Ant-mediated seed dispersal in a warmed world

Climate change affects communities both directly and indirectly via changes in interspecific interactions. One such interaction that may be altered under climate change is the ant-plant seed dispersal mutualism common in deciduous forests of the eastern US. As climatic warming alters the abundance and activity levels of ants, the potential exists for shifts in rates of ant-mediated seed removal. We used an experimental temperature manipulation at two sites in the eastern US (Harvard Forest in Massachusetts and Duke Forest in North Carolina) to examine the potential impacts of climatic warming on overall rates of seed dispersal (using *Asarum canadense* seeds) as well as species-specific rates of seed dispersal at the Duke Forest site. We also examined the relationship between ant critical thermal maxima (CT_{max}) and the mean seed removal temperature for each ant species. We found that seed removal rates did not change as a result of experimental warming at either study site, nor were there any changes in species-specific rates of seed dispersal. There was, however, a positive relationship between CT_{max} and mean seed removal temperature, whereby species with higher CT_{max} removed more seeds at hotter temperatures. The temperature at which seeds were removed was influenced by experimental warming as well as diurnal and day-to-day fluctuations in temperature. Taken together, our results suggest that while temperature may play a role in regulating seed removal by ants, ant plant seed-dispersal mutualisms may be more robust to climate change than currently assumed.

1 Ant-mediated seed dispersal in a warmed world

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19 Abstract

20 Climate change affects communities both directly and indirectly via changes in interspecific

21 interactions. One such interaction that may be altered under climate change is the ant-plant seed

22 dispersal mutualism common in deciduous forests of the eastern US. As climatic warming alters

23 the abundance and activity levels of ants, the potential exists for shifts in rates of ant-mediated

24 seed removal. We used an experimental temperature manipulation at two sites in the eastern US

25 (Harvard Forest in Massachusetts and Duke Forest in North Carolina) to examine the potential

26 impacts of climatic warming on overall rates of seed dispersal (using *Asarum canadense* seeds)

27 as well as species-specific rates of seed dispersal at the Duke Forest site. We also examined the

28 relationship between ant critical thermal maxima (CT_{max}) and the mean seed removal temperature

29 for each ant species. We found that seed removal rates did not change as a result of experimental

30 warming at either study site, nor were there any changes in species-specific rates of seed

31 dispersal. There was, however, a positive relationship between CT_{max} and mean seed removal

32 temperature, whereby species with higher CT_{max} removed more seeds at hotter temperatures. The

33 temperature at which seeds were removed was influenced by experimental warming as well as

34 diurnal and day-to-day fluctuations in temperature. Taken together, our results suggest that while

35 temperature may play a role in regulating seed removal by ants, ant plant seed-dispersal

36 mutualisms may be more robust to climate change than currently assumed.

37 **Keywords:** ants, climate change, myrmecochory, seed dispersal, warming

Introduction

Understanding how organisms will respond to ongoing changes in climate, leading to subsequent changes in key ecological processes, is essential in order to predict the structure and function of ecosystems in the future. For example, the alteration of interspecific interactions is one important mechanism by which climate change may ultimately alter the structure and function of ecosystems (Tylianakis et al. 2008, van der Putten et al. 2010, Walther 2010, Harley 2011). The majority of studies on the effects of climate change on interspecific interactions have focused on negative interactions, such as competition (Suttle et al. 2007), predator-prey interactions (Rothley and Dutton 2006, Barton and Schmitz 2009, Harley 2011), and herbivory (Bale et al. 2002). Though rare relative to studies that focus on physiological responses (Norby and Luo 2004, Dillon et al. 2010) or aggregate community-level responses (Klein et al. 2004, Villalpando et al. 2009, Fitzpatrick et al. 2011, Sheldon et al. 2011), empirical studies of the effects of climate on interactions among species have found that climate change can alter the nature and outcomes of interspecific interactions through a variety of mechanisms such as altered abundance and fitness levels of key species (Suttle et al. 2007), shifts in phenology (Both et al. 2009), and species range shifts (Harley 2011). Each of these mechanisms can decouple interspecific interactions by altering the frequency and intensity of interactions among species.

As with most studies in ecology, work on the effects of climate change on positive interactions is lacking, even though mutualisms play fundamental roles in structuring communities and ecosystems (Callaway 1995, Stachowicz 2001). Mutualisms including plant-pollinator interactions and mycorrhizal interactions have been altered by climate change (Parrent et al. 2006, Memmott et al. 2007, Hoover et al. 2012). However, the influence of climate change on other types of positive interactions is not as well studied.

61 One such mutualism that may be altered by climate change is the ant-plant seed dispersal

62 mutualism, which includes hundreds of ant species and thousands of plant species around the

63 world (Beattie and Hughes 2002; Gove et al 2007; Rico-Gray and Oliviera 2007, Lengyel et al.

64 2010). In deciduous forests of the United States approximately thirty percent of understory herb

65 species might be ant-dispersed (Beattie and Culver 1981), and a proposed keystone seed-

66 dispersing ant species, Aphaenogaster rudis, is responsible for upwards of 90% of ant-mediated

67 seed dispersal (Ness et al. 2009; Zelikova et al. 2008). Such specialization in interactions can

68 make interaction networks more vulnerable to disruption as a result of low levels of functional

69 redundancy within a system (Aizen et al. 2012). Myrmechorous plant species that rely on a

70 single ant species for seed dispersal may be at increased risk for disruption by ongoing climatic

71 change (Pelini et al. 2011a, Warren et al. 2011) if that ant species is negatively affected by

72 warming. Inversely, systems in which multiple species are responsible for removing seeds may

73 prove to be more resistant to disruptions because of functional redundancy in the system

74 (Peterson et al. 1998). However, despite the importance and ubiquity of ant-plant seed-dispersal

75 mutualisms in ecosystems around the world and the importance of temperature in regulating ant

76 foraging, experiments examining the consequences of climatic change on plant-seed dispersal

77 mutualisms are rare (but see Pelini et al. 2011a).

78 To examine the potential for climate change to alter seed dispersal mutualisms, we

79 experimentally manipulated temperature at two sites in the eastern United States (North Carolina

80 and Massachusetts) and examined overall rates of seed removal as a function of temperature. At

81 the North Carolina site, we also examined species-specific rates of seed dispersal. We test two *a*

82 *priori* predictions:

83 *Prediction 1:* Rates of seed removal by ants would decrease as a result of experimental warming

84 at the southern site where species, including A. rudis, are closer to their critical thermal maxima

85 (CT_{max}) (Deutsch et al. 2008, Diamond et al. 2012a, Diamond et al. 2012b, Huey et al. 2012), a

86 pattern previously documented in this study system ([Diamond et al. 2012a](#)). Rates of seed

87 removal can be expected to increase at the northern site, where most species, including A. rudis,

88 are well below their CT_{max} ([Diamond et al. 2012a](#)) and perhaps even below their thermal optima.

89 *Prediction 2:* Species with higher CT_{max} would remove seeds more readily under warmer

90 conditions as compared to species with lower CT_{max} as these species are more tolerant of higher

91 temperatures and have been found to be more active as temperatures increase (Stuble et al.

92 2013).

93 Methods

94 Site description

95   This experiment was conducted at Duke Forest (southern site) in North Carolina and

96 Harvard Forest (northern site) in Massachusetts, USA, in order to examine the potential impacts

97 of climate change on seed dispersal mutualisms near the southern extent and northern extent of

98 the ranges of several ant species. The Duke Forest site consists of a closed-canopy oak-hickory

99 (Quercus spp., Carya spp.) forest with a mean annual temperature of 15.5°C and approximately

100 1140 mm of precipitation annually. The Harvard Forest site is in a closed-canopy oak-maple

101 (Quercus spp.-Acer spp.) forest with a mean annual temperature of 7.1°C and 1066 mm of

102 precipitation a year. Though not present in the chambers, several myrmecochorous plant species

103 are common in these forests. These species include *Asarum canadense*, *Hexastylis arifolia*,

104 *Trillium* spp., *Violia rotundifolia*, and *Sanguinaria canadensis*, among others. Seeds of these

105 plant species are typically dispersed by ants in the spring (Thompson 1981).

106   The two sites share ~30 ant species, with the North Carolina site near the southern range

107 edge and the Massachusetts site near the northern range edge for many of these species ([Pelini et](#)

108 [al. 2011b](#)). The most abundant ant species at both sites is the proposed keystone seed disperser *A.*

109 *rudis* (Ness et al. 2009) (or at least a species in the A. rudis complex). *Crematogaster lineolata*, a

110 behaviorally aggressive species, can be abundant at the southern site in warmer months while

111 *Formica subsericea* and *Camponotus pennsylvanicus* (also behaviorally aggressive) are the two

112 next most abundant ant species at the Harvard Forest site (Stuble et al. 2013b). For the purposes

113 of this study we are combining *A. rudis, A. picea,* and *A. carolinensis* into the *A. rudis* complex

114 due to the difficultly of identifying these closely related species in the field.

115   At each site, there are twelve experimental open-top warming chambers (Fig. 1). Each

116 chamber is 5 m in diameter and 1.2 m tall with a 2-3 cm gap at the bottom to allow ants and other

117 organisms to move in and out. The chambers are approximately 1000 ant body lengths in

118 diameter. The chambers contain about 1 colony per square m, and the average foraging distance

119 of an *A. rudis* colony is ~70cm. Moreover, during the summer of 2012, we watched 72 *A. rudis*

120 workers visiting baits and returning to their colonies. Out of those 72 observations, only 1 worker

121 visited a bait in the chamber and returned to a nest outside the chamber (L. Nichols, unpublished

122 data). So, most of the activity we see is from ants in the chambers. Nine chambers at each site are

123 warmed from 1.5°C to 5.5°C in 0.5°C steps using air warmed by hydronic radiators, while the

124 three control chambers blow air at ambient temperatures into the plots (see Pelini et al. (2011b)

125 for a detailed description of the chambers). Warming treatments have been maintained

126 continuously since January of 2010 and have been successful at maintaining the targeted

127 temperature increases. For 2011, a significantly positive relationship between the target

128 temperature increase and actual temperature increase was maintained ($p < 0.01$, $R^2 = 0.99$).

129 Significant shifts in levels of ant foraging activity at food baits have been documented in the

130 chambers across the temperature treatments, with more thermally tolerant species exhibiting

131 higher levels of foraging activity in warmer chambers than species with lower thermal tolerances

132 (Stuble et al. 2013a). Those results suggest that temperature does mediate foraging behavior.

133 Such a result, that environmental context can mediate foraging behavior, is in line with previous

134   work in this system (Pelini et al. 2011) and others (Cerdá et al. 1997, Sanders and Gordon 2000,

135   2003, Gibb and Parr 2010).

136   Seed removal

137   To assess the impact of temperature on rates of seed dispersal, we haphazardly positioned

138   one seed cache in each of the 12 chambers at Duke Forest and Harvard Forest. Each cache

139   contained 20 seeds of the myrmecochorous species Asarum canadense. The range of Asarum

140   canadense extends from New Brunswick, Canada to North Carolina in the southern US (Cain and

141   Damman 1997). Seeds of *A. canadense* are similar in mass to many other myrmecochorous plant

142   species (Michaels et al. 1988). Seeds used in the trials at Duke Forest were collected at North

143   Carolina State University's Schenck Forest in Raleigh, North Carolina on May 11, 2011 and

144   those used in the Harvard Forest trials were collected from Mt. Toby in Massachusetts on June 8,

145   2011. We covered each seed cache with a mesh cage to allow ants to access the seeds while

146   preventing access by rodents. Caches were left out for one hour, after which time the number of

147   seeds remaining in the cache was counted and any remaining seeds were removed from the

148   chamber. Though observing seed removal for an hour limits our ability to account for the fate of

149   all seeds, using this standard timeframe allowed us to compare relative rates of seed removal

150   across treatments. A total of ten trials were conducted at Duke Forest between May 12 and May

151   25, 2011, with five trials conducted during the day (between 0900 and 1900) and five during the

152   night (between 2100 and 0500). Another five trials were conducted at Harvard Forest between

153   June 16 and June 30, 2011; three during the day and two at night. These dates corresponded with

154   the time periods during which the seeds were naturally released at each site, as opposed to

155   conducting this experiment in the hottest part of the year when the impacts of warming might be

156   expected to be greater, but when any results might be less ecologically relevant.

157   We calculated the average seed dispersal rate (number of seeds removed in an hour) for

158 each chamber at each site. We used ANCOVA to examine differences in seed dispersal rates as a

159 function of temperature treatment (which we refer to as Δ°C, included as a continuous variable)

160 and site. The number of seeds removed per hour was square root transformed to meet

161 assumptions of normality. All statistics were performed in SAS, version 9.2.

162   To determine the ant species responsible for removing the seeds, we continuously

163 observed caches of 10 A. canadense seeds within the chambers at Duke Forest for one hour, or

164 until all seeds were removed. Four seed removal observations were conducted in each chamber:

165 two during the day and two during the night. Nighttime observations were conducted using red

166 lights, which is typical in studies of ant behavior at night (Hodgson 1955, Narendra et al. 2010).

167 We recorded the identity of the ant species removing the seeds. When possible, we also followed

168 the seed back to the nest (or under leaf litter in some cases) and noted the distance it had been

169 moved. At the beginning of each observation, we took four ground surface temperature

170 measurements using a handheld infrared thermometer (Raytek® Raynger ST, +/- 1 □C), one at

171 each corner of the seed cache, which were averaged together. These temperature readings

172 provided us with estimates of ground-surface temperature conditions in the immediate vicinity of

173 the seeds. Ground-surface temperature has been shown to be an important driver of foraging

174 activity in ants (Whitford and Ettershank 1975, Crist and MacMahon 1991). We calculated the

175 percentage of seeds removed by each species overall, as well as separately for day and night. We

176 also calculated the mean number of seeds removed by each species in each chamber across all

177 trials.

178   We used linear regressions to examine differences in seed dispersal rates across

179 temperature treatments for each ant species. (We examined several polynomial regressions, but

180 found none of them to be a better fit than simple linear regressions.) Mean numbers of seeds

181 removed were log transformed to meet assumptions of normality for A. rudis and C. lineolata.

182   Finally, we calculated the average ground surface temperature (based on temperatures

183   collected with the infrared thermometer) at which each species removed seeds across all

184   treatments and times. We then examined the relationship between the average temperature at

185   which a species removed seeds and the CT_{max} of that species (as calculated by Diamond et al.,

186   2012) across all species observed removing seeds in the system. *A*phaneogaster lamellidens was

187   excluded from this analysis as it was only observed removing seeds from two seed caches and

188   was an outlier (as indicated by a plot of residuals by predicted values).

189   Results and Discussion

190   Seed removal rate did not depend on temperature treatment and did not vary between sites

191   ($F_{2,21} = 0.93$, p = 0.41; Fig. 2). This is despite the fact that most of the foragers observed in this

192   study were from colonies within the experimental chambers. At the southern site, where seed

193   dispersal observations were conducted, the mean seed removal distance was 51 cm, and only 2%

194   of observed seeds were removed more than 2 m. The lack of response to experimental warming

195   contrasts with the prediction that, based on the thermal limits of A. rudis and its disproportionate

196   role in seed dispersal, seed dispersal rate should decline with increasing temperatures. Regardless

197   of temperature treatment or site, ants removed ~ 23% of seeds per hour (an average of 4.6 seeds

198   out of 20). At the southern site, we observed seven ant species removing seeds across a range of

199   ground surface temperatures from 17ºC to 30ºC (Table 1). Aphaenogaster rudis was the most

200   common seed disperser, removing approximately 45.5% of seeds (Table 2). However, there was

201   no relationship between the rate of seed dispersal by A. rudis and temperature treatment (Table

202   1). With the exception of C. lineolata, which showed a marginally significant increase of

203   approximately 0.1 seeds removed per degree of warming, seed removal did not vary

204   systematically with temperature treatment for any ant species (Table 1). This is despite

previously observed shifts in foraging under experimentally warmed conditions (Pelini et al. 2011a, Stuble et al. 2013a). Pelini et al. (2011) found an approximately 50% decrease in several types of foraging, including seed removal, as a result of 1°C of warming at the southern site, though no change was observed at the northern site. Using the same warming chambers as in this study, Stuble et al. (2013) found species-specific shifts in foraging activity as a result of experimental warming consistent with the thermal tolerances of the foraging species. Further, ant community composition shifts in response to experimental warming, demonstrating the importance of temperature in regulating the ant community (Diamond et al. 2012a). Despite this, experimental warming apparently does not affect the aspects of the seed-dispersal mutualisms we studied in this system. This begs the question - why isn't this seed-dispersal mutualism disrupted by experimental warming?

One possible answer is that foraging behavior by Aphaenogaster rudis may be more tolerant to experimental warming than previously thought. A. rudis is a keystone mutualist in this and other systems, responsible for the majority of ant-mediated seed dispersal (Zelikova et al. 2008, Ness et al. 2009, Canner et al. 2012). The abundance and activity of *A. rudis* declines with elevation (i.e., lower temperatures) at biogeographic scales (Zelikova et al. 2008). Additionally, the relatively low thermal tolerance of this species accurately predicts its activity relative to other species (Stuble et al. in press). However, when exposed to experimental warming, the abundance (Pelini et al. 2011a) and foraging activity (Stuble et al. 2013) of *A. rudis* apparently do not decline at either study site. Importantly, the average foraging distance of *Aphaenogaster* spp. was ~70cm at the study site (L. Nichols, unpublished data). Further, based on the proportion of these ants observed foraging into the chambers from outside in observations, we'd predict that only about one of the eighty seeds observed being removed by *A. rudis* was likely to have been removed by a worker originating outside of the chambers. Thus, it is not likely the case that ants

229 are coming to baits from nests that are outside the chambers. However, even in cases in which

230 individual workers do forage at the experimental baits from colonies outside of the chambers,

231 these individuals are still exposed to the experimental temperature conditions while discovering,

232 foraging at, and recruiting to the seed caches. These results suggest that temperature does not

233 substantially alter this foraging behavior. The apparent tolerance of the foraging activity of this

234 important seed dispersing species to warming may play a major role in promoting the stability of

235 ant-plant seed dispersal in light of global change.

236   It is important to note that six ant species other than A. rudis were observed removing

237 seeds in this study, and they removed > 50% of the seeds. This runs counter to several studies

238 suggesting seed dispersal mutualisms may be highly specialized (Gove et al. 2007, Ness et al.

239 2009). Both the foraging activity and abundances of several of these species, including C.

240 lineolata and Formica pallidefulva, shift with warming (Pelini et al. 2011a, Diamond et al. 2012a,

241 Stuble et al. 2013a), resulting in an altered community of foragers (Diamond et al. 2012a). By

242 having multiple ant species interacting with myrmecochorous plants, this ant-plant seed dispersal

243 mutualism may be relatively resistant to the effects of warming as some ant species increase in

244 activity and abundance while others decline in abundance with temperature. Previous work on

245 ant foraging and community composition as a result of the experimental warming at these sites

246 suggests quite a bit of variability in species-specific responses to warming which may, in fact,

247 play a role in moderating the effects of climatic warming (Stuble et al. 2013a).

248   In addition to the apparent (and of course relative) resistance of the foraging of *A. rudis* to

249 warming, along with the diversity of ants engaging in this mutualism, another factor possibly

250 strengthening the resistance of the ant-plant seed dispersal mutualism may be the timing of ant-

251 mediated seed dispersal within deciduous forests of the eastern US. Ant-dispersed seeds in these

252 forests, including those of *Asarum canadense*, are primarily dispersed in the spring (Thompson

253 1981). Temperatures in May in North Carolina and June in Massachusetts at the study sites are

254 far from the critical thermal maxima of ant species in the system. For example, the critical

255 thermal maximum for *A. rudis* is 38ºC and 40ºC for populations at the northern and southern

256 sites, respectively (Diamond et al. 2012b), as opposed to the mean environmental temperatures

257 during the sampling period, which were 20ºC at the northern site and 22ºC at the southern site.

258 The thermal buffer between CT_{max} and the environmental temperature during the time of year

259 when seeds are dispersed may confer some degree of tolerance on this mutualism. Pelini (2011a)

260 found that rates of seed removal decreased in a passive experimental warming at the same two

261 sites, despite achieving warming of only 0.3˚C above ambient. However, the seed removal trials

262 in Pelini et al.'s experiment were conducted mostly in August when ambient environmental

263 temperatures are hotter than those experienced in the present study. We suggest that the

264 proximity of ants to their upper thermal limits in August may have driven the effects of warming

265 observed in the Pelini et al. (2011a) study while seed dispersal occurring in the spring when our

266 study was conducted may be less likely to be detrimentally impacted by warming. However, this

267 protection assumes that the peak of *A. rudis* activity and seed set coincide. Phenological shifts in

268 plant reproduction caused by ongoing warming (Price and Waser 1998, Dahlgren et al. 2007,

269 Inouye 2008, Liu et al. 2011, Wolkovich et al. 2012) have the potential to result in seeds

270 appearing before ants become active (Warren et al. 2011). Warren et al. (2011) suggest that while

271 both seed release by plants and onset of foraging in ants seem to be driven by temperature,

272 variability in activation temperatures among ant species may result in situations in which early

273 seeding plant species may become decoupled from their foragers in some areas.

274   Despite the apparent tolerance of the ant-plant seed dispersal mutualism to experimental

275 warming in this study, there was a significant relationship between the ground-surface

276 temperature at which a species removed seeds and the critical thermal maximum of that species

277 ($F_{1,4} = 7.35$, $p = 0.05$, $R^2 = 0.65$, Fig. 3). That is, those species with high thermal tolerances were

278 most active under the warmest temperatures. The positive relationship between CT_{max} and seed

279 removal temperature suggests that while chronic experimental warming may not affect rates of

280 seed dispersal, temperature does relate to rates of seed removal. This finding incorporates both

281 temperature variability associated with the temperature treatments as well as daily temperature

282 variability and complements other studies that have shown physiological tolerance to be an

283 important predictor of ant activity (Diamond et al, in press).

284   One important caveat to our study (and to most studies of ant-seed dispersal mutualisms)

285 is that we do not know the ultimate fate of the seeds once they were removed by the ants. It is

286 possible that warming could still alter the dynamics of plant populations by altering rates of

287 germination and seedling survival post-germination (De Frenne et al. 2012), even in cases in

288 which seed dispersal remains unaffected as temperatures increases. Additionally, some species,

289 including C. lineolata, dispersed seeds very short distances (only a few centimeters) while other

290 species, such as C. castaneus, often carried seeds several meters. Even slight shifts in dispersal

291 rates among these species may alter plant population dynamics if dispersal distances differ

292 substantially among species. Finally, by observing seed caches for an hour, we fail to collect data

293 on the fate of seeds not removed in that time frame. However, a considerable proportion of the

294 seeds that will be removed by ants are, in fact, removed soon after release from the parent plant

295 (Turnbill and Culver 1983, Beaumont et al. 2013) and seeds not dispersed by ants are at risk of

296 predation by rodents (Heithaus 1981). Additionally, as in most studies of ant-seed interactions,

297 we focus on seeds of only a single plant species. Including more seeds from more species

298 would be ideal, but would have been beyond what was possible in this (or in most) studies.

299   It has become axiomatic that interactions among species are being affected by ongoing

300 climatic change. However, in this study, we found no reduction in overall rates of seed removal

301 as a result of experimental warming. Moreover, there were no differences in species-specific seed

302 removal rates at the southern site. We suggest that the ant-plant seed dispersal mutualism may be

303 resistant, at least in part, to climatic warming as a result of the diversity of ants active in this

304 mutualism as well as the seasonal timing of this mutualism in the spring when most ant species

305 are far from their upper thermal limits. Importantly, however, if phenological mismatches arise,

306 or if the fate of seeds after dispersal is altered, the consequences of warming on plant populations

307 and communities could emerge in unexpected ways.

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Table 1. Test statistics are from linear regressions examining the influence of temperature treatment on the number of seeds removed by each ant species (d.f. = 11 for all species).

Species	F	p
Aphaenogaster lamellidens	2.58	0.58
Aphaenogaster rudis	2.45	0.15
Camponotus castaneus	0.10	0.75
Camponotus pennsylvanicus	0.24	0.64
Crematogaster lineolata	4.14	0.07
Formica pallidefulva	0.34	0.58
Formica subsericea	0.02	0.90

Table 2. Percentage of seeds removed by each species overall, during the day, and the night.

Species	Overall percent	Day percent	Night percent
Aphaenogaster lamellidens	8.5	17.2	0.0
Aphaenogaster rudis	45.5	48.3	42.7
Camponotus castaneus	26.7	0.0	52.8
Camponotus pennsylvanicus	2.8	2.3	3.4
Crematogaster lineolata	6.8	12.6	1.1
Formica pallidefulva	2.3	4.6	0.0
Formica subsericea	7.4	14.9	0.0

Figure 1

Figure 1. Warming chamber at Duke Forest.

Figure 2

Figure 2. Number of seeds removed in the course of an hour as a function of temperature treatment. Black dots represent Duke Forest and gray dots represent Harvard Forest.
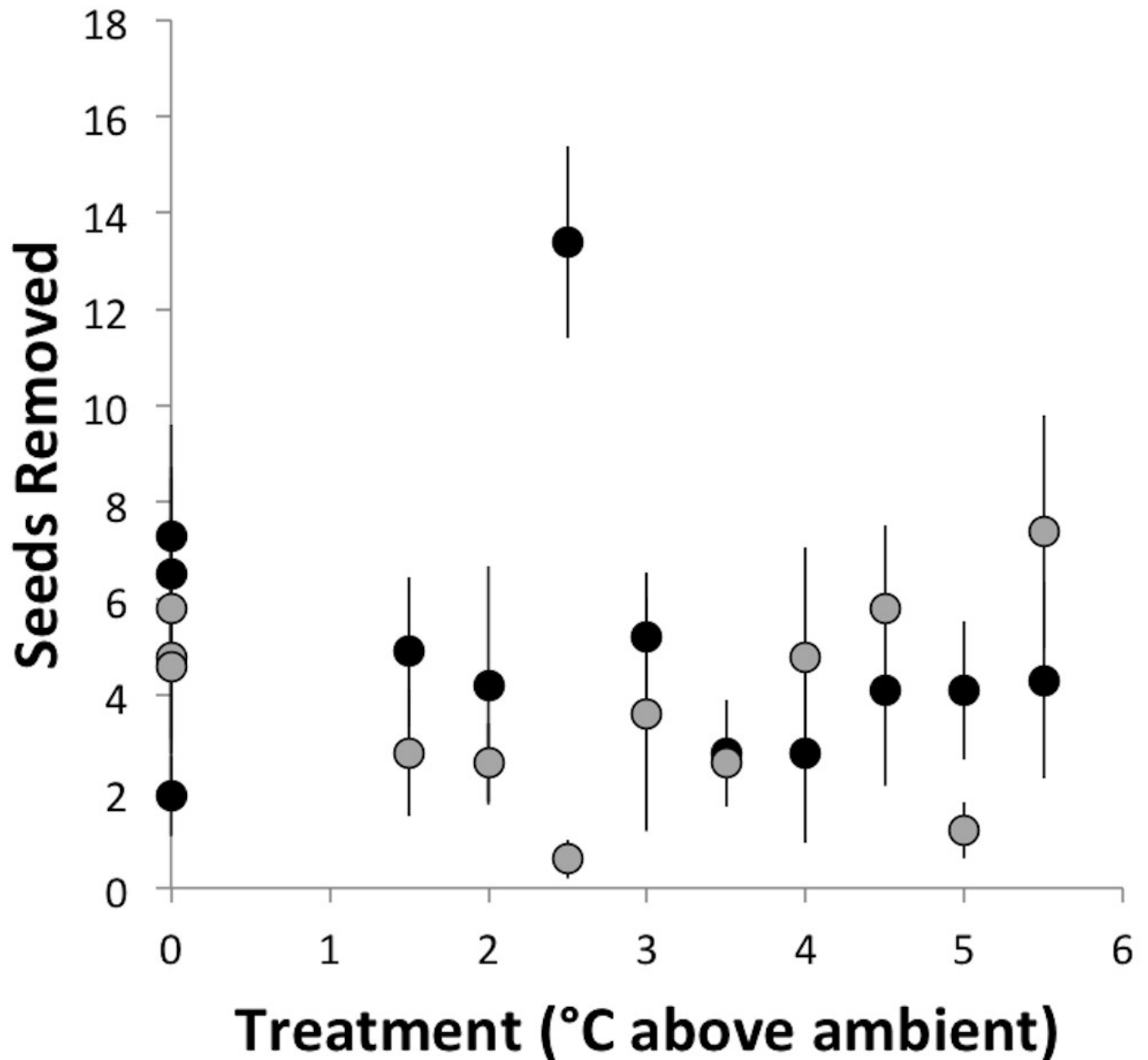
Figure 3

Figure 3. Temperature at which seeds were removed as a function of a species' critical thermal maximum (CT_{max}).