Species Interactions and Thermal Constraints on Ant Community Structure

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1 SPECIES INTERACTIONS AND THERMAL CONSTRAINTS ON ANT COMMUNITY

2 STRUCTURE

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Abstract

Patterns of species occurrence and abundance are influenced by abiotic factors and biotic interactions, but these factors are difficult to disentangle without experimental manipulations. In this study, we used observational and experimental approaches to investigate the role of temperature and interspecific competition in controlling the structure of ground-foraging ant communities in forests of the Siskiyou Mountains of southwestern Oregon. To assess the potential role of competition, we first used null model analyses to ask whether species partition temporal and/or spatial environments. To understand how thermal tolerances influence the structure of communities, we conducted a laboratory experiment to estimate the maximum thermal tolerance of workers and a field experiment in which we added shaded microhabitats and monitored the response of foragers. Finally, to evaluate the roles of temperature and interspecific competition in the field, we simultaneously manipulated shading and the presence of a dominant competitor (*Formica moki*). The foraging activity of species broadly overlapped during the diurnal range of temperatures. Species co-occurrence patterns varied across the diurnal temperature range: species were spatially segregated at bait stations at low temperatures, but co-occurred randomly at high temperatures. The decreased abundance of the co-occurring thermophilic *Temnothorax nevadensis* in shaded plots was a direct effect of shading and not an indirect effect of competitive interactions. Thermal tolerance predicted the response of ant species to the shading experiment: species with the lowest tolerances to high temperatures showed the greatest increase in abundance in the shaded plots. Moreover, species with more similar thermal tolerance values segregated more frequently on baits than did species that differed in their thermal tolerances. Collectively, our results suggest that thermal tolerances of

39 ants may mediate competitive effects in habitats that experience strong diurnal temperature

40 fluctuations.

Introduction

42   A major goal of ecology is to identity the processes that control patterns of community

43 structure. At large spatial scales, historical processes determine properties of the regional

44 species pool (Ricklefs 2004), which in turn influence the composition of local communities

45 (Webb et al. 2002, Wiens and Donoghue 2004). At smaller spatial scales, both abiotic filtering

46 (pH, temperature, water availability, etc.), and biotic interactions (interspecific competition,

47 parasites, herbivory, etc.) may operate to determine which species occur, and co-occur, together

48 within the local community (Weiher and Keddy 1999, Cavendar-Bares et al. 2009).

49   Within local communities, theory predicts either separation or aggregation of important

50 ecological traits among closely related species, depending on the relative role of biotic

51 interactions vs. the abiotic environment, respectively, on community membership. Closely

52 related species occurring in the same habitat often have similar requirements and share similar

53 ecological traits. Thus, classical niche theory of limiting similarity (Hutchinson 1959, MacArthur

54 and Levins 1967) predicts that species with similar traits cannot coexist due to competition for

55 limiting resources. Competitive exclusion may occur between species sharing similar ecological

56 traits, resulting in segregation of species with similar traits (e.g. Winston 1995). On the other

57 hand, if tolerance to abiotic conditions is more important than biotic interactions, then species

58 can only occur if they possess specific ecological traits. When environmental conditions

59 primarily determine community membership, we expect to find positive associations of species

60 with similar traits across sites (e.g. Jackson et al. 1992).

61   Ants are an ideal taxon with which to study the relative influence of biotic and abiotic

62   environment, as there is good evidence that both interspecific competition (reviewed in

63   Hölldobler and Wilson 1990) and thermal constraints on foraging activity and colony

64   performance (Bestelmeyer 1997, Cerdá et al. 1998, Holway et al. 2002) control ant community

65   structure. Ant responses to temperature and competition have been used to describe dominance-

66   diversity patterns on continental scales (Andersen 1992, Parr et al. 2005), responses to

67   disturbance (Andersen 1991, York 2000, Farji-Brener et al. 2002), and the invasion success of

68   non-native species (Holway et al. 2002).

69   In this study, we first measured statistical patterns of ant species co-occurrence and

70   activity at food resources. We then measured the thermal tolerance of the eight most common ant

71   species in a laboratory experiment. Finally, we added shade and removed a dominant ant

72   competitor in a controlled field experiment to understand how thermal tolerance and interspecific

73   competition shape ant communities. Specifically, we asked: (1) Is there statistical evidence that

74   species partition their temporal or spatial environment over a range of temperatures? (2) Does

75   physiological thermal tolerance predict how species respond to changes in their thermal

76   environment? (3) Are species with more similar thermal tolerance traits more or less likely to co-

77   occur within sites? (4) Do temperature and the presence of a behaviorally dominant species

78   interact to affect the foraging activity of a subordinate species?

79   **Methods**

80   **Study Area**

81   This research was conducted in the Siskiyou Mountains of southwestern Oregon and

82   northern California, USA, during the summers of 2003 – 2005. This area is part of the Klamath-

83   Siskiyou ecoregion that has a Mediterranean climate with cool winters (mean January minimum

4

84   temperature = 0 °C) and warm dry summers (mean July maximum temperature = 31.7 °C; mean

85   annual precipitation = 154 cm, with only 4 cm falling between June and August). During the

86   summer months there is a large diurnal variation in temperature (soil surface temperature range

87   of 10-75°C), but relatively little monthly variation (mean monthly temperatures of June, July,

88   August between 21.1 and 26.6°C). Forests are mostly open stands of *Pinus jeffreyi*; other

89   sclerophyllous trees are reduced to a shrub layer (Whittaker 1960).

90   **Temporal and Spatial Partitioning**

91   We first assessed whether species partitioned their temporal or spatial environments. We

92   used null model analysis of patterns of species occurrence and worker abundance throughout day

93   across 16 environmentally homogeneous, representative forest sites. During the summer of 2003,

94   we sampled the ant community by establishing in each site an 8×8 m sampling grid of 25 bait

95   stations arranged in a 5×5 grid with 2-m spacing. Each bait station consisted of two laminated

96   7.6×12.7 cm index cards, one baited with ~5.5 g of tuna and the other with a 6,280 mm^3 volume

97   cotton ball soaked in honey water. Each bait station was censused a total of 9 times (3

98   observations in each of 3 time blocks). Time blocks began at 08:30, 13:00, and 18:30h, and the

99   three observations within each time block were separated by 30 minutes (i.e., 08:30, 0:900,

100   09:30).

101   Species occurrences at baits may be dominated by behaviorally aggressive or mass-

102   recruiting species, so that baits can potentially under-sample trophic specialists, solitary foragers,

103   and behaviorally subordinate species. We used several baits in each site and made multiple

104   observations throughout the day to minimize these potential omissions (Bestelmeyer et al. 2000).

105   We supplemented the bait-station data by visually searching the plots during all 9 sampling

106   periods, but only one ant species that did not occur at baits, *Lasius flavus*, was found by visual

107   searching. Thus, we are confident that our sampling strategy captured the potential changes in

108   the activity of foraging ants over the course of the day and adequately sampled the community.

109   During each of the nine sampling periods, we observed each bait station for

110   approximately 20 seconds, recorded the number and identity of each species present, and

111   estimated the soil surface temperature to the nearest 0.1°C using a Raytek® Raynger ST20 XB

112   hand-held infrared thermometer (Santa Cruz, CA USA). Individual workers were collected at the

113   end of a time block if they could not be readily identified in the field. Phil Ward at the University

114   of California, Davis confirmed the species identifications. Voucher specimens are deposited at

115   the University of Tennessee in Knoxville. Nomenclature follows Bolton (2003).

116   **BACI Shading Experiment**

117   During June–August, 2004, we conducted a shading experiment at a single site (SE)

118   within the sampling area of the 2003 census (42.49°N, 123.78°W, elevation 430 m.a.s.l.). Rank

119   abundances and behavioral profiles of ants at the shading experiment site were similar to those of

120   ants sampled at other sites in the region in 2003 (Wittman 2007). Fifteen pairs of shade and no

121   shade (=control) blocks were established throughout the site in a randomized block design. Each

122   block was located in a relatively homogenous environment, and treatments were randomly

123   assigned to plots within the block. Within a block, two treatment areas of 0.5m × 0.5m were

124   delineated with four 25-cm metal stakes driven into the ground on each of the four corners.

125   Control plots received no further manipulation. Shade plots were covered with heavy-duty brown

126   industrial polyethylene tarps (CMS Quality Tarps, Baxter, MN) that were taped to the four stakes

127   at a height of 15 cm above the substrate. Treatments within each block were separated by 5 m,

128   and blocks were separated by 15 to 25 m.

129   Less than 20% of the shaded plots contained nest entrances (of those shade additions

130   covering nest entrances, about half belonged to *Temnothorax nevadensis* and half to *Solenopsis*

131   *molesta*). Moreover, we followed foragers from baits back to nest entrances and found that nest

132   entrance locations did not change during the duration of our experiment.

133   We sampled once every five weeks in a Before-After-Control-Impact (BACI) design

134   (Underwood 1994). The control stations were observed over the entire five week period while

135   the treatment stations were observed before (2 weeks) and after (3 weeks) shading (= "impact").

136   Shade treatments had covers added the night before sampling and removed the evening after

137   sampling.

138   On sampling days, baits were set under control and shade stations at 07:30 and censused

139   seven times throughout the day (three morning, one afternoon, and three evening samples).

140   Sampling periods began at 08:15, 14:30, and 18:15, and periods with multiple censuses were

141   sampled every 45 minutes. Baits consisted of ~5 g of tuna in oil placed on 7.6×12.7 cm

142   laminated index cards. At each census, we recorded the number and identity of each species and

143   estimated the soil surface temperature under and around each bait station to the nearest 0.1°C

144   using a Raytek® Raynger ST20 XB hand-held infrared thermometer (Santa Cruz, CA USA).

145   To assess competitive ability of each species, we quantified species interactions and

146   behavioral dominance at the control baits. Pairwise interactions between workers of two different

147   species were categorized as "attacks" or "avoidances" (see Fellers 1987). An attack consisted of

148   active participation of at least two workers in which one individual bit, chased, lunged, or used

149   chemical spray to cause the other individual to retreat. Occasionally an attack would result in a

150   severe injury or death. Avoidance behavior occurred when workers of one species retreated from

151   the bait card after making contact with another in the absence of an obvious attack. A species

152   was characterized as dominant if it attacked or if its presence elicited avoidance behavior in

153   individuals of another species. Using the method of Fellers (1987), the dominance index for each

154   species was defined as the percentage of times it was dominant during all instances of its attacks

155   and avoidances (Table 1). Note that some dominance indices are based on only one observation;

156   however, the general pattern of dominance and bait occurrence displayed in Table 1 is consistent

157   with behavioral and occurrence data collected at 16 other sites in the region (Wittman 2007).

158   **Thermal Tolerance Experiment**

159   We measured thermal tolerance of all eight species observed during the BACI shading

160   experiment (species listed in Table 1). We collected workers of each species from nest entrances

161   and vegetation that was well beyond the area of the shading experiment. Within four hours of

162   field collection, individual workers were exposed to slowly increasing temperatures in a VWR

163   Scientific heat block (Batavia, IL USA). Eight workers of each species were placed into

164   individual 1.5-mL microcentrifuge tubes and randomly assigned to a well within the heat block.

165   Temperature exposure began at 40°C and was increased in 2° intervals to 50°C. Individuals were

166   exposed to each temperature for 10 minutes, and the temperature was recorded when individuals

167   died or permanently lost muscle coordination. Each species trial was replicated six times. The

168   mean temperature of death for the eight individual workers was calculated as an index of thermal

169   tolerance for each species.

170   **Shading and Species Removal Experiment**

171   To determine if the reduction in *T. nevadensis* abundance in the shading experiment was

172   due to the direct effect of the shade or due to the indirect effects of changes in a competitively

173   dominant species, we conducted a full factorial shading and species removal experiment. The

174   shading and removal experiment was conducted during June – August, 2005, at the same site as

8

175   the 2004 BACI shading experiment. From the census data in the BACI shading experiment,

176   *Formica moki* was the most widespread and behaviorally dominant species (Table 1), so it was

177   the focal removal species in 2005. We located *F. moki* nests by baiting with Keebler Pecan

178   Sandies™ and following workers to their nest. After locating 24 nests, we randomly assigned the

179   area around the nest entrance to one of the four treatments: 1) shading; 2) *F. moki* removal; 3) *F.*

180   *moki* removal and shading; 4) control (neither shading nor *F. moki* removal). Shading treatments

181   were the same as in the BACI shading experiment, but tarps were kept in place permanently to

182   allow more time for the application of the species removal treatments. As in the BACI shading

183   experiment, very few shade tarps covered nest entrances, and there was no evidence of nest

184   entrance relocation during the experiment.

185   We denied *F. moki* workers access to removal treatments by installing temporary fencing

186   and setting temporary "distraction" baits close to the nest entrance(s) to lure *F. moki* workers

187   away from the removal plots. Once treatments were in place, we sampled for a total of 7 days;

188   each sampling day was separated by 2-3 days. Baits were set at 07:30 and we sampled stations

189   every hour from 08:00 until 11:00. Data from one removal plot was not included in the analysis

190   because we were not able to successfully remove *F. moki*. Data from two control stations were

191   also excluded because foragers in these plots were affected by the "distraction" baits used in the

192   removal experiment.

193   **Analyses**

194   *Temporal Overlap and Spatial Partitioning*

195   *Temporal Niche Overlap*—To determine whether species segregate or aggregate their activity

196   over the diurnal timeframe, we used null model analyses to examine the temporal overlap of

197   species at each of the 16 plots sampled in 2003. Matrices were constructed with species (n = 5 to

198   12 species) as rows and time of day (n = 9) as columns for each plot. Matrix entries were the

199   number of baits (max = 25) occupied by each species at each observation period in each plot.

200   We used the Czekanowski index (Feinsinger et al. 1981), which quantifies the

201   overlapping histogram area of temporal niche use for a pair of species. It is a symmetrical index

202   that ranges from 0 (no overlap) to 1 (complete overlap) and is calculated for each unique species

203   pair in the assemblage. For species 1 and 2, the Czechanowski index is defined as:

$$O_{12} = O_{21} = 1.0 - 0.5 \bullet \sum_{i=1}^{n} |p_{1i} - p_{2i}|$$

204

205   where p_i is the proportion of occurrences of species 1 in time interval = 1 to 9.

206   The average pairwise niche overlap was then compared to the average calculated for

207   randomized assemblages. Communities were randomized 1000 times using Randomization

208   Algorithm 2 (RA2) of the niche overlap model in EcoSim, version 7 (Gotelli and Entsminger

209   2006). RA2 retains zero states: if a species never occurred naturally during a specific time

210   period, it would not in the randomized assemblage either (Winemiller and Pianka 1990). RA2

211   also relaxes niche breadths, substituting a random uniform number for bait occupancy

212   throughout the day. This algorithm is recommended when certain resource states are unavailable

213   for some species (e.g. when physiological constraints prevent activity during hot times of the

214   day) but there are no other constraints on resource use (Gotelli and Entsminger 2006). Resource

215   states were set as equiprobable, as time is assumed to be equally "available" to all species in the

216   absence of species interactions. If species are partitioning the time of day in which they are

217   active, then the niche overlap index should be smaller than expected by chance (i.e. smaller than

218   the indices generated from the null assemblages).

219   S*patial Partitioning*—To determine whether species co-occurrence patterns were segregated or

220   aggregated in space, we analyzed species co-occurrence patterns at baits within each of the 16

10

221   forested sites. Furthermore, to determine whether the spatial pattern of co-occurrence varied

222   among diurnal times and temperatures, we analyzed species occurrence patterns during one

223   sampling period in the morning, afternoon, and evening. Presence-absence matrices were

224   constructed with species (n = 1 to 9) as rows and bait locations (n = 25) as columns. A total of 48

225   (3 times of day × 16 replicates) matrices were evaluated.

226   We used the C-score of Stone and Roberts (1990) to evaluate species co-occurrence

227   patterns. This score measures the average number of "checkerboard units" of all species pairs of

228   an assemblage. Each checkerboard unit is calculated by $(r_a - S)(r_b - S)$ where S is the total

229   number of 'sites' (e.g. bait locations) shared by the species pair, and r_a and r_b are the row totals

230   for species a and b, respectively. Species that always occur together (complete aggregation) will

231   have a C-score of zero. The greater the segregation in species, the larger the C-score will be.

232   Observed C-scores were compared to average C-scores generated from 5,000 randomized

233   matrices. Null assemblages were created in EcoSim using a fixed-equiprobable model (SIM2),

234   an algorithm robust to both Type I and Type II error (Gotelli 2000). In this model, row totals (=

235   number of baits a species occupies) are held constant and the 25 bait stations are treated as

236   equally suitable for species occupation. Differences in the standard effect size (SES) were

237   compared among times of day with a one-way Analysis of Variance (ANOVA). The SES reports

238   the number of standard deviations the observed index is above or below the mean of the

239   randomized assemblage to allow comparison among multiple tests (Gurevitch et al. 1992). It is

240   calculated as $(I_{obs} - I_{sim})/S_{sim}$, where I_{obs} corresponds to the index for the observed assemblage, I_{sim}

241   corresponds to the index for the null assemblages, and S_{sim} is the standard deviation of the null

242   assemblages. Assuming a normal distribution of deviations, approximately 95% of the SES

11

243   values should fall between -1.96 and 1.96. Values larger than 1.96 indicate non-random species

244   segregation, and values lower than -1.96 indicate non-random species aggregation.

BACI Shading Experiment

246   Differences in abundance between shade and control groups were evaluated with a

247   randomized block ANOVA. Shade was considered to be a fixed effect, and analyses were run

248   separately for each week, i.e. during times when all stations were unshaded (weeks I and II) and

249   during times when half of the stations were shaded (weeks III-V). We estimated abundance as

250   both bait occurrence and abundance. Bait occurrence values were defined as the number of baits

251   visited by different species, regardless of the number of workers present. Abundance was defined

252   as the total number of workers recorded at baits, and was log transformed to meet assumptions of

253   ANOVA. We analyzed the abundance of all species combined as well for the abundance of *T.*

254   *nevadensis*, the only species common enough to analyze separately.

Thermal Tolerance Experiment

256   We evaluated differences in thermal tolerances among species with a one-way ANOVA,

257   and compared individual species' responses with Tukey's Honest Significant Difference (HSD)

258   test. We also determined whether laboratory-determined thermal tolerance values were

259   representative of foraging behavior observed in the field. Using each species as an observation,

260   we regressed thermal tolerance against the observed temperature of maximum foraging activity

261   of each species. A positive relationship with a slope = 1 would suggest perfect correlation

262   between thermal tolerance and foraging activity.

263   To determine whether thermal tolerance predicts how species respond to shade additions,

264   we first quantified the change in abundance of each species after application of shade tarps as the

265   average percent change in worker numbers in the treatment plots from the unshaded period

266   (weeks I-II) to the shaded period (weeks III-V). To ensure effects of shade treatments we not

267   confounded with any unmeasured variable that varied through time, we also calculated the

268   change in abundance of all species in the control plots through time (= average percent change in

269   abundance of control plots from weeks I-II to weeks III-V). Using each species as an

270   observation, we regressed the change in abundance after shade application (treatments) and

271   through time (control) against thermal tolerance. We used a randomization test implanted in

272   EcoSim (Gotelli and Entsminger 2006) to test for the statistical significance of the slope.

273   To test whether species with similar traits were more likely or less likely to co-occur, we

274   paired the thermal tolerance results with analyses of species co-occurrence. We quantified co-

275   occurrence patterns of each species pair at the SE site. Matrices consisted of 2 rows (=species)

276   and 15 columns (=baits). A species was considered "present" if it occurred at the baits at any

277   sampling period during the initial, unshaded portion. We used the same null model parameters

278   as in the previous co-occurrence analysis. Using each species pair as an observation, we

279   regressed the absolute difference in thermal tolerance against the SES values from the co-

280   occurrence analyses. If species with more similar traits co-occur more often than expected by

281   chance (large negative SES values), then we expect a positive relationship between similarity in

282   thermal traits and SES values. If species with more similar traits co-occur less often than

283   expected by chance (large positive SES values), then we expect a negative relationship between

284   similarity in thermal traits and SES values.

285   **Shading and Species Removal Experiment**

286   We performed a two-way ANOVA with shade and removal of *F. moki* as fixed effects on

287   the abundance of *F. moki* and *T. nevadensis*. Abundance values were log-transformed to meet

288   assumptions of ANOVA. We used a two-factor factorial nominal logistic model to investigate

289 the effects of *F. moki* removal and shade addition on the bait occupancy of all other species

290 observed. Analyses were run separately on each of the four sampling periods (=times of day).

291 These analyses were conducted in JMP, version 4.0.2 (SAS Institute, Cary, North Carolina,

292 USA).

293 **Results**

294 **Community Composition**

295   In 2003, we observed in the forested habitat a total of 34,942 ants from 24 species and 11

296 genera at 16 sites (Ratchford et al. 2005). Mean local richness per site was usually approximately

297 8 species (range = 5 to 12). *Aphaenogaster occidentalis*, *Camponotus vicinus*, *Tapinoma sessile*,

298 and *Temnothorax nevadensis* occurred at the majority of sites and collectively constituted

299 between 29% and 86% of the species occurrences observed at bait stations within a site. Less

300 regionally-widespread species that were locally numerically dominant included *Crematogaster*

301 *coarctata, Formica subelongata*, and *F. moki*. *Camponotus essigi*, *C. laevigatus*, *Formica*

302 *neogagates*, *F. accreta*, *Liometopum occidentale*, and *Solenopsis molesta* were rare and were

303 observed only at one site. At the experimental study site, 8 species were collected, and the

304 numerically dominant species were *F. moki*, *Ta. sessile*, and *Te. nevadensis*.

305 **Site Characteristics**

306   Temperature did not vary widely among baits within sites during a sampling period

307 (average coefficient of variation among sites = 0.160; range = 0.027 to 0.328). Average

308 temperature during morning, afternoon, and evening time blocks did not vary among sites ($F_{15,47}$

309 = 0.452, P = 0.948). Soil surface temperature varied significantly throughout the day ($F_{2,47}$ =

310 50.336, P < 0.001) with hot afternoon temperatures (mean afternoon temperature °C ± 1 SE =

14

311   49.16 ±1.67) higher than either morning (30.02 ± 1.36) or evening (26.37 ± 1.36) temperatures

312   (Tukey's HSD test, $P < 0.05$)

Temporal and Spatial Partitioning

314   *Temporal Niche Overlap*— The temporal niche overlap index was larger than expected by

315   chance in 13 of the 16 sites ($P_{obs} > P_{exp}$; $P < 0.05$), indicating that species broadly aggregated

316   their activities throughout the day.

317   *Spatial Partitioning*—Species occurrences were segregated among baits during cool, but not

318   warm, hours of the day. There was significant segregation among species (SES values >1.96) at

319   3 of the 16 sites in the morning, 0 of 16 sites in afternoon, and 7 of 16 sites in the evening (Fig.

320   1). Co-occurrence patterns differed significantly throughout the day ($F_{2,40} = 17.059$, $P < 0.001$),

321   with the highest SES values occurring in the evening (mean SES = 1.581), intermediate values in

322   the morning (mean SES = 0.921), and the lowest values in the afternoon (mean SES = 0.088;

323   Tukey's HSD test, $P < 0.05$).

BACI Shading Experiment

325   Average soil surface temperature did not differ among baits assigned to treatment groups

326   before shade additions ($F_{1,89} = 1.86$, $P = 0.176$; mean temperature in control vs. treatment baits

327   before shading = 41.28 and 40.34°C, respectively). Treatment groups did differ after shade

328   additions ($F_{1,89} = 132.21$, $P < 0.001$; mean temperature in control vs. shaded baits =33.68 and

329   41.03°C , respectively). Average reduction in temperature in shaded plots was 4.6°C in the

330   morning, 16.1°C in the afternoon, and 2.9°C in the evening. Bait occupancy did not differ

331   significantly between control and treatment plots for any week (Week I: $F_{1,14} = 0.09$, $P = 0.769$;

332   Week II: $F_{1,14} = 0.16$, $P = 0.699$; Week III: $F_{1,14} = 0.30$, $P = 0.592$; Week IV: $F_{1,14} = 2.37$, $P =$

333   0.146, Week V: $F_{1,14} = 0.95$, $P = 0.345$). Total number of workers, however, was five times

334   greater in shaded plots than in control plots during Week IV (mean workers number $\pm$ SE = 30.9

335     $\pm$ 7.63 in control plots, 151.6 $\pm$ 42.3 in shade plots; $F_{1,14} = 5.36$, $P = 0.039$), and there was a trend

336   of greater worker numbers in shaded plots during Week V (45.9 $\pm$ 23.3 in control plots, 112.2 $\pm$

337   31.6 in shade plots; $F_{1,14} = 4.42$, $P = 0.057$). On average, half as many *Temnothorax nevadensis*

338   workers recruited to shaded vs. control baits during shading weeks (Week III: $F_{1,10} = 222.00$, $P <$

339   0.001; Week IV: $F_{1,10} = 7.07$, $P = 0.045$; Week V: $F_{1,10} = 7.57$, $P = 0.04$; Fig. 2). There was no

340   difference in *T. nevadensis* abundance between control and treatment baits during the two-week

341   pre-treatment period (Week I: $F_{1,10} = 1.52$, $P = 0.272$; Week II: $F_{1,10} = 0.12$, $P = 0.741$; Fig. 2).

342   **Thermal Tolerance Experiment**

343   The average maximum temperature tolerances ranged from 44.0 to 48.1°C (Fig. 3).

344   *Aphaenogaster occidentalis* was the least thermally tolerant species and *Temnothorax*

345   *nevadensis, Crematogaster coarctata,* and *Liometopum luctuosum* were the most thermally

346   tolerant (Fig. 3). Thermal tolerance measured in the laboratory was marginally associated with

347   maximum foraging temperatures observed in the field (observed $r = 0.524$, mean of simulated = -

348   0.025, $P = 0.073$).

349   Thermal tolerances of species predicted changes in abundance in shaded plots (observed

350   slope = -8.371, mean of simulated slopes = -0.220, $P = 0.007$; Fig. 4). Species with low thermal

351   tolerances increased in abundance in shaded plots relatively more than did species with high

352   thermal tolerance. Thermal tolerance was not associated with natural changes in abundance over

353   time as measured in the control plots (observed slope = -3.746, mean of simulated slopes = -

354   0.040, $P = 0.138$).

355   Similarity of thermal traits predicted patterns of co-occurrence among species pairs

356   (observed slope = -0.3155, mean of simulated slops = -0.0004, $P = 0.042$; Fig. 5). Species pairs

357 with similar thermal tolerances were more likely to be spatially segregated (large positive SES

358 values) within the SE site.

359 **Shade and Removal Experiment**

360 Removal treatments were successful, as 94.8% fewer *F. moki* workers were present at

361 baits in removal plots than at baits in control plots (mean workers number $\pm$ SE = 13.9 $\pm$ 2.42 in

362 control plots, 0.69 $\pm$ 0.87 in removal plots; $F_{1,15}$ = 20.29, *P* < 0.001). There was no effect of

363 shade (7.5 $\pm$ 2.3 in control plots, 7.0 $\pm$ 2.4 in shade plots; $F_{1,15}$ = 3.49, *P* = 0.139) or treatment

364 interaction ($F_{1,15}$ = 3.48, *P* = 0.139) on *F. moki* worker abundance. On average 78% more

365 *Temnothorax nevadensis* workers recruited to baits in removal plots ($F_{1,13}$ = 18.58, *P*<0.001) and

366 68% fewer workers to shaded baits ($F_{1,13}$ = 8.92, *P* = 0.015; Fig. 5). There was no interaction of

367 shade and removal treatments ($F_{1,13}$ = 1.22, *P* = 0.290).

368 Removal of *F. moki* increased the likelihood of bait occupancy by 2 of the 7 other ant

369 species: *Temnothorax nevadensis* occupied more baits in the removal treatment during three

370 sampling periods (= times of day), and *Tapinoma sessile* occupied more baits in the removal

371 treatment during two sampling periods (Table 2). Shading increased the likelihood that

372 *Aphaenogaster occidentalis* occupied baits during two sampling periods but decreased the

373 likelihood that. *Te. nevadensis* occupied baits (Table 2). Shade and removal treatments had no

374 effect on bait occupancy by *Solenopsis molesta*.

375 **Discussion**

376 In the Siskiyou Mountains, community organization and foraging abundance of ants at

377 the local scale appears to be controlled primarily by the thermal environment, and secondarily by

378 biotic interactions. Species aggregate foraging activity across the diurnal timeframe (Results:

379 Temporal Niche), with activity levels dropping in the hottest part of the day and increasing

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380   during cooler hours (Wittman 2007). In our study area, diurnal temperature fluctuates widely

381   (Results: Site Characteristics), likely setting hard boundaries to activity levels. Temperature is a

382   cue for ants to leave the nest to forage (Muser et al. 2005, Azcarate et al. 2007), and ants

383   generally forage within a limited thermal range (Garcia-Perez et al. 1994, Cerdà et al. 1997, Pol

384   and de Casenave 2004). Humidity may also interact with temperature to form a "temperature-

385   humidity envelope" (Hölldobler and Wilson 1990) that dictates when workers can be active

386   (Talbot 1946, Kuate et al. 2008).

387   Our study provides evidence that physiological thermal tolerance predicts how ant

388   species respond to changes in their thermal environment: the less thermally tolerant a species

389   was, the greater was its change in abundance after shade additions (Fig. 4). Due to the short

390   duration of the shading experiment, the abundance changes we documented likely are not

391   measures of change in population size of ant colonies, but rather measures of changes in foraging

392   behavior at baits. Because abundance was quantified as the sum of workers observed throughout

393   the day, if a species increased recruitment or total time spent foraging at a bait, it would be

394   recorded as an overall increase in abundance. Thus, we conclude that shading most greatly

395   impacted the foraging behavior of species most physiologically restricted by temperature (Fig 4).

396   That thermal tolerance predicted changes in foraging abundance to shade additions is

397   striking, considering the relatively small differences in thermal tolerance (Fig. 3), the small size

398   of shade tarps (0.25 m^2), which rarely covered nest entrances, and that physiologically driven

399   responses were not drastically altered by any competitive interactions. Thermal control of

400   forging activity is also very apparent in *T. nevadensis*, as evident in both the BACI shading

401   experiment (Fig. 2) and the shading and removal experiment (Table 2, Fig. 6). Although its

402   abundance increased in the removal experiment (Fig 6), interactions between shading and *F.*

403 *moki* removal were not statistically significant, suggesting additive effects of shading and

404 competitors (Fig. 6).

405   Temperature determined when species were generally active (Results: Temporal Niche

406 Overlap), setting the stage in which competitive interactions occurred. Co-occurrence patterns

407 differed during different times of day, with more segregation across baits during cooler times of

408 day (Fig. 1). When fewer species were active in the hot afternoon, we found random co-

409 occurrence patterns. Our sites appeared structurally homogenous, we found little variation in

410 temperature throughout a site (Results: Site Characteristics), and interspecific aggression was

411 conspicuous (Wittman 2007); thus, segregation likely resulted from competitive interactions

412 rather than from responses to habitat or environmental heterogeneity. Competitive interactions

413 also appear to be contingent upon temperature in other ant communities, and these interactions

414 may vary with season (Retana and Cerdá 2000, Albrecht and Gotelli 2001) and habitat structure

415 (Yanoviak and Kaspari 2000, Farji-Brener et al. 2002, Gotelli and Ellison 2002). For example,

416 Retana and Cerdá (2000) found competition is more prevalent in communities occurring in

417 cooler habitats or during cooler seasons.

418   Thermal tolerance also influenced patterns of species co-occurrence. Species pairs more

419 similar in thermal tolerances showed greater segregation at baits (Fig. 5). These results make

420 sense, given (1) the strong connection between thermal tolerance and the ability to forage in the

421 thermal environment (Fig. 4); (2) that activity levels are broadly defined by temperature

422 (Results: Temporal Niche Overlap); and (3) that competitive interactions were more prevalent

423 during times of greatest activity level (Fig. 1). Species with more similar thermal tolerance

424 foraging during the same time were more likely to encounter competitors. Thus, we demonstrate

425 how similarity in ecological traits defines the prevalence of competitive interactions (Johansson

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426   and Keddy 1991, Fig. 5) and that biotic interactions may change with abitoic conditions (Dunson

427   and Travis 1991, Pennings 2003, Fig. 1).

428   Our results confirm the power of using a "functional ecology" approach (McGill et al.

429   2006) to "bridge the gap of physiological and community ecology" (Dunson and Travis 1991)

430   and yield insights into how biotic and abiotic factors interact to determine spatial and temporal

431   patterns of community structure. In the Siskiyou Mountains, communities assemble and

432   disassemble along the thermally variable environment, and co-occurrence patterns at the local

433   appear to be determined, in part, by species thermal tolerance, a functional trait that strongly

434   determines when a species can be active.

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563 **Table 1.** Species list and summary results of behavioral observations at baits at the SE site.

564 Entries display the total number interactions with other species, the number of dominant

565 behaviors exhibited during those interactions, percentage of interactions in which a species was

566 dominant (= Dominance Index, *sensu* Fellers 1987), the number of species with which each

567 species interacted (max = 7), and the number of bait stations each species visited (max = 30).

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Species	Total No. Interactions	No. Dominant Interactions	Dominance Index	No. Species Interacted	No. Bait Stations
Formica moki (Fm)	18	12	67	6	14
Temnothorax nevadensis (Tn)	14	2	14	4	26
Tapinoma sessile (Ts)	5	0	0	2	10
Aphaenogaster occidentalis (Ao)	5	3	60	3	5
Crematogaster coarctata (Cc)	5	5	100	2	4
Solenopis molesta (Sm)	3	2	67	1	9
Camponotus vicinus (Cv)	1	1	100	1	2
Liometopum luctuosum (Ll)	1	1	100	1	4

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574 **Table 2**. Results of nominal logistic analysis of the effects of shading and *F. moki* removal on

575 bait occurrence data collected during four separate sampling periods (08:00-11:00). Analyses

576 were run separately for each species. *Crematogaster coarctata* and *L. luctuosum* did not occur at

577 sufficient baits for the analysis. Cells boxed with a solid line indicate a greater chance of bait

578 occupancy, while cells boxed with a dashed line indicate a reduced chance of bait occupancy. No

579 interactions between shading and removal treatments were found were found (*P*>0.05). Species

580 abbreviations as in Table 1.

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Species	8:00		9:00		10:00		11:00	
	Removal	Shade	Removal	Shade	Removal	Shade	Removal	Shade
Ao	0.162	0.046	0.167	0.004	1.000	1.000	0.958	0.945
Cc	.	.	.	.	.	.	.	.
Fm	0.570	0.767	0.002	1.000	0.047	0.999	<0.001	0.063
Ll	.	.	.	.	.	.	.	.
Sm	0.328	0.328	0.098	1.000	0.098	1.000	0.345	0.262
Tn	0.307	0.019	0.034	0.034	0.046	0.162	0.014	0.932
Ts	0.047	0.999	0.887	0.887	0.047	0.999	0.098	1.000

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Figure Legends

Figure 1. Co-occurrence values for ant communities at three temporal snapshots. Points

represent sites' Standard Effect Scores (SES) across the three sample periods. Sites with SES

values greater than 1.96 indicate significant species segregation, and SES values less than -1.96

indicate significant species aggregation.

Figure 2. Response of *Temnothorax nevadensis* workers to the BACI shading experiment. Error

bars represent standard error values. Closed symbols represent shaded baits; open symbols are

control baits. Dotted, vertical line denotes application of shade treatments. Fewer workers visited

shaded baits after treatment application (weeks III, IV and V; *=$P<0.05$).

Figure 3. Mean death temperature of all species observed during the BACI Shading Experiment.

Thermal tolerances of species under the same horizontal line were not significantly different

from each other (Tukey's HSD test). Species abbreviations as in Table 1.

Figure 4. Thermal tolerance values predict percent changes in abundance after the addition of

shade (observed slope = -8.371, mean of simulated slopes = -0.220, $P = 0.007$). Points represent

individual species (see Table 1 for species abbreviations).

Figure 5. Relationship between similarity in thermal tolerance and patterns of co-occurrence

between all species observed at one local site. Points represent unique species pairs; see Table 1

for species abbreviations. Similarity in thermal tolerance was calculated as the absolute

difference in laboratory measured thermal tolerance values. Co-occurrence patterns were

613   determined from field observations at baits and are expressed as Standard Effect Sizes (SES).

614   SES values greater than 1.96 indicate significant species segregation, and SES values less than -

615   1.96 indicate significant species aggregation. Species pairs with similar thermal tolerances were

616   more likely to be spatially segregated (observed slope = -0.3155, mean of simulated slops = -

617   0.0004, $P = 0.042$).

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619   **Figure 6**. *Temnothorax nevadensis* worker numbers in the shade (dark markers) and no shade

620   (light markers) treatments in areas where *F. moki* was removed and not removed. Adding shade

621   decreased workers numbers on baits while removing *F. moki* increased *T. nevadensis* abundance.

622   The interaction of shade and removal treatments was not significant ($P=0.290$).

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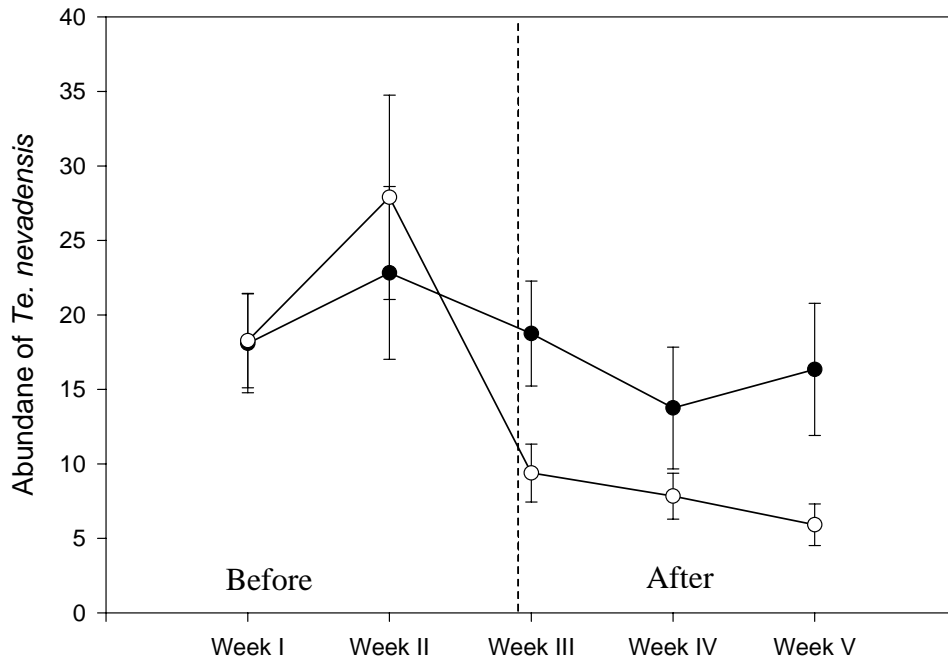
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Figure 1.

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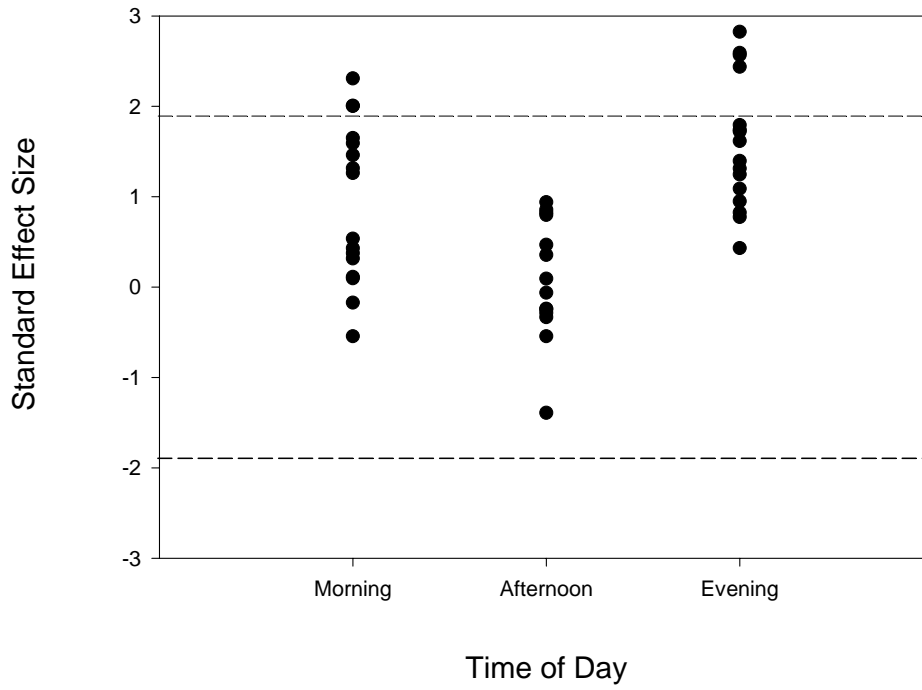
650   **Figure 2.**

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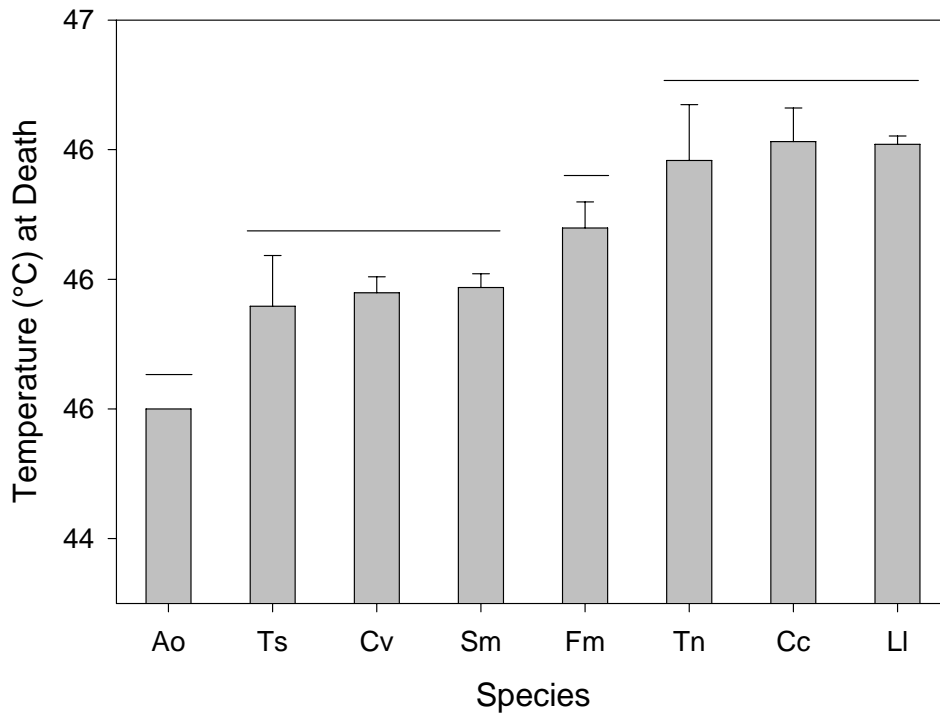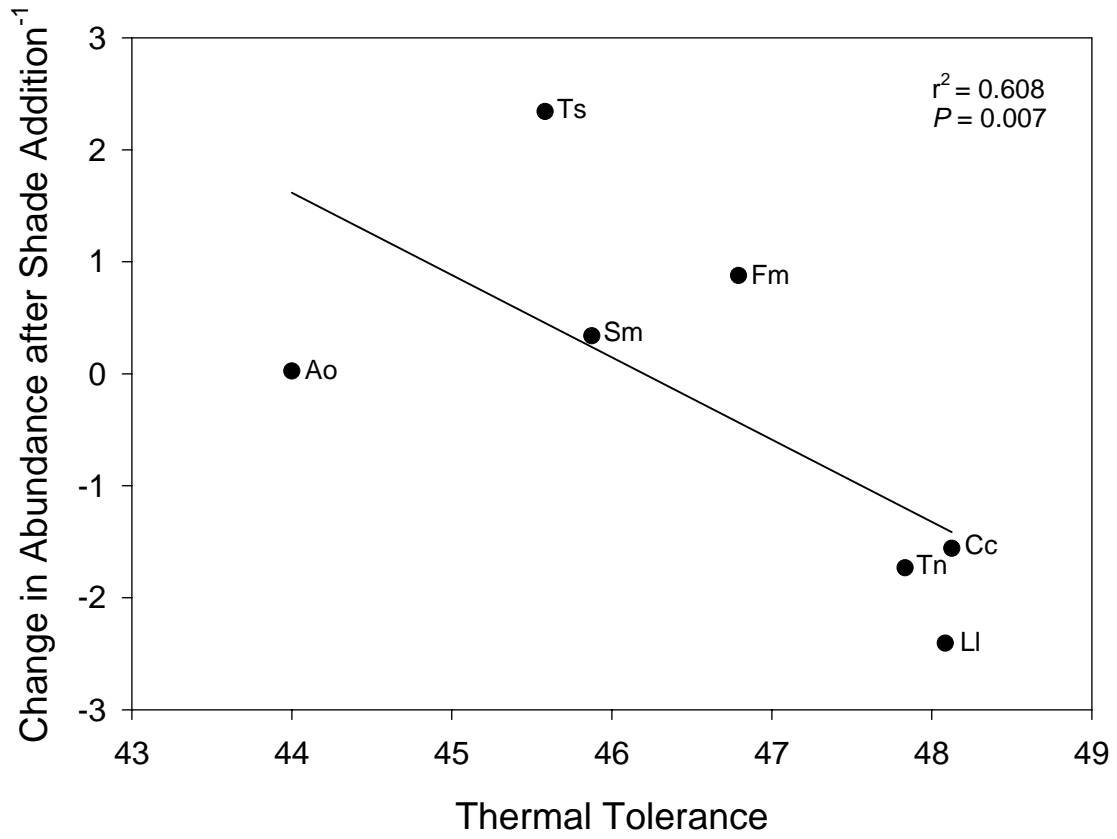
Figure 3.

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677   **Figure 4.**
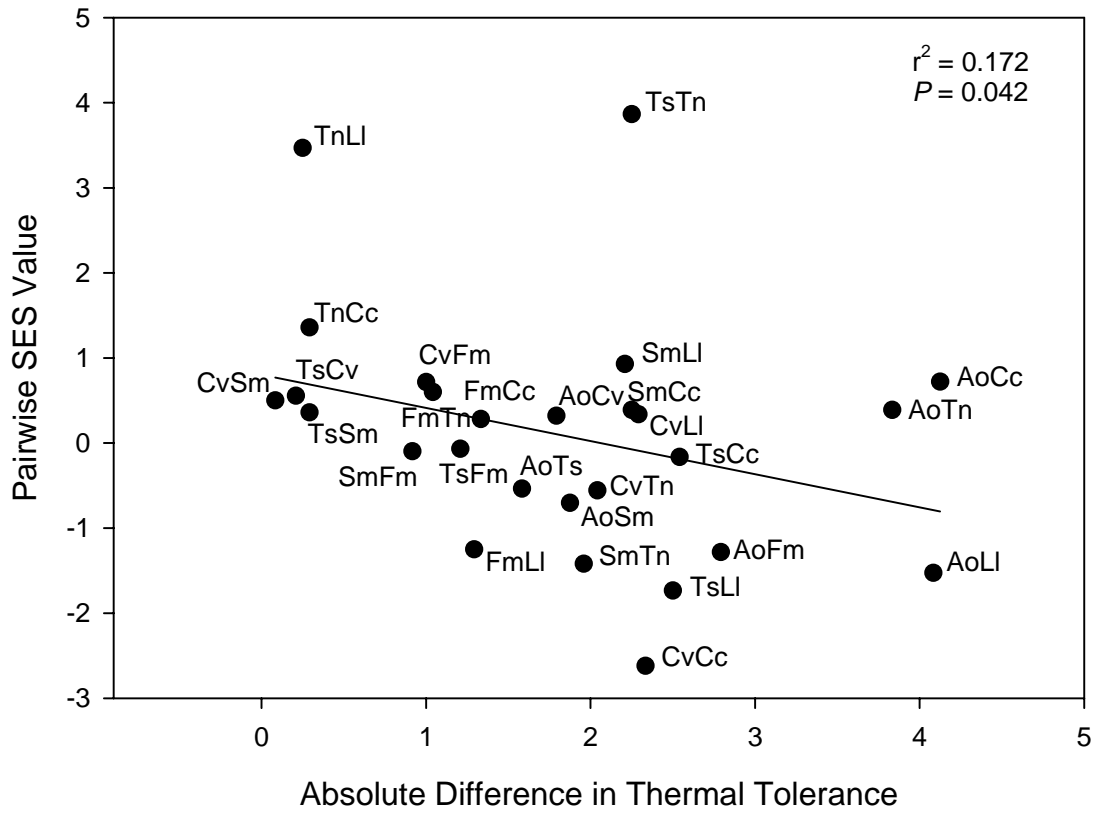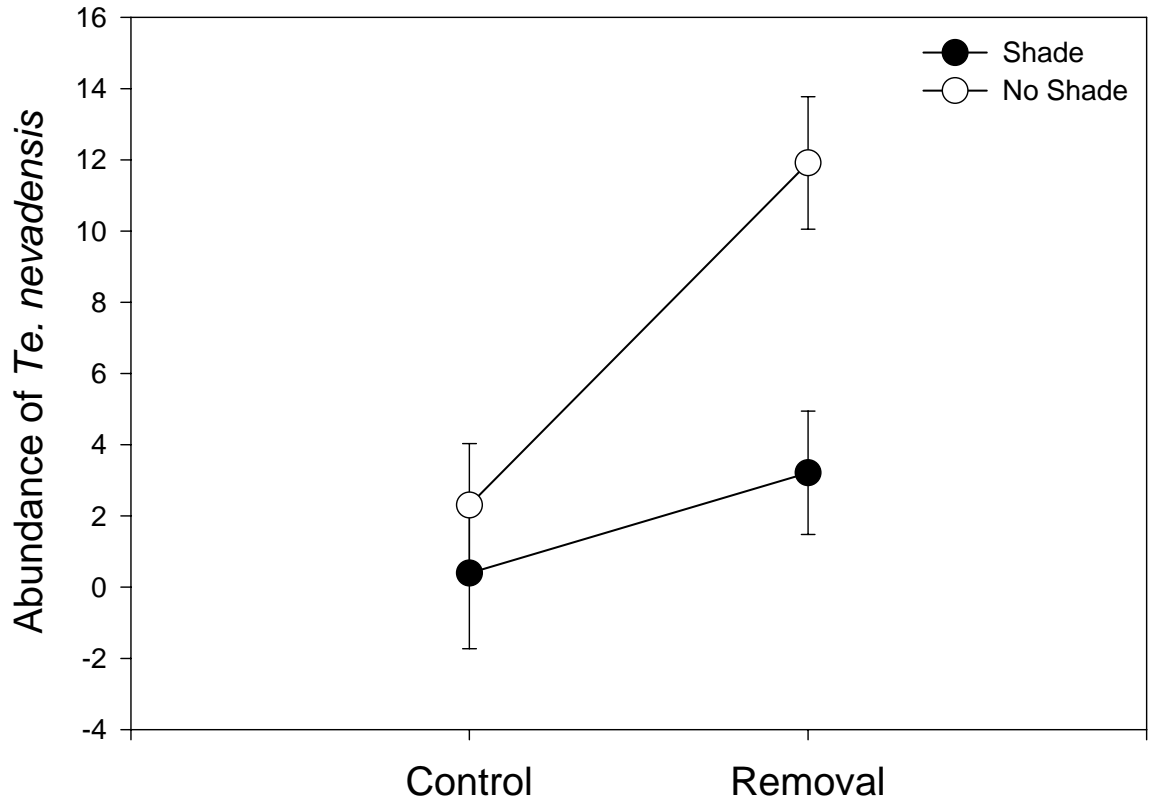
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689   **Figure 5.**

691   **Figure 6**.

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