Temperature Alters the Relative Abundance and Population Growth Rates of Species within the *Dendroctonus frontalis* (Coleoptera: Curculionidae) Community

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Insect-Symbiont Interactions

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ABSTRACT Temperature has strong effects on metabolic processes of individuals and demographics of populations, but effects on ecological communities are not well known. Many economically and ecologically important pest species have obligate associations with other organisms; therefore, effects of temperature on these species might be mediated by strong interactions. The southern pine beetle (*Dendroctonus frontalis* Zimmermann) harbors a rich community of phoretic mites and fungi that are linked by many strong direct and indirect interactions, providing multiple pathways for temperature to affect the system. We tested the effects of temperature on this community by manipulating communities within naturally infested sections of pine trees. Direct effects of temperature on component species were conspicuous and sometimes predictable based on single-species physiology, but there were also strong indirect effects of temperature via alteration of species interactions that could not have been predicted based on autecological temperature responses. Climatic variation, including directional warming, will likely influence ecological systems through direct physiological effects as well as indirect effects through species interactions.

KEY WORDS species interactions, indirect interactions, climate change, community structure, physiological ecology

Climate is a major determinant of arthropod distributions and demography (Ayres 1993, Bale et al. 2002, Parmesan 2006). Understanding how climate change will affect arthropod populations remains a priority (Dale et al. 2001, Easterling et al. 2007). Both interactions among species and autecological factors, such as climatic variables, strongly affect populations (Ayres 1993, Wootton 1994, Bale et al. 2002, Nahrung et al. 2004). Although evidence exists that species will respond individually to climate change (Bale et al. 2002, Parmesan 2006) such individual responses can disrupt interactions, leading to changes in communities (Petchey et al. 1999, Walther et al. 2002, Voight et al. 2003). Because of such disruptions, species' responses within communities might be qualitatively different from individual responses (Davis et al. 1998, Petchey et al. 1999, Walther et al. 2002, Voight et al. 2003, Barton et al. 2009, Hoekman 2010); therefore, a major goal of global change research is to understand effects within a community context.

Understanding how pest species will respond to climate change is a critical challenge (Dale et al. 2001, Crozier et al. 2006, Easterling et al. 2007, Seppäätä et al. 2009). The frequency and severity of insect pest outbreaks are expected to be influenced by climate change, resulting from the strong effects of abiotic factors (e.g., temperature and plant water stress) on insect development (Easterling et al. 2007, Seppäätä et al. 2009). However, many pest species have direct and indirect interactions with numerous other species, providing multiple pathways for climate change to affect the system (Ayres and Lombardero 2000). For example, bark beetles in the genus *Dendroctonus* harbor phoretic mites and fungi that affect beetle population dynamics (Goldhammer et al. 1990, Paine et al. 1997, Six and Paine 1998, Hofstetter et al. 2006a, Adams and Six 2007, Cardoza et al. 2008). Because demographic effects of temperature differ among these species (Lombardero et al. 2003, Hofstetter et al. 2006a, Six and Bentz 2007), how climate change will affect beetle dynamics might not be easily predicted. Other examples of pest species with intimate associates include *Angusticarpus* fungi and woodwasps (Slippers et al. 2003), pine nematodes and cerambycid beetles (Linit 1988), and bacterial endosymbionts of numerous insects including termites, aphids, and whiteflies (Moran and Telang 1998). Responses to temperature may differ among these interacting species, making it necessary to consider effects on inter-
actions when studying the effects of climate change. Here, we studied the effects of temperature on an economically important insect pest, Dendroctonus frontalis Zimmermann, and its associated mites and fungi within communities.

The southern pine beetle, Dendroctonus frontalis Zimmerman, is native to North America and attacks and kills native pines from New Jersey to Honduras. It occasionally reaches epidemic abundances, making it among the most important forest pests in North America (Thatcher et al. 1980). Population fluctuations in D. frontalis are partly the result of delayed negative feedback from coupled interactions with a specialist predator (Turchin et al. 1991), but the tendency for endogenous cycles is weaker than previously thought (Friedenberg et al. 2007), and there is accumulating evidence for strong demographic effects from interactions involving symbionts of D. frontalis (Klepzig et al. 2001, Hofstetter et al. 2006a).

Dendroctonus frontalis has a strong mutualism with two species of mycangial fungi, Entomocorticium sp. A and Ceratoxytiopsis ranactdosus Hausnier. The fungi receive selective transport (within mycangia) to new host trees and the beetle larvae feed on fungal-enriched phloem within trees (Barras and Perry 1972). The fungi only occur in association with the beetles and almost all female adult beetles (>90%) carry one or the other of these fungi (Hofstetter et al. 2006a). Entomocorticium tends to be a better nutritional source than C. ranaculosus (Coppedge et al. 1995), and beetle populations grow faster when a higher proportion of females carry Entomocorticium (Bridges 1983). Dendroctonus frontalis also transport many species of phoretic mites among host trees (Moser 1975). Tarsonemus mites, which are particularly common, are mutualists with a bluestain fungus (Ophiostoma minus Hedegcock), which they selectively transport to new host trees, propagate within trees and then consume (Bridges and Moser 1983, Lombardero et al. 2000). Ophiostoma minus might initially aid beetles in overcoming tree resistance (Klepzig et al. 2005), but overall is a strong antagonist of D. frontalis larvae, apparently because it outcompetes the mycangial fungi and is itself of poor nutritional value for beetles (Barras 1970, Klepzig and Wilkins 1997). Natural populations of D. frontalis tend to grow when O. minus is rare and decline when O. minus is abundant (Hofstetter et al. 2006a). Because Tarsonemus mites promote O. minus, they are strong indirect antagonists of D. frontalis (Lombardero et al. 2003, Hofstetter et al. 2006a).

Because of the number and complexity of strong interactions, there are multiple pathways through which temperature could affect the southern pine beetle system. For example, aetiological studies show that the growth rate of Tarsonemus populations is more sensitive to temperature than the development time of D. frontalis, implying that the antagonistic effects of mites on beetles would be greatest at 27°C and drop off rather sharply as temperatures increase or decrease from there (Lombardero et al. 2003). Furthermore, the two mycangial fungi differ in their temperature responses (Klepzig et al. 2001). Based on their autoecological responses, cooler temperatures should favor Entomocorticium relative to C. ranaculosus (Hofstetter et al. 2007), which should be beneficial to D. frontalis. Alternatively, the most important effects of temperature might arise from more complex mechanisms: e.g., interactions between Tarsonemus and other species of mites that alter interactions among fungi that influence beetles. To evaluate these possibilities we manipulated the temperature experienced by communities within trees naturally colonized by D. frontalis and their associates.

Materials and Methods

Experimental Design. We conducted two similar experiments. In both cases, we identified a set of similar adjacent trees (6-7, =25 cm diameter at breast height (dbh) and 18 m tall) that were being simultaneously attacked by the same population of D. frontalis, sampled the parental attacking beetles to characterize the incoming community of phoretic mites and fungi, waited until all attacks had ceased (indicating the period of oviposition and egg hatch within the phloem), then felled the trees, cut 6-8 replicate 40-cm bolts from the mid-bole of six or seven trees, and transported those to environmental chambers where they were distributed across temperature treatments. We collected, counted, and measured the emerging adult progeny, and examined them for phoretic symbionts. Our first study (experiment 1) began in July 2004 with seven slash pine (Pinus elliottii Engleman) in the Chickasawhay Ranger District, DeSoto National Forest, MS. The second study (experiment 2) began in October 2004 with six loblolly pine (Pinus taeda L.) in the Oakmugee Ranger District, Talladega National Forest, AL. Both Pinus species are suitable hosts for D. frontalis, though P. taeda is generally regarded as more susceptible and perhaps more suitable (Thatcher et al. 1980). In both studies, we placed four Lindgren funnel traps (unbaited) among the study trees to collect 150-200 live free-flying attacking beetles (collected over 2-4 d during the peak of attacks on study trees) that we stored individually at 1°C and later examined for phoretic mites and fungi Hofstetter et al. 2006a). We identified mites to genus (chiefly Tarsonemus, Dendrolaelaps, Trichonopoda, and Histiogaster; identity confirmed by Dr. John Moser, USDA Forest Service Southern Research Station, Pineville, LA), and also scored each beetle for presence of O. minus (experiment 1 only) and each female beetle for presence of the two mycangial fungi, C. ranaculosus and Entomocorticium sp. A (both experiments), following the methods of Hofstetter et al. (2006). We dissected and mounted the mycangium of each female in lactophenol blue dye to identify C. ranaculosus and Entomocorticium sp. A under a compound microscope (Barras and Perry 1972, Bridges 1983, Hofstetter et al. 2006a). To determine presence of O. minus on the beetles, we plated each individual on 10% malt agar to grow cultures of the fungus.

We randomly assigned two bolts per tree (one each from the lower and upper region of the mid-bole) into...
each of four or three (experiments 1 and 2, respectively) temperature regimes. The target temperatures were 23, 25, 27, and 32°C for experiment 1 and 23, 28, and 33°C for experiment 2. Mean daily temperatures in our study region range from 7 to 28°C over the year, and daily maxima regularly exceed 30°C during summer (www.noaa.gov). Thus, our experiment spanned temperatures from cool to warm relative to typical summer conditions in the Gulf Coastal region of the United States. Our treatments were also designed to range above and below 27°C, which was the predicted optimum for reproduction by *Tarsanemus* mites based on autecological measurements (Lombardero et al. 2003). We conducted experiment 1 at the USDA Forest Service Research Station in Pineville, LA, and experiment 2 at Dartmouth College in Hanover, NH. Facilities permitted one more temperature treatment in Louisiana but somewhat better temperature regulation at Dartmouth. We recorded the actual temperatures every 5 min throughout the experiment with one or more HOBO (Onset Computer Corporation, Pocasset, MA) temperature loggers per treatment: mean temperatures ± SD were: 22.8 ± 2.4, 25.5 ± 2.7, 26.0 ± 1.9, and 31.5 ± 2.6°C for experiment 1, and 23.6 ± 0.8, 28.4 ± 0.9, and 33.4 ± 1.6°C for experiment 2.

**Beetle, Mite, and Fungal Measurements.** We placed each beet in a container with a collection cup for emerging beetles. We collected emerging beetles daily and kept them at -5°C. After beetle emergence, we measured the length and circumference of each beetle and estimated the number of attack holes. We estimated the number of attacks per log by sequentially slicing thin layers of the outer bark and marking entrance holes (each representing the attack of one male-female pair). *Dendroctonus frontalis* entrance holes are usually within bark fissures, tend to enter somewhat obliquely, and generally show evidence of resin flow (hardened resin or crystals), whereas exit holes tend to be perpendicular to the bole of the tree and are frequently within rather than between bark plates. For each beetle, we removed two 20.5 by 16 cm sections of bark and measured percentage of phloem with bluestain (indicating *O. minus*) and length of oviposition gallery by tracing onto mylar acetate (Hofstetter et al. 2006a). We digitized the tracings and measured them using the program Raster to Vector® (www.raster-vector.com). To determine mite abundance within the phloem, we also counted *Tarsanemus* and non-*Tarsanemus* mites on three randomly placed one-cm² squares in areas within bluestain and three in areas with no bluestain (Lombardero et al. 2003). We multiplied the average abundance per 1-cm² by the total area within each bolt for bluestained and non-bluestained phloem separately, and then summed to give the total number of *Tarsanemus* per bolt at the end of the experiment.

We collected over 4,000 emerged beetles in each experiment. The first emergences were parent beetles that reemerged after mating and oviposition. Subsequent emergences were the progeny, which had developed from egg to adult during the experiment. We separated the reemerging beetles from progeny based upon a clear trough in the number of emerging beetles (Fig. 1). We calculated the development time (day of emergence), per capita reproductive success (λ = progeny per attacking adult), and the mean day of progeny emergence for each bolt. We compared development time to the time predicted by the biophysical model of Wagner et al. (1984).

To allow for possible patterns with respect to timing of beetle development, we subsampled beetle progeny from three stages of beetle emergence (early, peak, and late). We defined peak emergence for each bolt as the date of maximum emergence per day ± 1 d, and early and late as dates (± 1 d) when cumulative emergence was 40% less or more (respectively) of that on the date of maximum emergence. We examined this subset of beetles for phoretic mites and fungi as before and also measured female beetle length because length is positively correlated with fecundity (Coppegge et al. 1985).

We estimated *Tarsanemus* reproductive success within each bolt, R, calculated from mite abundance within the phloem at the end of experiment. We estimated the initial population size of mites per beetle in the parent generation multiplied by the number of adult beetles that entered the bolt (twice the number of attack holes), and R was calculated as $\ln(N_{\text{initial}} + 1) - \ln(N_{\text{initial}})/d$. The addition of one was required to avoid excluding a few bolts from which no mites were recorded in the phloem. For comparison, we also calculated the expected mite R for each temperature treatment. Lombardero et al. (2003) estimated mite population growth rate (mites per mite per day) at different temperatures in the laboratory. Using the recorded temperature in each of our treatments at 5-min time steps and these growth rate estimates (calibrated to 5-min time steps), we calculated the expected mite growth rate (R) in each temperature treatment. Because variation will introduce bias in nonlinear relationships (Jensen's Inequality; Ruel and Ayres 1999), using 5-min time steps allowed us to accurately account for imperfect temperature regulation, and is why our predictions of mite growth rates do not exactly match those of Lombardero et al. (2003).

**Statistical Analyses.** For most response variables, we tested for temperature effects with an analysis of variance (ANOVA) model that included temperature, tree, and temperature x tree as fixed effects. Because of unequal sample sizes for each bolt, we averaged response variables within each bolt. No beetles emerged from two trees at the highest temperature, so we excluded these trees from the analyses. We log transformed a and arc-sine-square root-transformed proportion of bluestained in phloem. We analyzed mites per beetle for each mite genus using an ANOVA with full factorial design including temperature, stage, and tree as fixed effects, as well as the interaction terms. To analyze the effect of temperature treatment on the proportion of beetles with each fungus, we used $\chi^2$ tests (Sokal and Rohlf 1995). We performed the statistical tests by using JMP V. 5 (SAS Institute 2002).
Fig. 1. The number of *D. frontalis* emerged each day varied among temperatures in experiment 1 (A) and experiment 2 (B). The first peak represents reemerging adults from the parental generation, while the second peak represents emerging adult progeny beetles.

## Results

**Initial Conditions.** Attack densities did not differ among temperature treatments: grand mean ± 1SE = 2.91 ± 0.13 and 3.33 ± 0.08 attacks per dm² in experiments 1 and 2 (Table 1). The length of oviposition gallery did not vary with temperature in experiment 1 (91.45 ± 0.10 cm/dm²) and varied among temperatures in experiment 2 (59.77 ± 2.55, 60.80 ± 2.55, and 43.68 ± 2.55 cm/dm² at 23, 28, and 33°C) (Table 1).

In both experiments, the parental female beetles were about equally split between those carrying *Entomocorticium* versus *C. ranaculosus* in their mycangia, but there were more females that carried neither in experiment 1 (number of individuals in each category 21:25:12 and 11:8:1 in experiments 1 and 2, respectively; Fig. 3). The percentage of attacking beetles carrying the bluestain fungus, *O. minus*, was 15.5 and 40.1% for each experiment. Phoretic mites were also common: the mean ± SEM initial abundances of *Tarsomermus, Dendrobaenoptes, Trichouropoda*, and *Histiosporus* per beetle were 1.79 (0.26), 1.04 (0.18), 1.87 (0.34), and 0.43 (0.07) in experiment 1 and 3.56 (0.88), 0.27 (0.15), 0.40 (0.14), and 0.00 (0.00) in experiment 2, respectively.

**Beetle and Mite Reproduction and Transmission of Fungi.** Beetle reproduction was higher in experiment 2 than in experiment 1, but declined markedly with increasing temperature, from λ of ≈ 0.8–0.2 in exper-
Table 1. ANOVA F-ratios of D. frontalis bolt attack density, no. of re-emerging parental beetles, gallery density, reproduction, and proportion of bluestain phloem

<table>
<thead>
<tr>
<th>Source</th>
<th>df</th>
<th>Attack Density (df = 6, P = 0.00076; df = 2, P = 0.009)</th>
<th>Gallery Length (df = 6, P = 0.00076; df = 2, P = 0.009)</th>
<th>Beetle λ (df = 6, P = 0.00076; df = 2, P = 0.009)</th>
<th>Proportion O minus Phloem (df = 6, P = 0.00076; df = 2, P = 0.009)</th>
</tr>
</thead>
<tbody>
<tr>
<td>Temp.</td>
<td>3.2</td>
<td>1.61 2.14 8.90** 2.10**</td>
<td>0.05 14.20*** 4.93**</td>
<td>13.31*** 47.90***</td>
<td>0.91 ** 3.79*</td>
</tr>
<tr>
<td>Tree</td>
<td>6.5</td>
<td>2.26 0.39 7.70** 0.11</td>
<td>0.02 6.37**</td>
<td>1.20</td>
<td>0.93 2.90***</td>
</tr>
<tr>
<td>Temp. x Tree</td>
<td>18, 10</td>
<td>0.15 1.24</td>
<td>1.20 2.15</td>
<td>0.54</td>
<td>1.10</td>
</tr>
</tbody>
</table>

Degrees of freedom, df, refer to slash and loblolly experiments, respectively. Asterisks signify statistical significance: * P < 0.05, ** P < 0.01, *** P < 0.0001. Error degrees of freedom are 25 for slash pine and 35 for loblolly pine.

Temperature effects were conspicuous compared with variance among individual trees, which was undetectable (Table 1). Temperature did not affect size of adult progeny in experiment 1 (mean ± SEM = 2.81 ± 0.02 mm) and only slightly in experiment 2 (2.99 ± 0.02 mm versus 2.98 ± 0.02 mm at 23 versus 28°C; Table 2). Beetle development time generally matched predictions of the model of Wagner et al. (1984), with the greatest departure being that beetles in the 23°C treatment in experiment 2 emerged 4 d earlier on average than predicted (Fig. 2B; Table 2).

Temperature manipulations altered the relative abundance of mycangial fungi in adult progeny beetles (experiment 1: χ² = 23.12, df = 6, P = 0.00076; experiment 2: χ² = 5.35, df = 2, P = 0.069; Fig. 3). In both experiments, the percentage of beetles with Entomocorticium in their mycangium declined with increasing temperature. In experiment 2, this was compensated by an increase in C. ranaculoides, whereas in experiment 1 the proportion of beetles without mycangial fungi increased (to 36% at 32°C).

In both experiments, the abundance of the bluestain fungus, O. minus, decreased from 20 to 5% of the phloem colonized with increasing temperature (Fig. 2C; Table 1). The proportion of emerging progeny beetles with O. minus inoculum on the exoskeleton also decreased at higher temperatures, but this trend was not significant (experiment 1: 26.8, 22.2, 21.9, 10.5% with inoculum at 23, 25, 27 and 32°C, respectively: χ² = 4.20, df = 3, P = 0.24). Beetle reproduction decreased with increasing proportion of bluestain phloem only at the lowest temperature in experiment 2 (F = 10.85; df = 1, 10; P = 0.008); however, in all other treatments there was no relationship (P > 0.05; Fig. 4).

The per capita reproduction of Tarsonomus mites decreased with increasing temperature (Fig. 5; Table 3). The pattern was a poor match to the aetiological prediction that reproduction should have been greatest at intermediate temperatures. Realized per capita growth rate was negative in all treatments except 25°C in experiment 1.

Temperature affected phoretic mite abundance, but the patterns varied among genera of mites (Fig. 6; Table 4). The abundance of phoretic Tarsonomus declined as temperatures increased in experiment 1 but not experiment 2. In contrast, the abundance of

Fig. 2. (A) D. frontalis reproduction observed at each temperature treatment. No beetles emerged at the highest temperature in experiment 2. (B) Observed D. frontalis development time at each temperature treatment. Dashed line represents the predicted development time from a biophysical model (Wagner et al. 1984). (C) The proportion of phloem colonized by O. minus. In all panels means ± SEM are shown.
Fig. 3. Relationships between beetle reproduction (A) and phloem bluestain abundance within experiment 1 (A) and experiment 2 (B) for each temperature treatment.

Trichostrongyloidea, Histiogaster, and to a lesser extent, Deudroloelaps, tended to increase from 23 to 26°C. With further temperature increases, the abundance of Deudroloelaps and Trichouropoda remained stable, while that of Histiogaster dropped sharply, and were not found in experiment 2.

Table 2. ANOVA F-ratios of D. frontalis size and development time (mean day of emergence)

<table>
<thead>
<tr>
<th>Source</th>
<th>Beetle length (mm)</th>
<th>Mean day of emergence</th>
</tr>
</thead>
<tbody>
<tr>
<td></td>
<td>df</td>
<td>Slash</td>
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<td>0.61</td>
</tr>
<tr>
<td>Tree</td>
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<td>1.57</td>
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<tr>
<td>Temp. × Tree</td>
<td>12.5</td>
<td>0.31</td>
</tr>
<tr>
<td>Error</td>
<td>12.1</td>
<td>18.11</td>
</tr>
</tbody>
</table>

Degrees of freedom, df, refer to slash and loblolly experiments, respectively.
Asterisks signify statistical significance: * $P < 0.05$, ** $P < 0.01$, *** $P < 0.0001$.

Discussion

Experimental manipulation of temperature altered the relative abundance and relative population growth rates of species within the D. frontalis community. *Deudronotous frontalis* population dynamics are influenced by both climate (Ungerer and Ayres 1999, Gan 2004) and interactions with other species (Barras 1973; Bridges 1983; Goldhammer et al. 1990; Turchin et al. 1991; Lombardero et al. 2003; Hofstetter et al. 2006a, 2007). Results indicated direct effects of temperature on species' development and survival, and suggested further indirect effects from changes in species interactions, supporting the view that communities are structured by both autecological responses of species to environmental factors as well as effects on strong interactions among species.

Direct effects of Temperature on Beetles. *Deudronotous frontalis* reproduction decreased at higher temperatures in both experiments, possibly from direct physiological consequences. Even though attack densities were similar among treatments fewer parental
beetles reemerged at higher temperatures, indicating increased mortality (Fig. 1; Table 1). As reemerged females might oviposit in other host trees (Thatcher et al. 1980), higher temperatures might directly reduce lifetime beetle reproduction because of increased mortality.

Temperature affected beetle reproduction through direct effects on progeny. Gallery length (a surrogate for egg number, Lashomb and Nebeker 1979) was similar among treatments (Table 1); thus, differences in the number of progeny reflected differences in survival during development. Temperature had little effect on progeny size, but median development time decreased with increasing temperature in experiment 1. Treatment effects on development time were less evident in experiment 2 (probably partly because logs spent 4 d en route to New Hampshire and therefore spent somewhat less time in temperature treatments), but in both experiments, development time approximated the projected development time based on a biophysical model of D. frontalis development (Fig. 2B; Wagner et al. 1984). Temperatures were relatively constant during both experiments, compared with natural diurnal fluctuations in field conditions. Even the highest temperature treatment encompasses temperatures regularly experienced by beetles in the field, but high field temperatures have been reported to reduce beetle population growth and brood survival (Thatcher and Pickard 1964, Gagne et al. 1980, Friedenberg et al. 2008). Our results support this and other earlier work (Wagner et al. 1984), despite differences in diurnal temperature fluctuations. Host species might have also driven differences observed between the two experiments, because pines differ in suitability for Dendroctonus (Langor et al. 1990, Veysey et al. 2003). The tendency for better beetle reproduction in experiment 2 (Fig. 2A) might have occurred because P. taeda is a better host than P. elliottii (Hodges et al. 1979, Thatcher et al. 1980). Collectively, these results indicate strong direct effects of temperature on D. frontalis reproductive success.

Effects of Temperature on Species Interactions. In addition to the direct effects of temperature, interactions with O. minus, Tarsenomus, or mycanial fungi might have affected beetle reproduction. High abundance of O. minus (bluestain) generally yields poor survival of beetle larvae (Barras 1970, Lombardero et al. 2003, Hofstetter et al. 2006a). We found a significant relationship between bluestain and beetle A in only one treatment, probably because the abundance of bluestain in phloem was generally below the threshold of ∼40% where effects tend to be strongest (Figs. 2C and 4; Hofstetter et al. 2006a). Differences among pine species affect the performance of Ophiostomatoid fungi (Cook and Hain 1988, Hofstetter et al. 2005, Rice et al. 2007); therefore, the slightly higher proportion of bluestained phloem in the second experiment might have resulted from higher host quality of P. taeda for O. minus. However, overall there was little bluestained phloem, and little evidence that temperature effects
However, the effect of temperature on *Tarsonomus* populations did not match the predicted autecological measurements (Fig. 5; Lombardero et al. 2003) indicating that temperature effects on *Tarsonomus* within a community are more complicated than expected from direct physiological effects. *Tarsonomus* mite abundance was not directly related to *O. minus* abundance in phloem (Figs. 2C, 5 and 6), contrary to other studies with higher bluestain abundances (Lombardero et al. 2003, Hofstetter et al. 2006a).

Temperature effects on interactions among species might explain patterns in *Tarsonomus* reproduction. *Histioaster* and *Trichouropoda* (fungivores and scavengers) and *Dendrolaelaps* (predators) all have the potential to interact with *Tarsonomus* through resources competition or predation (Moser and Roton 1971, Moser 1975). In experiment 1, *Tarsonomus* reproduction decreased sharply from 25 to 26°C (Figs. 5 and 6), which coincided with sharp increases in *Histioaster*, *Dendrolaelaps*, and *Trichouropoda* abundances (Fig. 6). In experiment 2, where *Histioaster* was rare or absent, *Tarsonomus*, *Dendrolaelaps*, and *Trichouropoda* abundances were positively correlated across temperatures (Fig. 6). We speculate that *Histioaster* might be a strong antagonist of *Tarsonomus*, presumably via resource competition, and that temperature mediates their interactions.

Experiments indicated further indirect effects of temperature related to mycangial fungi (nutritional symbionts) abundance on *D. frontalis*. Both fungi showed clear responses to temperature, but results differed slightly between the two experiments (Fig. 3). This might be because of host differences in secondary metabolites that could alter the relative performance of the fungi (Hofstetter et al. 2005, Rice et al. 2007), though we are aware of no studies that have examined differences between *P. radiata* and *P. elliottii* on fungal performance. Regardless of the potential tree effects, *Entomocorticium* sp. A performed poorly at high temperatures. The decrease in *D. frontalis* at high temperatures could be a direct result of poor mycangial fungal growth (Goldhammer et al. 1990, Coppege et al. 1995). Furthermore, future reproduction at the highest temperatures would be limited as a proportion of emerging beetles had no mycangial fungi, which leads to decreased reproductive success. Constant temperatures in the treatments depart from field conditions, and periodic, rather than constant, high temperatures might buffer their effects. However, our experimental results match expectations from observations in the field for fungi associated with both *D. frontalis* (Hofstetter et al. 2006b) as well as *D. ponderosa* (Adams and Six 2007, Six and Bentz 2007); thus, experimental results are likely relevant to field dynamics. While temperature might have had direct effects on *D. frontalis*, indirect effects via mutualistic fungi had clear consequences for beetle reproduction, which could then affect associated species (e.g., phoretic mites).

Temperature had an opposite effect on *C. ranaculous*, the other nutritional symbiont of *D. frontalis*. *Ceratothrips* *ranaculous* was either not affected by
भोवणी ३/६, बोपेंकुंड, पुणे - ४१२ ००७

(५८४) ३६२ ८०००

"बोपेंकुंड" येथे स्थापित केलेले जागीरदारी पुणे जिल्ह्यातील "पुणे नगरपालिकेच्या भागात" येथे म्हणजेच "पुणे शहर" येथे आहे। येथे जुन दिलीले "पुणे सिटी" म्हणजेच "पुणे शहर" येथे आहे। येथे जुन दिलीले "पुणे सिटी" म्हणजेच "पुणे शहर" येथे आहे। येथे जुन दिलीले "पुणे सिटी" म्हणजेच "पुणे शहर" येथे आहे। येथे जुन दिलीले "पुणे सिटी" म्हणजेच "पुणे शहर" येथे आहे। येथे जुन दिलीले "पुणे सिटी" म्हणजेच "पुणे शहर" येथे आहे। येथे जुन दिलीले "पुणे सिटी" म्हणजेच "पुणे शहर" येथे आहे। येथे जुन दिलीले "पुणे सिटी" म्हणजेच "पुणे शहर" येथे आहे। येथे जुन दिलीले "पुणे सिटी" म्हणजेच "पुणे शहर" येथे आहे। येथे जुन दिलीले "पुणे सिटी" म्हणजेच "पुणे शहर" येथे आहे। येथे जुन दिलीले "पुणे सिटी" म्हणजेच "पुणे शहर" येथे आहे। येथे जुन दिलीले "पुणे सिटी" म्हणजेच "पुणे शहर" येथे आहे। येथे जुन दिलीले "पुणे सिटी" म्हणजेच "पुणे शहर" येथे आहे। येथे जुन दिलीले "पुणे सिटी" म्हणजेच "पुणे शहर" येथे आहे। येथे जुन दिलीले "पुणे सिटी" म्हणजेच "पुणे शहर" येथे आहे। येथे जुन दिलीले "पुणे सिटी" म्हणजेच "पुणे शहर" येथे आहे। येथे जुन दिलीले "पुणे सिटी" म्हणजेच "पुणे शहर" येथे आहे। येथे जुन दिलीले "पुणे सिटी" म्हणजेच "पुणे शहर" येथे आहे। येथे जुन दिलीले "पुणे सिटी" म्हणजेच "पुणे शहर" येथे आहे।