generally robust in the face of statistical noise and has a low propensity for type I errors (Gotelli, 2000). This analysis was conducted

on the full data set including all 30 sites, as well as on the 15 green sites and the 15 red sites separately.

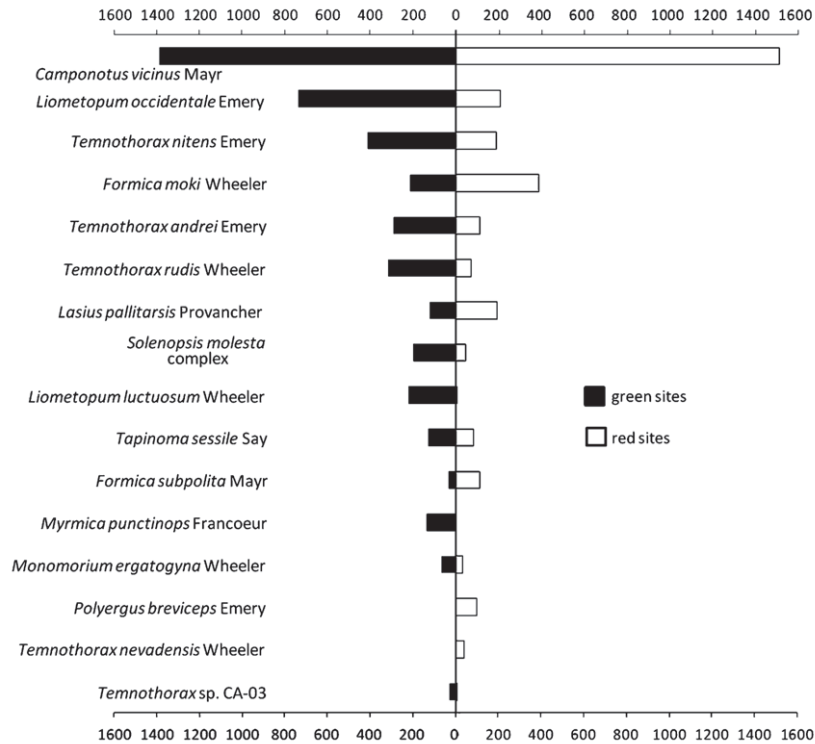
## Results

In our 30 sites, we collected 7372 ants, representing 24 species in 14 genera. Of these, 21 species (4292 individuals) were collected from green sites and 19 species (3080 individuals) from red sites, so species incidence overlapped greatly between red and green sites. The ant community in both red and green sites was dominated overwhelmingly by *Camponotus vicinus* Mayr, which was three times as abundant as any other species. Species in the genus *Liometopum* (*L. occidentale* Emery and *L. luctuosum* Wheeler) accounted for nearly a quarter of the individuals in green sites, but less than 10% of the individuals in red sites. Another quarter of the ants seen in green sites belonged to five species in the genus *Temnothorax*. These species, with the exception of *T. nevadensis* Wheeler, were caught in larger numbers in green sites than in red sites. Species in the genus *Formica* (*F. moki* Wheeler and *F. subpolita* Mayr) contributed considerably to the abundances in red sites. Figure 3 shows the abundances in red and green sites for all species with an overall abundance of more than 30 individuals.

Variation in abundance among sites was very high for almost all species, making it difficult to detect significant differences in species-specific abundance between green and red sites. After a sequential Bonferroni correction, only five such differences were significant. *Tapinoma sessile* Say, *Temnothorax* sp. CA-03, and *Liometopum luctuosum* were significantly more abundant in green sites, whereas *F. moki* and *F. subpolita* were more abundant in red sites. Two species had *P*-values that were below 0.05 but were not low enough to meet the sequential Bonferroni cutoff. These were *Monomorium ergatogyna* Wheeler and *Temnothorax andrei* Emery, both of which tended to be more abundant in green sites. The difference in total ant abundance between green and red sites was not significant.

Overall, the ant communities in green sites were strongly significantly different from those seen in red sites (ANOSIM, global  $R = 0.147$ ,  $P < 0.001$ ). About half of the dissimilarity in ant composition between green and red sites was as a result of four species: *C. vicinus*, *F. moki*, *Temnothorax nitens* Emery, and *L. occidentale*. This is unsurprising, as these species were the four most abundant species in our traps. There was a tendency for green sites to have a higher diversity than red sites, but the significance of this trend varied according to the metric being used: the difference in Shannon diversity only approached significance ( $F_{1,28} = 2.99$ ,  $P = 0.095$ ), whereas the difference in Simpson diversity was marginally significant ( $F_{1,28} = 4.34$ ,  $P = 0.047$ ). Species-accumulation curves, as shown in Fig. 4, had not reached an asymptote by the end of the sampling period, suggesting that considerable numbers of additional ant species remain unsampled in both habitat types. The first-order jackknife estimator for both green and red sites ultimately reached a value of around 26 species.

Overall, NMDS revealed that green and red sites generally tend to be separated from one another in terms of their ant



**Fig. 3.** Total abundances of ants captured across all sites, by species. Black bars to the left represent abundances in green sites. White bars to the right represent abundances in red sites. Totals are not corrected for numbers of trap days or fourth-root transformed.

communities, although there was some overlap between the two groups (Fig. 5).

When all sites were considered together, the observed  $C$ -score was significantly higher than expected owing to chance, suggesting that the ant associations in our sites are in fact highly structured ( $C = 10.53$ ,  $P = 0.001$ ). However, when red sites were considered separately, this trend only approached significance ( $C = 4.44$ ,  $P = 0.071$ ). The same was true for green sites when considered separately ( $C = 2.76$ ,  $P = 0.064$ ). This suggests that much of the apparent structure when all sites are considered together is caused by species affinities for the red or green habitats (Schoener & Adler, 1991).

## Discussion

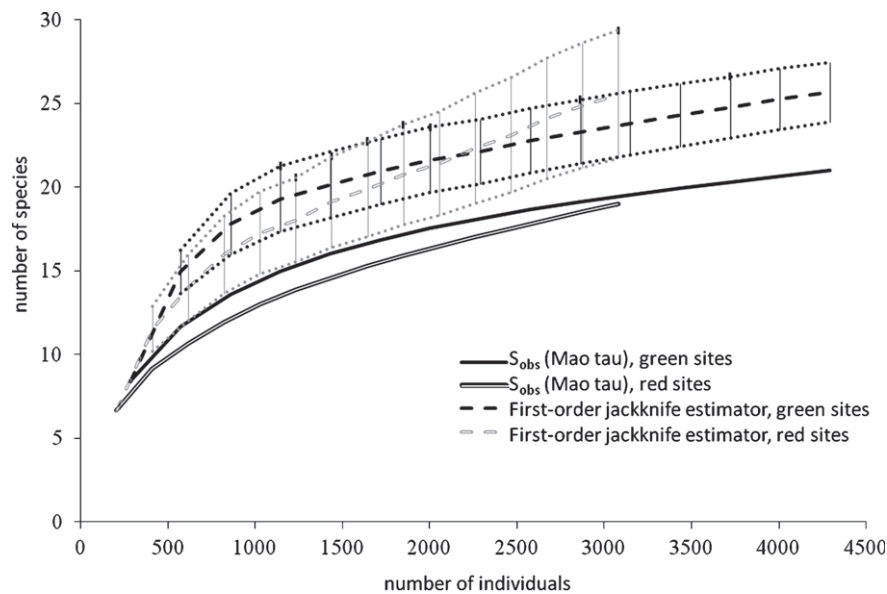
### Impacts of bark beetle outbreaks

While the tree mortality caused by the bark beetle outbreaks of 2003 had a dramatic impact on the local ant communities, this change does not appear to have been catastrophic or irreversible. It did not result in a drop in species richness, and there is no sign that it opened the way to invasive ants, as documented in some other cases of disturbance (e.g., Gibb & Hochuli, 2003; Zettler *et al.*, 2004; Bos *et al.*, 2008). Every species we collected in both types of site is native to southern California, suggesting that invasive ants such as the Argentine ant *Linepithema humile* Mayr may have lacked the opportunity

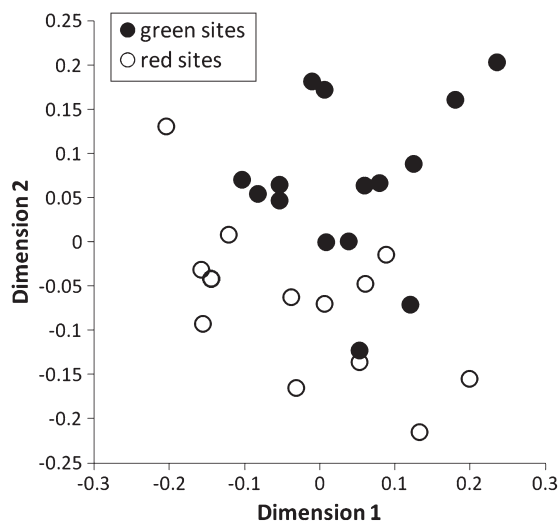
to encroach on the red sites. The outbreak also caused little turnover in ant species. Only a few species were collected exclusively from green or red sites, and those few occurred in only one or two sites, suggesting that these rare species might have been overlooked in the other type of site by chance alone. Nonetheless, the abundances of many species changed enough to significantly shift the composition of the ant community. The decrease in diversity as measured by the Simpson index reflects a drop in the evenness of the ant community; as shown in Fig. 3, a smaller number of species tend to be numerically dominant in red sites.

Our data may underestimate the impact of the outbreaks. Because the outbreaks resulted in a fine-scale mosaic of red and green patches, ant species with broad foraging ranges that chiefly inhabit one type of site may forage occasionally in the other. Captures of such foragers would blur the distinction between red and green areas. Because of the small grain of many of these patches, especially our green sites (which were generally small), edge effects have almost certainly altered the abiotic conditions in our green sites, probably further blurring this distinction. Moreover, we deliberately chose sites that varied with respect to a number of factors other than tree mortality; this made our sites more representative of the heterogeneous landscape, but also probably made it more difficult to detect statistically significant differences between red and green sites.

It should be reiterated that there were certainly numerous open areas similar to our 'red' sites before 2003, so this



**Fig. 4.** Species accumulation curves for green sites (black line) and red sites (white line). Dotted lines represent first-order jackknife estimators of species richness for these sites, with dark lines corresponding to the green sites and grey lines corresponding to the red sites. Error bars around jackknife estimators denote  $\pm$  one standard deviation.



**Fig. 5.** Dimensions 1 and 2 from non-metric multidimensional scaling (NMDS) of the Bray–Curtis dissimilarity matrix for our sampling sites, calculated from untransformed abundances corrected for the number of trap days.

disturbance event introduced nothing wholly new to the area. The effect has likely been to favour those ants that already did well in open areas (e.g. *C. vicinus* and *Formica*) and to reduce the numbers of others (*Liometopum*, *Solenopsis*, and most *Temnothorax*) that appear to prefer shaded habitats.

If we assume that other taxa in this ecosystem have had roughly similar responses, we can conclude that these forest ecosystems have experienced a dramatic change, but without widespread loss or turnover of species. It is quite plausible that some ecosystem functions have shifted significantly, and

the abundances of some species have probably changed dramatically. However, based on our data on the ant community, there is no evidence that these bark-beetle outbreaks have precipitated overwhelming change in the forest ecosystems of the San Bernardino Mountains, such as the collapse of food webs or the establishment of disruptive invaders.

#### *What factors structure ant communities in the San Bernardino Mountains?*

Inter-specific competition is considered to be a major, if not overriding, force determining ant community composition (Andersen, 1991; Cerda *et al.*, 1998; Sanders *et al.*, 2007b; Calcatera *et al.*, 2010). However, our data contain weak evidence at most for the idea that ant communities in the San Bernardino Mountains are structured by competition. The *C*-scores obtained from co-occurrence analyses of each habitat type separately are low enough that they only approach significance. Even if further investigation were to show that these *C*-scores are not as a result of chance, microhabitat associations and other ecological mechanisms besides competition can generate significant patterns of co-occurrence (Gotelli & Ellison, 2002; Sanders *et al.*, 2007a). Based on our data, inter-specific competition is certainly not an overwhelming force structuring these ant communities.

Some previous authors have suggested that thermal requirements largely govern ant community composition (Cerda *et al.*, 1998; Dunn *et al.*, 2007; Palladini *et al.*, 2007), or that temperature and competition interact to structure ant communities (Bestelmeyer, 2000; Wittman, 2007). Because our study site is at nearly 2000 m a.s.l., ants are certainly thermally limited during part of the year. Our red sites experienced much greater

insolation and higher temperatures (B. Spitzer, unpublished) than our green sites. It may be that thermal factors explain the relatively modest nature of the response of the ant community to the beetle outbreak; our sites contain primarily north temperate or boreal species (Fisher & Cover, 2007), which must tolerate severe annual temperature cycles and should therefore be relatively accommodating of temperature changes, including those that followed tree mortality.

However, the species-specific increases and decreases in abundance that we observed are not consistent with the hypothesis that thermal limitation is the chief factor structuring this community. For example, while some authors have suggested that greater ant abundances after disturbance are caused by increased insolation (e.g., Vanderwoude, 2000; Graham *et al.*, 2004; Palladini *et al.*, 2007), the average abundance in our red sites is slightly (though not significantly) less than that in our green sites. Moreover, certain ant taxa which are suggested to be dominant at high latitudes as a result of their ability to maintain nest temperatures above ambient (e.g. *Formica* and *Lasius*; Andersen, 2000) tend to be more common in red sites than in green sites.

Changes in nesting site availability appear to more accurately predict changes in the ant community between red and green sites than do changes in temperature or alterations of a dominance hierarchy. Ants such as *Liometopum* spp., which use hollows in living trees, are likely to have become limited by the availability of nesting sites after the bark-beetle outbreaks. *Temnothorax* spp. are also known to nest in plant cavities, and may have become similarly limited. Both of these genera declined, on average, in red sites. On the other hand, *Formica moki* is a soil-nesting species which favours moderately open areas, and its observed increase after tree mortality is consistent with the hypothesis that nest-site limitation is an important control on community composition in the San Bernardino Mountains. Other species, such as *C. vicinus*, which has the ability to nest in soil and downed wood alike, should not experience nesting-site limitation in either green or red areas; the relatively small shift in numbers of *C. vicinus* is consistent with this aspect of its natural history. Habitat requirements other than a need for suitable nesting sites may be responsible for the shift in some species; some ants, such as the *Solenopsis molesta* complex, are typical of a complex litter layer (Andersen, 2008), which decreased significantly with the deaths of the trees in many of the red sites (B. Spitzer, unpublished).

While the availability of nesting sites is generally recognised as an important factor with the potential to structure ant communities (Andersen, 2000, 2008; Armbrrecht *et al.*, 2006; Sanders *et al.*, 2007a), relatively little close attention has been paid to nest site availability in ant community assembly, except in a few specialised ant communities that depend on small, easily quantified nesting sites such as hollow trigs (Armbrrecht *et al.*, 2004), myrmecophytes (Davidson *et al.*, 1989; Fonseca, 1999), or other small cavities (Foitzik & Heinze, 1998; Houdeshell *et al.*, 2011). The traditional emphasis on inter-specific competition may have led to an underappreciation of the importance of forces such as nest site limitation in an ant community structure (Sanders *et al.*, 2007a). While further data must be collected to confirm that nest site limitation is

structuring ant communities in the San Bernardino Mountains, this mechanism certainly deserves more attention, perhaps not only in our study system but more generally in ant ecology as well.

Continued monitoring of these sites will be necessary to determine if the ant community shifts back towards a 'green site' profile as the vegetation recovers in the red sites. It would also be instructive for similar surveys to be made where bark beetle outbreaks have occurred farther to the north; as these outbreaks have extended all through the Rocky Mountains into Canada in recent years, the opportunity exists to compare the current study with the response of ant communities at higher latitudes, where thermal limitation may be a more important controlling factor.

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