Research Article

Exploitative Competition and Risk of Parasitism in Two Host Ant Species: The Roles of Habitat Complexity, Body Size, and Behavioral Dominance

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Habitat structural complexity can slow resource discovery by ants but can also lower the risk of parasitism during foraging. The relative importance of these two ecological facets of habitat complexity may differ in a species-specific manner and thus may be important in the outcome of exploitative competition over food resources. For the host ant species *Pheidole diversipilosa* and *P. bicarinata*, we used in situ experimental manipulations to explore whether the effects of habitat complexity on exploitative competition depended on host body size and behavioral dominance, two characteristics likely to affect mobility and utilization of refuge from specialist Dipteran parasitoids (*Apocephalus orthocladius* and *A. pugilist*, resp.). We found that habitat complexity affected the resource discovery and harvest components of exploitative competition in an opposing fashion for each species and discuss these results in light of the differences in body size and behavioral dominance between the two hosts.

1. Introduction

Characteristics of habitats in which animals forage influence their mobility, ability to compete, and the likelihood of encountering predators, among other things. The structural complexity of a habitat can act on several aspects of animal foraging simultaneously. In particular, exploitative competition or the consumption of a common resource without direct competitive interaction may be directly affected by habitat complexity because it constrains animal movement in a species-specific manner [1]. Architecturally complex substrates often take more energy and time to traverse [2–5], which can reduce a species' ability to find and efficiently harvest a resource. A given degree of habitat complexity will be more difficult for relatively small species to traverse because they must move around or through the substrate, instead of over it [1]. As a result, habitat complexity can mediate exploitative competition for a common resource because species of different sizes are differentially affected.

Although habitat complexity may have negative effects on exploitative competitive ability by constraining animal movement, it may also have positive indirect effects on competitive ability by providing refuge from predators or parasitoids during resource acquisition. Numerous studies on a wide range of taxa have noted the importance of habitat complexity in providing refuge from predators ([6–13], but see [14, 15], e.g., of habitat complexity increasing predation). By impeding movement and providing refuge, habitat complexity may have opposing effects on resource discovery and acquisition, but the degree to which this is true may depend on species-specific characteristics such as body size or use of refuge from predators.

Ant communities are well suited for studying the role of habitat complexity in exploitative resource competition and escape from predators. Evidence suggests that exploitative competition between species has fitness consequences and is important in determining community composition [16–19]. Ants exhibit a wide range of body sizes [1], with larger ants being able to navigate complexity in the microhabitat more easily than small ants [20–23]. Increased habitat complexity does not appear to have an energetic cost to foragers [24], but does increase the time required to harvest resources and necessarily decreases harvest rate [25].

Ant communities are not traditionally considered to be structured by top-down forces from predators. However, community composition can be influenced by specialist Dipteran parasitoids (Apocephalus: Phoridae) that attack host ant species, induce behavioral responses in their hosts, and alter the outcome of interspecific competition in the community [26–32]. Habitat complexity has been shown to benefit the host ant species *Pheidole diversipilosa* and *P. bicarinata* during interference competition with nonhost ant species by providing refuge from parasitoids. Refuge allows hosts to maintain similar numbers of soldiers during head-to-head competition as in competitive bouts without parasitoids [13]. These two host ants cooccur in the same habitat and are dominant to most other ants in the community, but *P. bicarinata* is behaviorally subordinate to *P. diversipilosa* [30]. This difference in dominance has the potential to impact benefits derived from habitat complexity during exploitative competition.

Previous research indicates that *P. diversipilosa* wins a majority of contests, has access to the majority of resources, and experiences a resource environment that is not restricted by competition [29]. If such a host is attacked by its specialist parasitoid while exploiting an uncontested resource, it can simply abandon the resource, wait for parasitoids to leave, and return to the resource at a later time [33]. As a result, any refuge provided by habitat complexity would have marginal benefit to the colony during exploitative competition.

Predictions are different for the more subordinate species, *P. bicarinata*. Subordinate species only have access to a limited proportion of total available resources because they often lose resources to dominants [29]. Previous work has shown that subordinate hosts simply cannot afford to leave a resource when parasitoids arrive because successful foraging bouts are too rare [33]. For subordinates, a higher mortality risk must be accepted in order to satisfy energy requirements. Work on damselfly, passerine bird and ant communities has demonstrated that solutions to this ecological trade-off have evolutionary repercussions: subordinate competitors or species with higher resource requirements display little predator avoidance regardless of any pressure from dominant competitors [33–35]. Such observations have led to the hypothesis that subordinate species, who typically experience a more limited resource environment than dominants, will sacrifice predator avoidance to a greater extent than dominants in order to meet energy requirements [33, 36, 37]. While harvesting uncontested resources, subordinate hosts are likely to benefit from refuge provided by habitat complexity to a greater extent than dominant hosts because subordinates under attack by parasitoids must continue to forage even when resources are not contested by competitors, whereas dominants can avoid parasitism by returning to the nest.

The ecological and evolutionary consequences of host dominance discussed above suggest that benefits derived from habitat complexity may depend on whether foraging is occurring in an interference or exploitative competitive context. The benefits derived from habitat complexity during interference competition (head-to-head competition for resources) are investigated in a previous study [13]. In con-

trast, this study focuses on whether habitat complexity affects the exploitative component of competition (depression of the resource base in the absence of competitors). We explored the benefits derived from habitat complexity separately in interference and exploitative contexts because parasitoids have a greater impact on hosts engaged in interference competition (versus exploitative harvest of uncontested resources), due to a positive feedback between recruitment pheromones used during defense of resources and parasitoid behavior [29].

In addition, this study expands upon a previous study [13] by exploring whether habitat complexity affects the "discovery" and "harvest" components of exploitative competition separately. The effects of habitat complexity on each component of exploitative competition are interpreted in light of the body size and behavioral dominance of two host ant species. Of the two focal species, *P. diversipilosa* is approximately twice as large as *P. bicarinata* (workers: 0.12 versus 0.05 mg, resp.; soldiers: 0.44 versus 0.26 mg, resp.), and wins 15% more of its interactions with all other species in the local assemblage [30]. First, we determine whether habitat complexity influences the time it takes each host species to find resources (the "discovery" component of exploitative competition, [38]). Second, we ask whether the benefits hosts receive from refuge during harvest of uncontested resources (the "harvest" component of exploitative competition) depends on their dominance within the community. Benefits provided by habitat complexity during harvest of uncontested resources are measured in terms of the number of soldier ants because (1) soldier ants are crucial for the defense and harvest of large resources and (2) only soldiers are attacked by parasitoids. We then interpret our findings in the context of variation in habitat complexity.

2. Materials and Methods

2.1. Study Site and System. This study was conducted in oak, pine, and juniper woodlands in the Chiricahua Mountains of Southeast Arizona. The two focal ant species *P. diversipilosa* and *P. bicarinata* coexist in this habitat and are hosts to species-specific parasitoids (*Apocephalus orthocladius* and *A. pugilist*, resp., [39]). In July-August of 2003, *P. diversipilosa* was studied on National Forest land surrounding the Southwestern Research Station (31°52′ N 109°14′ W). In August-September of 2004, *P. bicarinata* was studied nearby on land owned by the Southwestern Research Station (31°53′ N 109°12′ W). Colonies of *P. diversipilosa*, *P. bicarinata,* and their respective parasitoids are found at both of these sites within meters of each other, but their relative abundances at each site differ (see Section 4).

2.2. Experimental Design. To investigate how habitat complexity affects exploitative competition for resources and host-parasitoid interactions, we forced field colonies to forage up into plastic bins and recorded their behavior under different levels of habitat complexity and parasitism. Cookie baits measuring 2×2 cm were placed 50 cm away from the nest entrance, and the number of soldiers harvesting and

defending these baits was recorded every 10 minutes for 2.5 hours in all treatments. Cookie baits are examples of large resources that require soldiers to break them into small pieces for efficient transport by workers. Placing baits 50 cm away from colony entrances ensured that baits were discovered and that colonies traversed a distance during which they were susceptible to parasitoid attack.

Foraging bins were 30×60 cm Sterilite storage containers, and had a 6 cm diameter hole at one end that could be placed directly over colony nest entrances. Using foraging bins allowed us to (1) minimize disturbance around nest sites and control exactly which resources hosts were harvesting and (2) introduce or exclude parasitoids from treatments using bridal veil to cover the foraging bin. We used soldier number as a response variable because soldiers (1) are able to carve up large resources for transport to the nest by workers, and thus are critical to harvesting resources, (2) can defend resources against competitors, and (3) are the only caste attacked by parasitoids in this system. We also recorded the time it took colonies to discover cookie baits.

We used a multifactor design with two levels of habitat complexity (complex or simple) and parasitoid exposure (parasitoids present or absent). Complex habitat treatments contained 5000 cm^3 of leaf litter that had been ovendried for 72 h, while simple habitat treatments occurred in empty foraging bins. The addition of leaf litter closely approximated average leaf litter depth found in habitat where both species coexisted. Parasitoids were captured by aspiration during recruitment events instigated at unused host colonies nearby. In parasitoid-present treatments, two parasitoids were introduced after soldiers had recruited to resources. Foraging bins were covered tightly with bridal veil in all treatments to ensure that parasitoids could not escape from parasitoid-present treatments and that parasitoids could not gain access to parasitoid-absent treatments.

Treatments were replicated on seven colonies of *P. diversipilosa* and eight colonies of *P. bicarinata*. The experiment was performed in areas where *P. diversipilosa* and its specialist parasitoid *A. orthocladius* cooccurred with *P. bicarinata* and its specialist parasitoid *A. pugilist* in order to control for the surrounding competitive environment. Colonies were randomly assigned the order in which they received treatments such that all colonies on a given trial day received different treatments. This allowed us to control for the effects of environmental variation and cumulative treatment effects. In addition, we rested colonies for two days between treatments to control for energetic state after foraging on cookies. It was not possible to monitor all colonies at once due to time constraints and distance between colonies, so all replicates were divided roughly into two groups, and groups experienced treatments within 24 h of each other to control for environmental conditions. All treatments were shaded to control for temperature and humidity differences between colony locations.

2.3. Analysis. Exploitative competition can generally be divided into two components: discovery and harvest of resources. To determine the impact of habitat complexity on resource discovery for each host, we conducted paired *t*-tests on the time it took hosts to discover cookie baits (TTD) in complex and simple habitat treatments. This experiment resembles a randomized block or repeated measures design, in which colonies are blocks and treatments are implemented within blocks. Since parasitoid treatments were not implemented until after hosts discovered cookie baits, TTD values were averaged across both levels of parasitism (e.g., for each complexity treatment, TTD values for each colony were averages of TTD in parasitoid absent and parasitoid present levels). Paired *t*-tests were then performed to compare each colony's average values for complex and simple habitats. To compare discovery speed between hosts within either simple or complex habitat treatments, we used two-sample *t*-tests because hosts were not intrinsically paired. To control for the multiple comparisons made within habitat complexity treatments and maintain an experiment-wide α of 0.05, we used Bonferroni adjustments.

To determine whether the refuge benefits provided by habitat complexity during harvest of resources depend on host dominance level, we constructed a randomized block/repeated measures General Linear Model to test for differences among treatments. For each host, post hoc comparisons among means were conducted using Tukey's HSD method with degrees of freedom appropriate for randomized block/repeated measures designs and 0.05 experiment-wide α levels. Replicate means were calculated by averaging recorded values of soldiers at cookie baits over the 2.5 h foraging period. Recorded values were averaged from the time colonies discovered the cookie bait for treatments without parasitoids, and from the point of parasitoid introduction for treatments with parasitoids. Means were transformed [log (mean + 1)] to meet homogeneity of variance and normality assumptions.

3. Results

The time it took *P. diversipilosa* to discover cookie baits did not differ significantly between complex and simple habitat treatments ($t_{1,6} = -0.870$, $P > 0.05$; Figure 1), although *P. diversipilosa* discovered resources slightly faster in complex habitat treatments. In contrast, *P. bicarinata* discovered resources in simple habitats much more quickly than in complex habitats ($t_{1,7} = 5.276$, $P < 0.005$; Figure 1). Within complex habitats, *P. diversipilosa* discovered resources more quickly than *P. bicarinata* ($t_{1,13} = 2.538$, $P < 0.05$; Figure 1), but *P. bicarinata* discovered resources more quickly than *P. diversipilosa* in simple habitats ($t_{1,13} = -2.923$, $P < 0.005$).

For both *P. diversipilosa* and *P. bicarinata*, general linear models indicated that significant differences in the number of soldiers harvesting resources existed between at least two treatments ($F_{3,17} = 5.070$, $P < 0.05$; $F_{3,21} = 4.139$, $P < 0.05$ resp.). *P. diversipilosa* maintained significantly more soldiers at resources in complex habitats without parasitoids than either complex or simple habitats with parasitoids (closed circle compared to closed and open triangles in Figure 2(a): $Q_t = 4.244$, $P < 0.05$; $Q_t = 4.683$, $P < 0.05$). There was a little
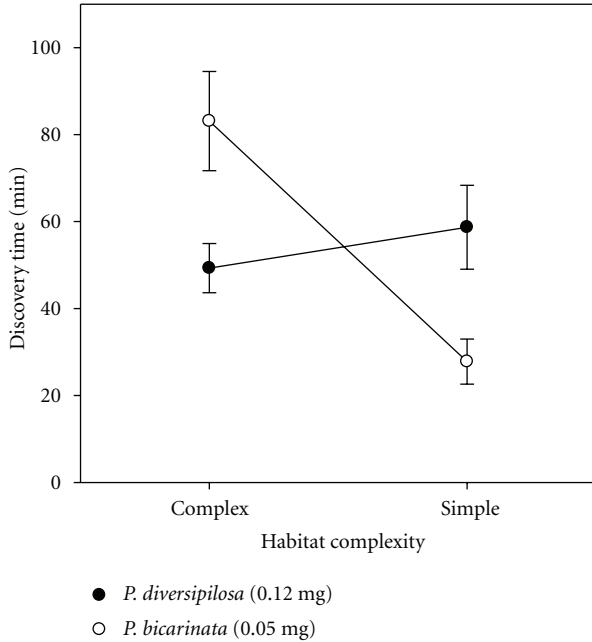
FIGURE 1: Differences in resource discovery time between *P. diversipilosa* and *P. bicarinata* in complex and simple habitats. Means and standard errors are presented.

difference in soldier number between simple and complex habitats without parasitoids (open and closed circles: $Q_t = 1.358$, $P > 0.05$). There was also no difference in soldier number between simple habitats without parasitoids and both simple and complex habitats with parasitoids (open circles compared to open and closed triangles: $Q_t = 3.379$, $P > 0.05$; $Q_t = 2.886$, $P > 0.05$).

P. bicarinata maintained significantly more soldiers at resources in complex and simple habitats without parasitoids than simple habitats with parasitoids (open and closed circles compared to open triangle in Figure 2(b): $Q_t = 4.199$, $P < 0.05$; $Q_t = 4.191$, $P < 0.05$). In contrast, no difference in soldier number existed between complex and simple habitats without parasitoids and complex habitats with parasitoids (open and closed circles compared to closed triangles: $Q_t = 2.355$, $P > 0.05$; $Q_t = 2.347$, $P > 0.05$). Soldier number was also statistically indistinguishable between complexity levels in both parasitoid and no parasitoid treatments (open compared to closed triangles and open compared to closed circles: $Q_t = 1.844$, $P > 0.05$; $Q_t = 0.008$, $P > 0.05$).

4. Discussion

4.1. Exploitative Competition. For a given habitat complexity level, such as the leaf litter used in this study, smaller species perceive their environment as more rugose than larger species. This theory, known as the size-grain hypothesis, predicts that larger species will traverse a moderately rugose habitat with greater ease than smaller species [1]. Results on resource discovery time show that smaller *P. bicarinata* take longer to discover resources in complex habitats than do larger *P. diversipilosa*, which is consistent with the size-grain

hypothesis. However, the observation that smaller *P. bicarinata* find resources in simple habitats more quickly than larger *P. diversipilosa* runs somewhat contrary to the predictions of the size-grain hypothesis. This observation suggests that, in addition to the limitations on movement predicted by the size-grain hypothesis, these two species either (1) differ in the degree to which they tolerate desiccation, (2) have different exploratory or recruitment strategies, or (3) exhibit differential sensory bias toward habitat complexity. First, differences in the degree to which species tolerate desiccation is not a plausible explanation for *P. bicarinata* discovering resources more quickly than *P. diversipilosa* in simple habitats because smaller ants such as *P. bicarinata* are more sensitive to desiccation stress than larger ants, and soil temperatures are much higher in more open, simplified environments [40–44]. Physiological limitations are also not a plausible explanation in the context of our experimental setup because physiological conditions between treatments were controlled (see Section 2). Second, *P. diversipilosa* and *P. bicarinata* may differ in their exploratory [45] or recruitment behaviors [46]. Unfortunately, the small scale of our experimental arena caused a rapid attenuation of recruitment curves, making insight into exploratory and recruitment behavior difficult in this study. Further work should be conducted to determine whether differences in exploratory or recruitment behavior can explain *P. bicarinata* discovering resources more quickly than *P. diversipilosa* in simple habitats. Finally, *P. diversipilosa* and *P. bicarinata* may exhibit differential sensory bias towards habitat complexity, a possibility that is discussed in detail below. Regardless of the mechanism behind these results, the ultimate consequence is that smaller *P. bicarinata* can discover resources faster in simple habitats, while larger *P. diversipilosa* can discover resources faster in complex habitats. Thus, habitat complexity has important but contrasting effects on the resource discovery component of exploitative competition for both species.

During initial attempts to find host colonies for this study, 44% of *P. bicarinata* and 64% of *P. diversipilosa* foraging bouts to cookie baits went unchallenged (data not shown). Thus refuge from parasitoids during uncontested harvest of resources may have important fitness consequences. *P. diversipilosa* and *P. bicarinata* harvesting resources in the absence of direct competition respond differently to habitat complexity, and this difference is best explained by the parasitoid avoidance behavior and dominance of each host. We predicted that *P. diversipilosa*, being behaviorally more dominant and having access to the majority of resources, would abandon uncontested resources when under attack by parasitoids regardless of the presence of refuge in complex habitats. This prediction follows from the resource loss-predation trade-off suggested to exist in a variety of systems [33, 36, 37]. We found that *P. diversipilosa* under attack by parasitoids do abandon uncontested resources regardless of whether refuge from habitat complexity is present. However, we also found that the number of soldiers *P. diversipilosa* maintains at resources in simple habitats without parasitoids is not statistically distinguishable from the number of soldiers maintained in simple habitats with parasitoids.

A lower physiological threshold for open habitats is one explanation for this pattern but is unlikely for reasons explained above. In addition, if desiccation tolerance were solely responsible for the observed foraging patterns of *P. diversipilosa* during exploitative competition, significant differences between complex habitat treatments in the presence and absence parasitoids should not exist. However, we cannot rule out the role of desiccation tolerance in *P. diversipliosa* foraging behavior. A more plausible explanation is that *P. diversipilosa* exhibits a sensory bias towards habitat complexity and is less willing to forage in any habitat that does not offer refuge from parasitoids. Numerous studies on a wide range of taxa suggest that animals make patch choices based on perceived predation risk ([47] and references therein, [48–50]). Work on vole, deer mouse and passerine bird populations suggests that competitive dominants may choose to forage in habitats with less predation risk, thereby forcing subordinates to forage in habitats with greater predation risk [50–53]. These patch choices take place in ecological time and are considered solutions to the problem of maximizing energy intake while minimizing mortality risk.

As predicted by the resource loss-predation trade-off, subordinates must accept a higher mortality in order to satisfy energy requirements. Therefore, we predicted that *P. bicarinata* under attack by parasitoids would benefit from refuge even while foraging on uncontested resources. The number of *P. bicarinata* soldiers at resources in complex habitats was similar regardless of parasitoid presence, but soldier number in simple habitats with parasitoids was much lower than without parasitoids. These observations support the predictions of the resource loss-predation trade off and suggest that refuge benefits associated with habitat complexity depend on host dominance during exploitative competition. Subordinate hosts harvesting uncontested resources benefit from habitat complexity because their need for resources does not allow them to avoid parasitism by ceasing foraging. In contrast, dominant hosts harvesting uncontested resources receive no benefit from habitat complexity because they can afford to cease foraging in the presence of parasitoids. The potential for resource loss increases when resources are directly contested by competitors (interference competition). As the potential for resource loss increases during interference competition, dominant hosts should become more willing to accept the risk of parasitism in order to retain resources, and refuge provided by habitat complexity may allow hosts to strike a balance between retaining resources and risking mortality. Prior work in this system has shown that *P. diversipilosa* under attack by parasitoids will not abandon resources if they are directly contested by competitors, as long as habitat complexity provides some refuge from attacking parasitoids [13]. This study expands upon previous work [13] by demonstrating that behavioral dominance and refuge provided by habitat complexity interact to influence how species balance the resource loss-predation trade-off in different competitive contexts. The acts of discovering resources and harvesting resources in the absence of competitors are two important components of exploitative competition between the focal species of this study. Habitat complexity provides an advantage to *P. diversipilosa* during the discovery phase of exploitative competition because *P. diversipilosa* is larger and can traverse complex habitats more easily than *P. bicarinata*. The opposite is true while harvesting resources: habitat complexity provides an important refuge benefit to *P. bicarinata*, but no refuge benefit to *P. diversipilosa*. During exploitative competition, habitat complexity plays a dual role in impeding movement and providing refuge. These mechanisms work in opposing manners in this system because the focal species differ in body size and behavioral dominance. The degree to which the discovery and harvest components of exploitative competition are opposing will depend on the relative strength with which habitat complexity impedes movement and offers refuge for *P. diversipilosa* and *P. bicarinata*.

4.2. Impact of Natural Heterogeneity on Movement and Benefits from Refuge. For ants, the degree to which movement is impeded by habitat complexity depends largely on the abundance and quality of litter on the ground surface. Natural heterogeneity in habitat complexity could lead to local pockets in which movement was strongly impeded by habitat complexity, favoring *P. diversipilosa's* resource discovery abilities, and other pockets where movement was unimpeded, favoring *P. bicarinata's* discovery abilities. In extremely heterogeneous environments, the relative discovery abilities of both species may, therefore, be similar when summed across the community. Further work is needed to determine whether natural heterogeneity in habitat complexity could facilitate coexistence between these host species.

The degree to which habitat complexity provides refuge depends both on variation in litter and on the abundance of parasitoids. While under attack by a constant number of parasitoids, *P. bicarinata* benefits more from refuge than *P. diversipilosa* (Figure 2). If there is reliable parasitoid pressure on both hosts, *P. bicarinata* would experience a greater relative benefit from refuge. Working in the same system, LeBrun and Feener [29] found that parasitoids discovered *P. diversipilosa* exploiting resources in the absence of competitors ~50% of the time. Parasitoid discovery of *P. bicarinata* is less predictable, as *A. pugilist* exhibits wide fluctuations in abundance through space and time, but is rarely more than 50% [33]. Based on observed parasitoid abundance for each host, it appears that the potential to benefit from refuge is greater for *P. bicarinata*. Pockets of low habitat complexity will not counteract benefits that *P. bicarinata* receives from areas nearby with higher habitat complexity because, unlike *P. diversipilosa*, *P. bicarinata* forages willingly in simplified habitats, and also unlike *P. diversipilosa*, *P. bicarinata* maintains some foraging presence at resources regardless of whether refuge from parasitoids is available (see Figure 2).

4.3. Conclusions. While *P. diversipilosa* should have greater relative discovery abilities in complex habitats, natural heterogeneity in structural complexity will minimize this advantage by favoring *P. bicarinata* in simpler habitats. *P. bicarinata* is also likely to benefit from refuge from parasitoids during harvest of uncontested resources to a greater degree than
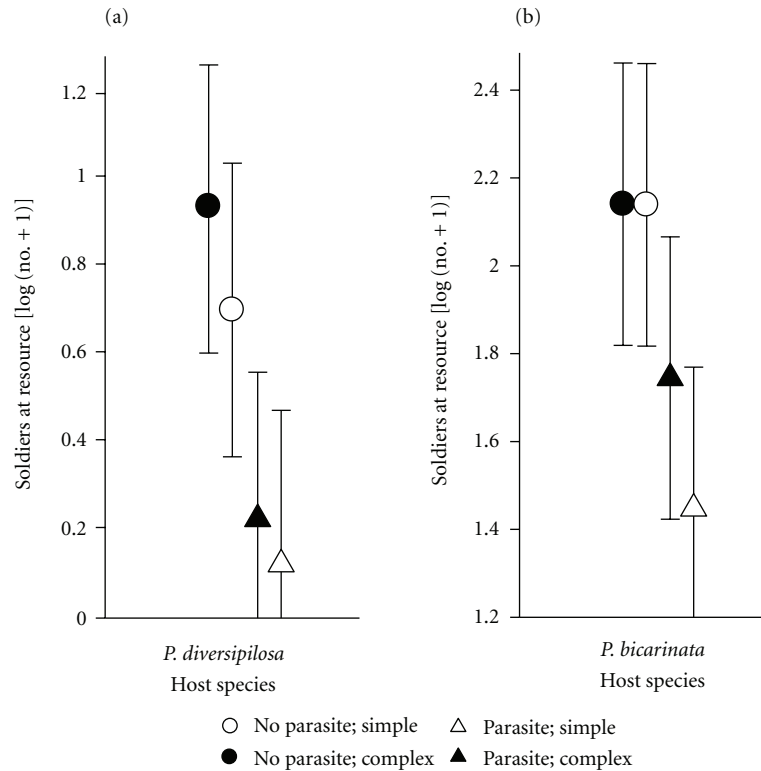
FIGURE 2: Number of (a) *P. diversipilosa* and (b) *P. bicarinata* soldiers harvesting resources in the absence of head-to-head competition when parasitoids are absent (*circles*) or present (*triangles*) in complex habitat (*filled symbols*) or simple habitat (*empty symbols*). Means and Tukey's minimum significant difference (MSD) comparison intervals are presented. Means whose comparison intervals overlap are not significantly different. Means whose comparison intervals do not overlap are significantly different at an experiment-wide α of 0.05.

P. diversipilosa, and this advantage will not be affected by natural heterogeneity in structural complexity. These advantages in exploitative competitive ability experienced by *P. bicarinata* may partially explain why it is able to coexist along with *P. diversipilosa*, who is a superior interference competitor [29].

This study demonstrates how the dual roles of habitat complexity in impeding movement and providing refuge from parasitoids impact the exploitative competitive abilities of two host ant species. These two mechanisms by which habitat complexity mediates competition may function in an opposing manner because of differences in host body size and behavioral dominance. However, further work should be conducted to determine whether differences in exploratory or recruitment strategies offer additional insight into the effects of habitat complexity on each host [45, 46]. Natural variation in habitat complexity or variation caused by disturbance such as fire [13] may impact the relative importance of these mechanisms for each host, the degree to which they are opposing, and therefore the potential for coexistence between these species. Knowledge of the prevalence of complex versus simple substrates within and between habitats is important for predicting the degree to which these mechanisms oppose each other, but is currently lacking.

Acknowledgments

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