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Enemy-Free Space for Parasitoids

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ABSTRACT

Animal trait patterns and variation in the structures of their communities have typically been explained in the context of competition for resources. Progress in research over past decades has shown the importance of mortality from natural enemies as community structuring forces. Selection towards enemy-free space through traits that aid in interactions with these natural enemies can be used to explain community patterns. Insect parasitoids that develop as larvae by continuously feeding within a host herbivore experience many of the same ecological pressures as these hosts, such as predation. Parasitoid communities may be structured by mortality from natural enemies of their hosts, and should avoid hosts with a high risk of mortality. Here, data from multiple field studies conducted in temperate Connecticut forests were combined to assess the impact of enemy-free space on parasitoid fly and wasp community patterns. Using generalized linear models, I examined the relationship between the risk of predation from birds and ants and the probability of parasitism across the community of caterpillar species found on eight deciduous tree hostplant species. I tested the prediction that probability of parasitism should be negatively correlated with risk of predation, while accounting for fixed effects on parasitism related to the caterpillar species and the host-plant species. Predation risk from birds had consistent negative relationships with all measures of parasitism (total, as well as fly and wasp separately) while the risk of ant predation had little to no relationship with probability of parasitism. These relationships were stronger for tachinid fly parasitoids than wasp parasitoids, potentially highlighting differences in their life-histories and the timing of predation. The results support the enemy-free space for parasitoids hypothesis: parasitoids generally avoid caterpillar and host-plant combinations with a high risk of bird predation. Therefore enemy-free space from birds in conjunction with host-plant and caterpillar species-based effects drive parasitoid host choice in this temperate community. These results highlight the importance of considering multiple and varied ecological effects simultaneously when investigating community-level patterns.

INTRODUCTION

Enemy-Free Space

Many pivotal ecological and evolutionary hypotheses for causes of ecological community structure have been posited in the context of direct interactions between organisms (e.g., predator-prey interactions, herbivore-hostplant associations, competition for resources), without considering how indirect and multi-trophic level interactions may play a role. For example, during much of the 20th century competition for resources was the conventional explanation as the major biotic force structuring communities. Many aspects of animal life-history such as body size, diet breadth, and feeding guild had been traditionally explained through the lens of interspecific competition (Jeffries and Lawton 1984, Chase and Leibold 2003) even though these traits are often mediated by the trade-off between mortality from natural enemies and resource acquisition (Ives and Dobson 1987, Werner at al. 1992). Bottom-up effects (effects that begin in lower trophic levels and propagate up the food web) such as competition for resources were assumed to have much stronger influence on animal communities and trait patterns than top-down effects (effects beginning with a higher trophic level that propagate down the trophic levels) from interactions like predation and parasitism. As research progressed, many ecologists noticed the limitations of focusing on resource competition, especially when discussing coexistence of organisms and their ecological niches. Although competition for resources is still known to be an important factor structuring animal communities, its primacy has mostly been exchanged for a more holistic view that includes other factors, such as predation, as well as indirect interactions (Chase and Leibold 2003, Pocheville 2015).

One aspect of this holistic perspective considers tri-trophic interactions as drivers of community patterns (Singer and Stireman 2005, Abdala-Roberts et al. 2019). The concept of enemy-free space figures prominently in tri-trophic interactions and community structure. Jeffries and Lawton (1984) presented the idea of enemy-free space as an alternative to the conventional resource competition explanation; proposing that components of a species ecological niche are influenced by its natural enemies and species traits will aid in avoiding interactions with these enemies, taking advantage of enemy-free space. Jeffries and Lawton (1984) made the important point that true enemy-free space is extremely rare in nature and define the term as “ways of living that reduce or eliminate a species vulnerability to one or more species of natural enemy.” The potential effects of predators on shaping a species’ ecological niche was not new, however. Holt (1977) coined the term “apparent competition” for cases where prey species interact via a shared enemy, and others had argued that the effects of shared natural enemies would generally be the same as interspecific competition for resources (Williamson 1957). Jeffries and Lawton (1984) hoped that this competition for enemy-free space could be used as an explanation for ecological and evolutionary patterns that could not or could only poorly be explained by resource competition. Their seminal paper sparked more critical attention to enemy-free space, and tests of this idea in ecological research have grown more common in many different environments and communities.

A well-known application of enemy-free space has occurred in the study of evolutionary ecology of host selection and specialization in insect herbivores (e.g., Price 1980, Singer and Stireman 2005, Mooney et al. 2012, Vidal and Murphy 2018a & 2018b). Insect herbivores frequently have diets restricted to a small set of host-plants, usually within the same family (Forister et al. 2015). Ecological studies and theory have attempted to explain this phenomenon by focusing on anti-herbivore traits of the host-plant, especially secondary metabolites that serve as deterrents or toxins (Ehrlich and Raven 1964, Thompson 1988, Jaenike 1990, Cornell and Hawkins 2003). It is expected that dietary specialists will be more efficient in utilizing their host-plants as food relative to dietary generalists, leading to a physiological advantage of specialization. This advantage is theorized to arise from co-evolved counter-adaptations not found in generalists that allow specialists to tolerate, detoxify, or sequester plant secondary metabolites (Thompson 1988, Karban and Agrawal 2002, Ali and Agrawal 2012). Bernays and Graham (1988) challenged this bi-trophic theory of insect specialization and expanded on the idea of enemy-free space posited by Jeffries and Lawton (1984). Generalist predators such as ants and birds are significant sources of mortality for herbivores (Roslin et al. 2017), which might cause strong selection on herbivores to use host-plants that provide the best anti-predator defenses. If this predation imposes stronger trade-offs in herbivore fitness across alternative host-plants than does anti-herbivore traits of plants, it is predicted that selection from predation will lead to host-specialist herbivore phenotypes that acquire enemy-free space on specific host-plants (Bernays and Graham 1988). If natural enemies pose strong selection, enemy-free space as a selective force can be applied to any species' enemies and may help better explain community dynamics.

Enemy-free space as a selective force on key ecological traits of organisms has been applied to terrestrial, freshwater, and marine ecosystems, with many studies focusing on invasive species that may utilize enemy-free space to replace competing native species (Söderbäck 1994, Roy et al. 2011). In terrestrial environments, a wide range of organisms has been studied in regard to enemy-free space, ranging from insect herbivores (discussed above) to bird (e.g., Suhonen et al. 1994, Schmidt and Whelan 1999, Hufbauer and Via 1999) and large mammalian species (e.g., Lawton and Woodroffe 1991, Doncaster 1992, Lingle 2002). By altering predator access (Persson and Eklöv 1995, Caley 1993), and habitat structures (Hixon and Beets 1993, Werner and McPeek 1994), studies have found support for selection towards maximizing enemy-free space in marine organisms and widespread effects of predation on species distributions. Communities in freshwater environments have received similar study to marine ecosystems (Fraser et al. 1995), and many of the same patterns of predator avoidance and utilization of protected, structurally complex habitats have been found (Pierce 1988, Christensen and Persson 1993, McPeek 1996).

The majority of researchers have moved on from the historical focus on competition for resources and test its selective effects alongside predation's. Many organisms face a foraging behavior trade-off between predator avoidance and increased resource acquisition; research has provided many examples of preference for habitat refuges or behaviors that provide enemy-free space at the expense of resource acquisition (e.g., Caraco et al. 1980, Werner et al. 1983, McPeek 1998, Persson 1993, Halpin 2000, Gonzáles et al. 2001, Singer et al. 2004, Moon et al. 2006). Studies on insect parasitoid host use have been some of the first attempts to expand enemy-free space and apply its predictions to organisms of higher trophic levels (Völkl 1992, Kaneko 2003, Murphy et al. 2014, Baer and Marquis 2020).

Parasitoid Life History

Parasitoids are organisms whose immature stages develop by feeding on a living host animal, often an insect, and usually result in the death of the host (Godfray 1994). Parasitoids are free-living as adults and must search for suitable hosts through a huge variety of environmental cues (Godfray 1994, Hawkins 1994). Lepidopteran larvae (caterpillars) face significant mortality from two main groups of parasitoids, wasps (commonly braconid and ichneumon) and tachinid flies. Hymenopteran parasitoids have ovipositors that pierce into their host where eggs are laid (Shaw 2006). Tachinid flies lack an ovipositor and will often lay their eggs directly on the host or on the plant nearby and newly hatched larvae must find a way into the host (Stireman et al. 2006). Many species of parasitoids are restricted in their host choice and specialize on a single host species or collection of usually closely related species (Hawkins 1994). As endoparasitic predators of herbivores, the parasitoids may face some of the same ecological pressures as their host insects, and tri-trophic interactions that structure the herbivore community may also influence parasitoid communities (Murphy et al. 2014).

Enemy-Free Space for Parasitoids

Relatively little study has been done on the potential effects of predators and other natural enemies in determining parasitoid host selection. Hawkins (1994) analyzed variation in host-parasitoid interactions across insect herbivore feeding guilds and found broad patterns of host-plant and herbivore traits as well as interactions between these traits that explained up to 50% of variation in parasitism rate of herbivores. This comprehensive book on parasitoid community patterns does mention that predators of the host herbivores may influence host selection by parasitoids but does not empirically address the issue. The possibility that selection due to predation plays a role in structuring parasitoid-host interactions cannot be ignored (Murphy et al. 2014). While a parasitoid larva develops within an insect herbivore host, traits of that herbivore and of the host-plant that reduce predation to the herbivore will also provide enemy-free space to the developing parasitoid. Therefore, selection is expected to favor parasitoid adults that preferentially utilize herbivore hosts facing lower risks of predation because this host selection behavior would provide the parasitoid larvae with enemy-free space. If multiple parasitoid species in a community choose hosts in this manner, enemy-free space as a structuring force of parasitoid communities predicts a negative relationship between predation risk and parasitism rate across host species.

Frago (2016) is one of the only review papers that considers how intraguild predation and natural enemies of parasitoids may influence the evolutionary processes that shape patterns of parasitoid host use. Many parasitoids alter their behavior in the presence of predators or predator cues, and the dominant parasitoid of an herbivore species has been shown to shift in the presence of hyperparasitoids (insects that utilize primary parasitoid larvae as their host) and other natural enemies (Nofemela 2013, Frago 2016). As far back as the inception of the hypothesis parasitoids have been mentioned as potential higher trophic level species that are heavily influenced by enemy-free space (Jefferies and Lawton 1984). While little work on enemy-free space for parasitoids followed since that pivotal paper, almost all studies have found results that support the hypothesis and its predictions (Völkl 1992, Kaneko 2003, Murphy et al. 2014, Baer and Marquis 2020). Ant attendance of an aphid species has been found to provide enemy-free space for both the aphid species and its primary parasitoids (Völkl 1992, Kaneko 2003). Ant-tended aphids were protected from one species of hymenopteran parasitoid but highly susceptible to a different species; their mutualist ants fought off ovipositing females of the first species but showed no response to flying females of the second. Aphids that were successfully parasitized then began to produce more honeydew than unparasitized aphids and suffered a drastically reduced rate of hyperparasitism (Völkl 1992). Similar work with a related species of aphid found that different ant mutualists provided different levels of protection against foraging primary and hyperparasitoids (Kaneko 2003). These parasitoids gain significant enemy-free space based on their aphid host selection and this research was some of the earliest to show the potential selective effects of higher trophic levels on parasitoid host selection (Völkl 1992, Kaneko 2003).

Murphy et al. (2014) offered a more expansive view of the enemy-free space for parasitoids hypothesis, which predicts that female parasitoids should seek enemy-free space for their offspring through the evolutionary ecology of host choice. They described three straightforward mechanisms by which parasitoids can gain enemy-free space through their host selection. The first mechanism is: hosts that are well protected with physical anti-predator defenses will also provide enemy-free space to a parasitoid larva that is developing within the host herbivore. The authors predict that parasitoids will target well-defended caterpillar hosts, and preferentially oviposit within these hosts to grant their larvae enemy-free space. Murphy et al. (2014) conducted comparisons across 14 limacodid and megalopygid caterpillar species from seven host-plants. Through collection of over 1,000 caterpillars, they found that well-defended caterpillar species possessing spines or other projections were significantly more likely to be parasitized than undefended species. In the Limacodidae, a family known for their defensive spines and hairs, the frequency of parasitism was positively associated with the level of physical defense among caterpillar species. The second method by which parasitoids may gain enemy-free space is by utilizing a chemically defended host. These herbivores that produce or sequester defensive compounds may provide similar defensive benefits as physically defended hosts; additionally, if the parasitoid is able to sequester and utilize chemicals from the host there may be a direct defensive benefit to the parasitoid. Through field collections of a specialist caterpillar that sequesters iridoid glycosides, Bowers and colleagues (in Murphy et al. 2014) found that increasing levels of sequestered chemicals did not negatively influence parasitoid success, and the results suggested a positive correlation of increased sequestration and parasitism.

The third mechanism that may provide parasitoids with enemy-free space is based on the idea that parasitoids will be subjected to most of the same ecological pressures as their herbivore hosts. Therefore, some of the same factors of host-plant choice that provide enemy-free space to herbivores can also provide enemy-free space to parasitoids. Different host-plant species or phenotypes will expose both the herbivore and any internally developing parasitoids to different rates of predation, and it is predicted that parasitoid adults will take advantage of microhabitat differences in enemy-free space and preferentially oviposit in herbivores that utilize their host-plant to gain enemy-free space. The enemy-free space for parasitoids hypothesis predicts a negative relationship between the rate of parasitism and risk of predation across host environments. An initial test in Murphy et al. (2014) using data from the Singer lab found support for this relationship. The frequency of parasitism of dietary generalist caterpillars (pooled as groups of species) varied across eight host tree species, and the frequency of parasitism from tachinid flies was negatively associated with the effect size of bird predation (measured for groups of species) and generalist caterpillar density across these tree species (Murphy et al. 2014). It is noteworthy for the present study that this initial test did not distinguish these measures of parasitism and predation among caterpillar species living in the same site and year.

Baer and Marquis (2020) tested the predictions of the enemy-free space hypothesis in a study of parasitoids that utilize shelter-building caterpillar hosts.

Shelter-building is a defensive phenotype of insect herbivores that is associated with increased parasitism (Hawkins 1994, Hrcek et al. 2013, Baer and Marquis 2020), potentially because these semi-concealed herbivores experience less predation than exposed caterpillars, providing enemy-free space for the developing parasitoid larvae. Baer and Marquis (2020) found a negative relationship between observational measures of predation and parasitism, consistent with predictions from the enemy-free space hypothesis. This support for the enemy-free space hypothesis was contrasted with a lack of evidence for shelter traits influencing parasitism. There was no effect of shelter type on parasitism, and the authors conclude that the most likely driver behind different rates of parasitism between functional groups of shelter-builders was the negative relationship with predation, and the effects the shelter type has on predation rates (Baer and Marquis 2020).

Given how complex interactions can be within these systems, using large datasets and searching for broad patterns may be the best way to analyze parasitoid communities and the factors that influence their composition, yet few researchers have a large enough dataset or suitable study system to further uncover tri-trophic effects on patterns of parasitism (Hawkins 1994). Previous studies have focused on specific species of parasitoids or hosts, and while these papers provide support for the enemy-free space for parasitoids hypothesis, they are relatively limited in scope. Volkl (1992) and Kaneko (2003) looked at only a few parasitoid species and host aphid species and their interactions with specific ant species, but their work provided preliminary evidence and some of the earliest work supporting the hypothesis. Baer and Marquis (2020) provide one of the most complete tests of the enemy-free space for parasitoids hypothesis as they measured predation and parasitism of shelter-building caterpillars simultaneously. Their study was restricted in scope through only looking at shelter-building caterpillars as they have unique interactions with their hostplants and natural enemies compared to the majority of caterpillars that feed exposed on the hostplant. The tests performed in Murphy et al. (2014) provide general support and information on potential mechanisms of enemy-free space for parasitoids and allow the present study to further elaborate on patterns. The present study expands on the initial test reported in Murphy et al. (2014), it takes a more fine-grained approach to measuring parasitism and predation by including dietary specialist as well as generalist caterpillar species in analyses and including the risk of ant predation as a predictor.

Parasitoid Host Selection

Parasitoid host selection is a topic of considerable interest in ecological and environmental literature, but the majority of work has focused on environmental factors or traits from the host herbivore and host-plant that propagate up trophic levels and influence parasitoid-host interactions. Beginning in the 1880s, parasitoids have been extensively studied for their potential uses in agricultural pest management, and only as recently as the late 1960s and 1970s has research begun to focus on non-pest species (Hawkins 1994, Harvey et al. 2015). Parasitism rates may vary across herbivore host species and host-plants due to differences in traits of the herbivore host, attributes of the host population, traits of the host-plant, traits of the parasitoid, and the interactions between these potential effectors. Bottom-up factors have been central in explanations while top-down effects of predators have been largely ignored.

Effect of Host Traits

Research in parasitoid host selection has focused on how the bi-trophic interactions of the herbivore host with the parasitoid adult influence patterns of parasitism, and how traits inherent to the herbivore may make them more susceptible to parasitism (e.g., Barbosa and Caldas 2007). Defensive traits of host caterpillars, for example, can directly prevent oviposition through concealment or deterrent behaviors, but many physiological processes, like herbivore immune responses to parasitoid eggs or larvae, can lead to the death of the parasitoid (Gross 1993, Smilanich et al. 2009a, Greeney et al. 2012, Kaplan et al. 2016). Behavioral defenses (e.g., thrashing, dropping from host-plant, regurgitation, etc.) are complex and varied between herbivore species, and their efficacy in preventing parasitoid attack has been rigorously studied in the lab and field. Almost all of these studies find that specific defensive behaviors increase survival in interactions with parasitoids, and in general, herbivores possessing greater behavioral defensive capabilities avoid parasitism (Stamp 1982, Gross 1993, Brodeur et al. 1996, Gentry and Dyer 2002, Singer et al. 2009, Firlej et al. 2010). The main exceptions to this pattern are caterpillars that build shelters as protection from natural enemies.

Many studies find that concealed caterpillars suffer much higher rates of parasitism and lower predation rates than externally feeding herbivores, and generally attribute this pattern to differences in caterpillar availability between the two feeding guilds (Hawkins 1994, Le Corff et al. 2000, Hrcek et al. 2013). Alternatively, parasitoids may avoid exposed hosts, which may face higher predation risk (i.e., enemy-dense space), and hosts in shelters provide enemy-free space (Baer and Marquis 2020). Interestingly, insects that utilize tough plant structures for protection from parasitoids like root borers or galling species have a similar parasitism rate to that of non-concealed herbivores (Hawkins 1994). This leaves the case of externally feeding herbivores with a rather unsatisfying answer, as they do not have the benefits of tough plant material to protect them from parasitoid attack but still suffer less parasitism than partially concealed herbivores. Conventionally, the variability in parasitism rate across externally feeding herbivores has been attributed to other traits of the herbivore such as defensive morphologies, behaviors, chemicals, and crypsis (Hawkins 1994, Barbosa and Caldas 2007), but effects of predators on parasitoid host selection should not be ignored.

The effect of defensive traits of the host on parasitism rates and survival is dependent on the ecological context. Studies focus on how effective these traits are at preventing contact with or oviposition by adult female parasitoids to explain variation in parasitism rates (Gross 1993, Greeney et al. 2012), without considering how these traits may benefit developing parasitoid larvae (Murphy et al. 2014). Sequestered chemical defenses of hosts, such as caterpillars, may be toxic to parasitoids (e.g., Price et al. 1980, Sime 2002). Alternatively, if these compounds are not toxic to parasitoids but do deter predation, they may promote parasitism (e.g., Gentry and

Dyer 2002, Lampert et al. 2010) by protecting both host and parasitoid. Morphological defenses of caterpillars mainly consist of spines or hairs and coloration, which may be bold and contrasting with the background or camouflaged. Although these traits may make adult parasitoid foraging and oviposition processes harder (Gross 1993, Dyer 1997, Gentry and Dyer 2002, Barbosa and Caldas 2007, Greeney et al. 2012), parasitoids might utilize caterpillars possessing these morphological traits to take advantage of enemy-free space. Stireman and Singer (2003) found that hairy caterpillars supported larger communities of tachinid parasitoids, and attributed this result to the putative reduced predation that hairy caterpillars face, which would provide enemy-free space for the parasitoids. Many studies have found that the caterpillars most well defended from predators, either chemically (Gentry and Dyer 2002), morphologically (Stireman and Singer 2003, Murphy et al. 2014), or behaviorally (Hrcek et al. 2013, Baer and Marquis 2020), also suffer higher rates of parasitism. In these cases, it seems reasonable to hypothesize that parasitoids are taking advantage of enemy-free space for their offspring, but this requires more information on the top-down effects of predators as well as bottom-up impacts of host-plant and herbivore on the parasitoids in these systems. Further tests and studies are needed to determine if escape from generalist predators has driven these parasitoids to utilize well defended hosts.

Effect of Plant Traits

Plant traits can both directly and indirectly influence parasitoid-host interactions (Benrey and Denno 1996, Fritz et al. 1997, Gols et al. 2008a). In a landmark community-level study, Lill et al. (2002) showed a significant influence of host-plant taxon on parasitism frequency of 15 focal caterpillar species. When examined individually, each caterpillar species suffered significantly different parasitism rates across its set of host plants. Likewise, individual parasitoid species varied in their parasitism rate of caterpillars on different host-plant genera. Work following this paper has focused on the mechanisms driving this variation, chiefly focused on bottom-up effects, including herbivore density patterns (Umbanhower et al. 2003, White and Andow 2005), host-plant quality (Hunter 2003, Ode 2006, Coley et al. 2006, Gols et al. 2008a, Glassmire et al. 2016), the effects of secondary defense chemicals and other defense traits (Gols et al. 2008b, Smilanich et al. 2009b, Bukovinszky et al. 2009, Garvey et al. 2020), and volatile organic compounds used as cues by searching parasitoids (Bukovinszky et al. 2005, Hare 2011, McCormick et al. 2012).

Plants produce defense and signaling chemicals with a staggering amount of variation among species and individuals of the same species, and differences in host-plant chemistry have been used to explain variation in parasitism across host plant species (Barbosa et al. 1986, Gols et al. 2008a, Gols et al. 2008b, Glassmire 2016) even when plant chemistry is not directly tested (Ode 2006). These secondary defense chemicals can have a large impact on parasitoid fitness, whether directly through contact with the toxin in the host insect’s tissues (Garvey et al. 2020), or indirectly through reduced herbivore growth or impacted immune response (Hunter 2003, Ode 2006, Smilanich et al. 2009b, Stoepler et al. 2011, Kaplan et al. 2016). If these fitness effects are strong enough, then host-plant chemistry can select on parasitoid host choice (Lill et al. 2002, Kaplan et al. 2016).

In response to herbivory, plants release volatile organic compounds (VOCs) that are used as primary cues by searching natural enemies of the herbivore (Turlings and Erb 2018). The recruitment of parasitoids through herbivore-induced VOCs has been tested in both laboratory and agricultural settings. Generally, parasitoids have been shown to prefer volatiles released from host plants with actively feeding herbivores or herbivore damage, and they respond differently to host damage across plant species (Bradburne and Mithen 2000, Bukovinszky et al. 2005, Mumm et al. 2008, Poelman et al. 2009, Bruinsma et al. 2009). Effects of VOC recruitment on parasitism rates at the community level has been little studied, mainly due to the experimental challenges posed by a natural setting with many uncontrolled variables, including the parasitoids themselves (Poelman et al. 2009, Hare 2011, Turlings and Erb 2018). Despite difficulty in study, attraction through hostplant VOCs may be a driver of variation in parasitism of the same Lepidopteran host species across different plant species (Barbosa et al. 2001, Lill et al. 2002, Farkas and Singer 2013). Additionally, variation in VOCs may cause different recruitment of parasitoid natural enemies across host plants (Mäntylä et al. 2004, Hare 2011, Poelman et al. 2012), providing enemy-dense and enemy-free spaces in the community and indirectly influences parasitoid host choice (*Figure 1*).

Effect of Host Population Attributes

Herbivore host density and community structure is directly influenced by both traits of the host plant and herbivore. Generally, parasitism is predicted to increase as host density increases simply due to reduced time and effort in finding a suitable host (Hawkins 1994). Several empirical examples show this relationship (e.g., Umbanhower et al. 2003, White and Andow 2005) and others report congregation of parasitoids at larger patches of hosts (Bezemer et al. 2010). This does not seem to be a uniform pattern, as many studies have published evidence and theory of density-independent parasitism and negatively density-dependent parasitism (e.g., Cronin and Strong 1990, Connor and Beck 1993, Hassell 2000, Farkas and Singer 2013).

Tri-trophic Interactions

In Connecticut forests, caterpillars–and consequently their parasitoids–experience a huge variety of tri-trophic interactions between the host plant and various natural enemies (*Figure 1*). These interactions contribute to variation in caterpillar and parasitoid mortality from natural enemies and may shape parasitoid host choice. Caterpillars face significant levels of mortality from various invertebrate and vertebrate predators (Mooney et al. 2010, Remmel et al. 2011, Greeney et al. 2012). In forested environments, birds and ants are two of the most abundant predators of caterpillars and have different rates of predation across communities of caterpillars found on common tree species (Singer et al. 2017, Roslin et al. 2017). In our temperate study system, arthropod predators such as ants have much weaker predation effects on caterpillars than do avian predators (Singer et al. 2017). These generalist predators may shape parasitoid host choice through predation of caterpillars at two distinct points. Predation prior to parasitoid host choice (pre-oviposition) changes the community of caterpillars available for oviposition, and predation of caterpillars after oviposition (post-oviposition) will kill the parasitoid larva (*Figure 1*). Traits of the caterpillar, traits of its host-plant, or interactions between the caterpillar and plant traits can have significant impacts on a caterpillar's risk of predation.

Notable variation in bird predation across caterpillar species in temperate forest communities has been attributed to traits of the caterpillars. Smaller, dietary specialist caterpillars face significantly less bird predation than large, dietary generalist caterpillars (Singer et al. 2012, Singer et al. 2014, Singer et al. 2017). In contrast, ants only have detectable predation effects on smaller, dietary specialist caterpillars, and only in the presence of bird predation (Singer et al. 2017, Singer et al. 2019). Behavioral and defensive traits also strongly influence caterpillar-predator interactions (Dyer 1995). Caterpillar species with warning coloration, superior camouflage, and behavioral fidelity to particular microenvironments on the host plant gain enemy-free space from birds (Lichter-Marck et al. 2015). Caterpillar species with a higher frequency of anti-predator behavioral responses suffered less predation by ants (Singer et al. 2019), whereas the tendency to express those same behaviors is associated with high risk of bird predation (Lichter-Marck et al. 2015). Through these different caterpillar traits, parasitoids will face different degrees of mortality from predators based on their host species.

The host plant of the herbivore can influence predation through differences in plant quality and herbivore densities across tree species. Singer et al. (2012) found that dietary generalist caterpillars suffer varied predation risk by birds across eight common host tree species. This predation risk was correlated with differences in host-plant quality and caterpillar density across tree species. These results indicate that birds preferentially forage on tree species with relatively high caterpillar density, which is positively associated with the tree species' food quality for the caterpillars. Ant foraging options are much more limited compared to birds, as they cannot travel as far from their nest as birds. They cannot efficiently seek out areas with high caterpillar density as birds can, and in previous studies more abundant caterpillars in the community faced higher ant predation (Singer et al. 2017, Singer et al. 2019). This pattern of ant predation is likely to reflect the opportunistic nature of their predation on caterpillars.

Tachinid flies and hymenopteran parasitoids–the two main groups of parasitoids in our study system–have different behaviors and development times that may significantly impact their vulnerability to predators (Murphy et al. 2014). Parasitoid wasps typically oviposit in very young caterpillars and often exit their host in the early or middle instars (Godfray 1994, Shaw 2006). Tachinid flies usually take much longer to develop and remain in the host until the host's final instar or later (Stireman et al. 2006). Since tachinid parasitoids usually take longer to develop in their host caterpillar than hymenopteran parasitoids, they should be under stronger selection to avoid attacking hosts that face a high risk of bird predation (which targets later instar caterpillars). Their larvae will be exposed to bird predation for longer, and as their hosts get larger the risk of bird predation will also increase (Murphy et al. 2014). Parasitoid wasps usually inhabit smaller hosts and are thus predicted to face a higher risk of ant predation compared to tachinid flies. These parasitoids face significant mortality from these generalist predators, as well as more specialized natural enemies such as hyperparasitoids, parasitoids that utilize primary parasitoid larvae as their host insect (*Figure 1*).

Based on the litany of studies that focus on bottom-up effects that influence parasitoid host use, patterns of parasitism in the temperate Connecticut caterpillar community might be well explained by some of these studied effects of caterpillar and host-plant traits. It is also possible that these differences in parasitism may come from different top-down effects of predators across host-plant species, which has been rarely considered in studies of parasitoid communities. To better understand the ecological processes that drive parasitoid host selection, we must seek to combine knowledge and explanations from both the bottom-up and the top-down effects.

Hypotheses and Predictions

In this study, we will test predictions of the enemy-free space hypothesis as they apply to patterns of host use by parasitoids of caterpillars in temperate Connecticut forests. Interactions between life-history traits of the parasitoids and patterns of predation from birds and ants provide different predictions for parasitism of caterpillars when analyzed at the finer taxonomic scales. First, we predict a negative relationship between the probability of parasitism and the risk of predation from both birds and ants across the community of caterpillars and plants (caterpillar species-plant species combinations). Second, since birds pose stronger, more easily detectable effects of predation on caterpillars, we expect the relationship to be stronger for the risk of bird predation rather than ant predation. Along with this general prediction, we make two more specific predictions due to life-history interactions of the parasitoids and predators. Third, the probability of wasp parasitism should be more negatively associated with ant predation than should tachinid parasitism. Fourth, the probability of tachinid parasitism should be more negatively associated with bird predation compared to wasp parasitism.

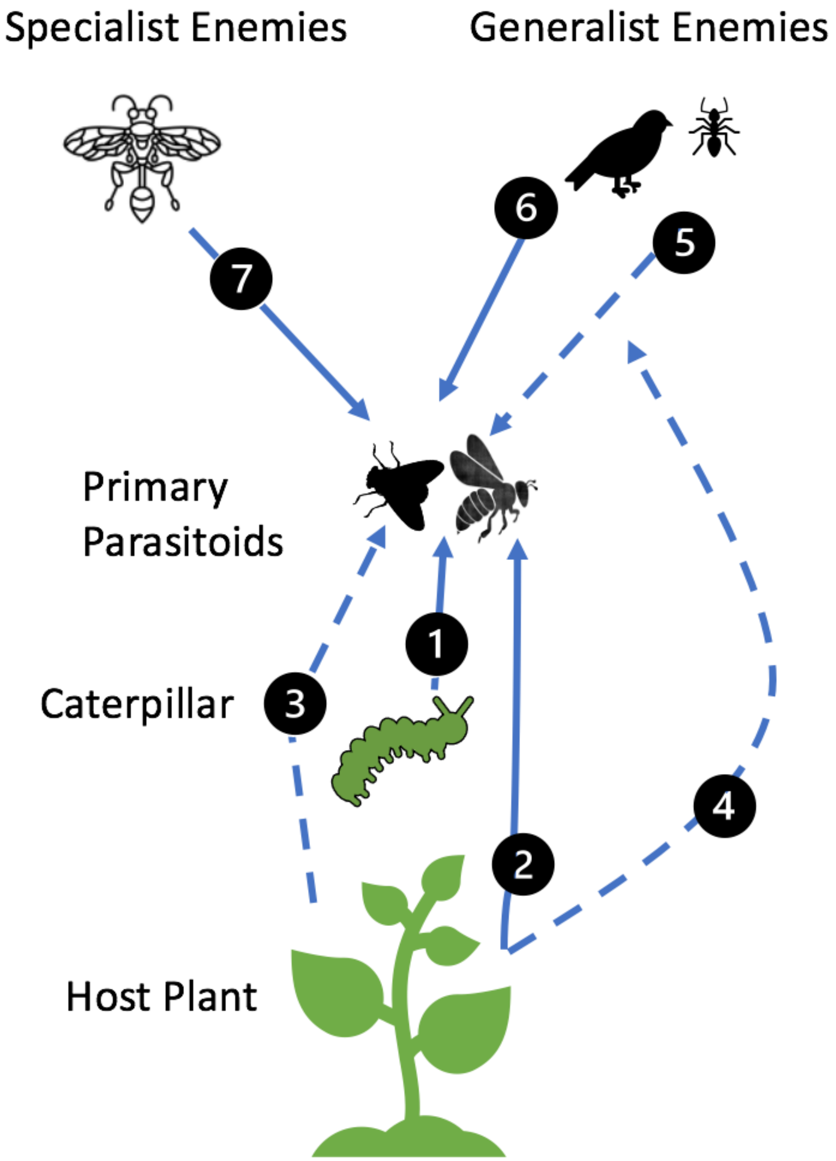


Figure 1: Tri-trophic diagram showcasing examples of the various direct (solid line) and indirect (dashed line) influences on parasitoid host choice. 1) Traits of the caterpillar can impact its suitability to a parasitoid, and directly influence parasitoid host choice. 2) Release of volatile organic compounds or other parasitoid attractants by plants can directly influence the detectability of hosts. 3) Interactions of plant and caterpillar traits give plants an indirect influence on parasitoid host choice (e.g., plant chemistry impacts on caterpillar immune resistance to parasitoids.) 4) Variation in volatiles across host-plants may influence attraction of enemies of parasitoids, giving the plant an indirect impact on parasitoid host choice. 5) Pre-oviposition predation indirectly influences host choice through altering caterpillar availability. 6) Post-oviposition predation and 7) Hyperparasitism directly affects host choice through mortality of immature parasitoids.

METHODS

Overview

Data from several community-level studies were combined to assess how variation in predation risk across a caterpillar community correlated with probability of parasitoid attack. The data for my project come from 10 seasons of field work, including both observational studies of parasitism and experimental studies of bird and ant predation on the caterpillar community of eight tree taxa in Connecticut forests. Parasitism events were documented by sampling caterpillars from the field and noting parasitoid emergence from the sampled caterpillars as they were reared in the laboratory on field-collected leaves of the host-plant species on which they were sampled. These rearing outcomes were used to calculate a probability of parasitism for each caterpillar species and host-plant species combination. Reared caterpillars used to calculate the probability of parasitism were not sampled from predator-exclusion branches to avoid direct effects of the experimental exclusions on parasitism. Predation effects were inferred from comparisons of caterpillar densities found on tree branches subjected to predator-exclusion treatments versus predator-access (control) conditions. These comparisons were used to calculate the effect size of predation by birds and ants for each caterpillar species and host-plant species combination. Using generalized linear models, I examined the relationship between the effect size of predation (predation risk) and the probability of parasitism for caterpillar species and host-plant species combinations to test the prediction that probability of parasitism should be negatively correlated with risk of predation.

Study System

Sites

The sites varied across each season of the study, in total consisting of 23 deciduous or mixed-deciduous forest patches with a large range of forest patch size and connectedness. These upland forests were mixtures of oak-hickory and maple-beech dominated canopies, typical of the Northeastern Coastal Forest ecoregion (Olson et al. 2001). The land use surrounding these forest patches ranged from agricultural and light to medium density suburban development. The majority are within Middlesex County and sit overtop brownstone or basalt bedrock, although some are out of the Connecticut River basin in neighboring counties such as Hartford or New London and have a metamorphic (gneiss or schist) bedrock. Most sites are relatively flat, but some are hilly with steep topographic changes due to the scouring and deposition of materials by glaciers in these sites' history.

Plants

The eight host-plant taxa include *Acer rubrum L.* (red maple, Sapindaceae), *Betula lenta L.* (black birch, Betulaceae), *Carya* spp. (hickories, Juglandaceae), *Hamamelis virginiana L.* (witch hazel, Hamamelidaceae), *Prunus serotina L.* (black cherry, Rosaceae), *Quercus rubra L.* (red oak, Fagaceae) *,* *Quercus alba L.* (white oak, Fagaceae) *,* and *Fagus grandifolia L.* (beech, Fagaceae). Hickories (*Carya* spp.) were not identified to species and include *Carya ovata* (Mill.) K.Koch (shagbark hickory), *Carya tomentosa* (Lam.) Nutt. (mockernut hickory), and *Carya glabra* (Mill.) Sweet (pignut hickory) (Singer et al. 2012). The set of trees that are called *Q. rubra* includes individuals within the hybridizing red oak group (Manos et al. 1999) ranging from typical *Q. rubra* to phenotypes resembling *Quercus velutina* Lindl. (black oak). This collection of species was chosen because they represent a large proportion of trees in the upland temperate forest and have been shown to host varied densities of phytophagous caterpillars (Futuyma and Gould 1979, Singer et al. 2012).

Parasitoids

The insect parasitoid community that attacks caterpillars in forests of Connecticut belong to two higher taxa, flies (Diptera) in the family Tachinidae, and wasps from several families in the Parasitica division, but primarily belonging to Braconidae (mostly Microgastrinae) and, to a lesser degree, Ichneumonidae. Both taxa of parasitoid adults fly and search for host caterpillars starting in late spring and continue into early summer, coinciding with the season of caterpillar sampling and predator exclusion in this study. All tachinids and the majority of wasps are endoparasitoids, with larvae developing and feeding from within the caterpillar, while some wasps feed and develop as ectoparasitoids. Any adult parasitoids that emerged from a collected caterpillar were identified as either hymenopteran or tachinid, and preserved in ethanol (hymenopteran) or pinned (tachinid) for potential further identification. I did not embark in further identification because identification at lower taxonomic levels using morphological traits requires specialized taxonomic knowledge and access to museum specimens. DNA barcoding libraries are being developed for these taxa, but using molecular methods for taxonomic identification of thousands of specimens would be a large and costly undertaking.

Caterpillars

The caterpillar community sampled on these tree taxa consisted of 125 species from 10 families and ranged from dietary specialists that feed on a single host-plant species to dietary generalists that feed on all eight plant taxa (Singer et al. 2012, Singer et al. 2017). The vast majority of caterpillars could be identified on collection or during the rearing process, but a few had to be identified after pupation and emergence as an adult.

Predators

Predation by foliage-gleaning birds is one of the largest sources of mortality for caterpillars in temperate Connecticut forests. The exclusion experiments were conducted during the breeding season for many songbirds, a period of very high bird density as both resident and migratory birds search for mates, nest sites, and prey. Avian surveys were conducted in 2010, 2011, 2017, and 2018, and a full list of the insectivorous species present can be found in Table 1 with foliage-gleaning birds in bold. The most abundant insectivorous birds that forage in the low canopy and understory are ovenbird (*Seiurus aurocapillus* L.), black-capped chickadee (*Poecile atricapilla* L.), red-eyed vireo (*Vireo olivaceus* L.), and tufted titmouse (*Baeolophus bicolor* L.) (Singer et al. 2012, Lichter-Marck et al. 2015, Singer et al. 2017). The most important ant predators of caterpillars in this community are *Formica neogagates* Viereck, *Camponotus chromaiodes* Bolton, and *Camponotus pennsylvanicus* (De Geer) (Singer et al. 2017, Singer et al. 2019)

Table 1: List of all relevant insectivorous bird species, with foliage-gleaning birds that may pose the highest risk to caterpillars in bold.

Common Name	Scientific Name
Acadian Flycatcher	**Empidonax virescens**
American Redstart	**Setophaga ruticilla**
American Robin	**Turdus migratorius**
Baltimore Oriole	**Icterus galbula**
Black-and-white Warbler	**Mniotilta varia**
Black-capped Chickadee	**Poecile atricapillus**
Blue-gray Gnatcatcher	**Polioptila caerulea**
Brown-headed Cowbird	Molothrus ater
Blackburnian Warbler	**Setophaga fusca**
Blue Jay	**Cyanocitta cristata**
Blackpoll Warbler	**Setophaga striata**
Black-throated Blue Warbler	**Setophaga caerulescens**
Black-throated Green Warbler	**Setophaga virens**
Blue-winged Warbler	**Vermivora cyanoptera**
Carolina Wren	Thryothorus ludovicianus
Cedar Waxwing	Bombycilla cedrorum
Chipping Sparrow	**Spizella passerine**
Common Yellowthroat	**Geothlypis trichas**
Downy Woodpecker	Picoides pubescens
Eastern Bluebird	Sialia sialis
Eastern Phoebe	**Sayornis phoebe**
Eastern Towhee	**Pipilo erythrophthalmus**
Eastern Wood-Pewee	**Contopus virens**
Great Crested Flycatcher	**Myiarchus crinitus**

Gray Catbird	**Dumetella carolinensis**
Hairy Woodpecker	Picoides villosus
Hermit Thrush	**Catharus guttatus**
House Wren	**Troglodytes aedon**
Indigo Bunting	**Passerina cyanea**
Louisiana Waterthrush	Parkesia motacilla
Northern Cardinal	**Cardinalis cardinalis**
Northern Flicker	Colaptes auratus
Northern Waterthrush	Parkesia noveboracensis
Ovenbird	**Seiurus aurocapilla**
Philadelphia vireo	**Vireo philadelphicus**
Pine Warbler	**Setophaga pinus**
Prairie Warbler	**Setophaga discolor**
Rose-breasted Grosbeak	**Pheucticus ludovicianus**
Red-bellied Woodpecker	Melanerpes carolinus
Red-eyed Vireo	**Vireo olivaceus**
Scarlet Tanager	**Piranga olivacea**
Song Sparrow	Melospiza melodia
Tufted Titmouse	**Baeolophus bicolor**
Veery	**Catharus fuscescens**
Warbling Vireo	Vireo gilvus
White-breasted Nuthatch	**Sitta carolinensis**
Worm-eating Warbler	**Helmitheros vermivorum**
Winter Wren	Troglodytes hiemalis
Wood Thrush	**Hylocichla mustelina**
Yellow-billed Cuckoo	**Coccyzus americanus**
Yellow-bellied Sapsucker	Sphyrapicus varius
Yellow Warbler	**Setophaga petechia**

Yellow-throated Vireo Vireo flavifrons

Experimental Design

From 2007 – 2019, predator exclusion experiments were conducted for 10 non-consecutive field seasons over 23 field sites across central Connecticut to test effects of predators on the caterpillar community. The sites, host-plants, and exclusion treatments of these experiments varied over the field seasons, but the design remained relatively consistent. The experiments were designed as factorial exclusions of birds and ants, either together (i.e., ant exclusion, bird exclusion, dual exclusion, and control), or separately (i.e., bird or ant exclusion and control), with experimental units that ranged from small saplings to low branches of mature trees, typically 1-3 m above ground.

Bird-exclusion branches were bagged with 13- or 20-mm nylon mesh secured around the branch (Mooney 2006, Lichter-Marck et al. 2015, Singer et al. 2012, 2014, 2017) and ant-exclusion branches were treated with sticky resin (Tanglefoot, Contech Enterprises) that resulted in a reduction of ant density of about 60% (Singer et al. 2017). The Tanglefoot was applied to a 10 to 20-cm wide plastic collar that was tightly wrapped around the base of the exclusion branch, and a collar without tanglefoot was wrapped around the control branches (Clark et al. 2019). The mesh size of the nylon bagging was large enough to allow invertebrate access but small enough to prevent bird access as well as potentially preventing access to omnivorous rodents, such as white-footed mice (Singer et al. 2012). Experimental branches in the same replicate (representing all treatments and controls) were selected to be closely situated, either on the same individual tree or using nearby trees that had similar light exposure and size, and branches with a similar size and number of leaves. Experimental blocks within sites covered roughly one hectare, and different blocks were separated by at least 100m to increase the likelihood that each block was in the home range of different foraging bird individuals (Singer et al. 2012).

The experimental branches were set up in early-mid May of each year and sampled either once or twice, with three weeks between the set-up and each sampling period (Singer et al. 2012, Singer et al. 2017). Branches were beaten during set up to dislodge any ants before treatments were applied, and any caterpillars were returned to the branch. Sampling consisted of beating the experimental branches with sheets held below to capture insects for identification and counts (Wagner 2010). During sampling, caterpillars were identified and collected for rearing if they were 1 cm in length or larger, and the number of leaves on each experimental branch was recorded at the last sampling event for caterpillar density calculations. Collected caterpillars were reared until pupation or the emergence of a parasitoid, and fed wild collected leaves from the host-plant species they were found on. Only caterpillars from non-bagged branches were used to calculate parasitism probabilities, in order to avoid effects of the nylon bagging on parasitoid searching or oviposition. Caterpillars were also collected opportunistically through beating or visually searching on non-experimental branches for more parasitism records. Prior to the exclusion experiments, an observational study was carried out from 2004-2007 where branches from each of the eight tree species were haphazardly chosen in sets of blocks, and the caterpillar community was quantitatively sampled (Farkas and Singer 2013). The caterpillars from these rigorous sampling events, along with caterpillars opportunistically found on non-sampled branches, were reared as described above to create the bulk of the parasitism dataset for the caterpillar community on our eight focal tree species.

The general methods as described above remained consistent across years, but the specific sites, host plants, number of replicates, number of blocks, and levels of predator exclusion varied across field seasons (Table 2). The largest divergences from the design were in 2010, 2011, 2016. In 2010 and 2011 half of the blocks contained factorial bird and ant exclusion, but half were not factorial exclusions. In 2010 half were bird-exclusion only and in 2011 half were ant-exclusions only. In order to increase the sample size of ant-treated branches in the presence of bird exclusion, all branches in 2016 were bagged. Standard ant exclusion and control treatments were applied but no branches were accessible to birds. Starting in 2017 field work was expanded geographically to additional sites across central and eastern Connecticut and restricted to *A. rubrum* and *H. virginiana* as focal tree species. In 2017 and 2018, 2 blocks, each containing a single replicate of both tree species were set-up at each site, and 2019 had 3 replicates. These replicates had 4 branches each with all combinations of predator exclusion treatments applied.

Data Analysis

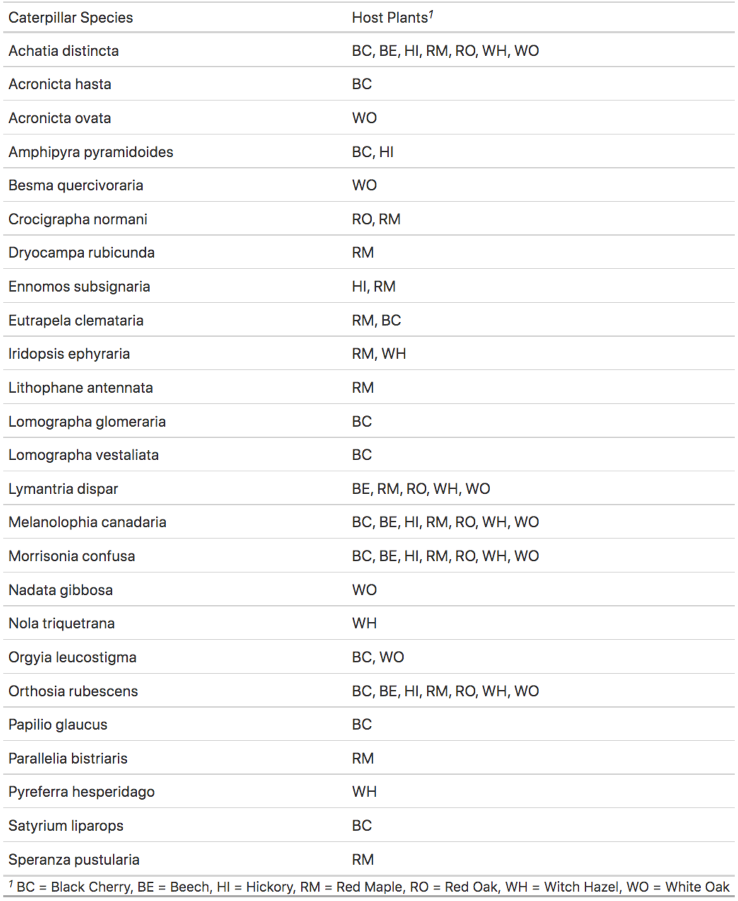
All analyses were performed in R, version 4.1.3 (R Core Team, 2022). The caterpillar and host-plant combinations included in our analyses were determined by sample size cut-offs from both the predator exclusion experiments and parasitism rearing records (See *Table 3* for full list of caterpillar species and host-plant combinations). These cut-offs were determined through re-iterated tests of overdispersion and qualitatively examining the predicted value trends and confidence intervals of our models. We were attempting to balance including as many caterpillar and hostplant species combinations as possible, while ensuring those combinations present in the analysis had suitable sample sizes. Any caterpillar species must have been present in an abundance of at least 10 individuals across bird or ant treated branches of a given host-plant species to calculate an effect size for the respective predator. At least 15 individuals of each caterpillar species must have been reared for parasitism from each host-plant species to be included in calculations of the probability of parasitism. These minimum sample size requirements excluded all samples from *B. lenta* plants, as caterpillars were so scarce on this host-plant species that no combinations reached the parasitism rearing threshold. These cut-offs restricted our dataset to a subset consisting of 59 caterpillar species and host-plant combinations, of which: 52 were included in the analysis of just bird predation risk, 46 in the analysis of ant predation risk, and 39 caterpillar and host-plant combinations had large enough sample sizes on ant treated and bird treated branches to be included in the analysis of both predation risks.

Table 2: Differences in experimental setup across field seasons.

Year	Number of tree species	Number of sites	Number of blocks per site	Number of replicates per block	Bird Treatment	Ant Treatment
2007	3	1	7	1	Yes	No
2008	8	3	6	3	Yes	No
2009	8	3	6	3	Yes	No
2010	8	3	6	2	Yes	Yes
2011	8	3	6	2	Yes	Yes
2012	8	3	6	2	No	Yes
2016	3	2	6	1	Yes, exclusion only	Yes
2017	2	11	2	1	Yes	Yes
2018	2	10	2	1	Yes	Yes
2019	2	15	3	1	Yes	Yes

Caterpillar density was calculated for each caterpillar and host-plant species combination at the site and year level for all predator treatments. For example, the density of *Melanolophia canadaria* on bird accessible and bird exclusion branches of *Prunus serotina* was calculated separately for each site and year combination with sufficient data. Caterpillar density was calculated for each predator-exclusion treatment (bagged, unbagged, tangled, untangled) by grouping at the site and year levels and summing caterpillar abundance across branches within the given treatment for each caterpillar species and host-plant species combination, and dividing these counts by total leaf area. Total leaf area was estimated by adding the number of leaves on all branches with the same treatment of a given host-plant species in each site and year combination, and multiplying by the average leaf area per tree species (Singer et al. 2012). These average leaf area measures were made with a leaf area meter for 10-20 undamaged leaves from varying sized experimental branches and saplings of each tree species from 2004-2008 at each site (Marquis and Whelan 1994, Singer et al. 2012). The number of leaves per branch was not recorded for some experimental branches from 2008 – 2011, and these branches had their total leaf area imputed from a simple model based on host-plant and bird treatment.

Table 3: List of caterpillar species and host-plant combinations included in analyses.



Caterpillar Species	Host Plants[1]
Achatia distincta	BC, BE, HI, RM, RO, WH, WO
Acronicta hasta	BC
Acronicta ovata	WO
Amphipyra pyramidoides	BC, HI
Besma quercivoraria	WO
Crocigrapha normani	RO, RM
Dryocampa rubicunda	RM
Ennomos subsignaria	HI, RM
Eutrapela clemataria	RM, BC
Iridopsis ephyraria	RM, WH
Lithophane antennata	RM
Lomographa glomeraria	BC
Lomographa vestaliata	BC
Lymantria dispar	BE, RM, RO, WH, WO
Melanolophia canadaria	BC, BE, HI, RM, RO, WH, WO
Morrisonia confusa	BC, BE, HI, RM, RO, WH, WO
Nadata gibbosa	WO
Nola triquetrana	WH
Orgyia leucostigma	BC, WO
Orthosia rubescens	BC, BE, HI, RM, RO, WH, WO
Papilio glaucus	BC
Parallelia bistriaris	RM
Pyreferra hesperidago	WH
Satyrium liparops	BC
Speranza pustularia	RM

[1] BC = Black Cherry, BE = Beech, HI = Hickory, RM = Red Maple, RO = Red Oak, WH = Witch Hazel, WO = White Oak

Note that these host-plant species do not represent the full host range of these Lepidopteran species, only the host-plant species with enough predation and parasitism samples to be included in the analyses.

Calculating probability of parasitism involved combining the various sampling and rearing records, and excluded caterpillars sampled from bird-exclusion (bagged) branches due to concerns that the bird exclusion bags artifactually reduced parasitism of caterpillars. For each caterpillar species and host-plant species combination, the rearing records from the 2004 – 2007 observational study, unbagged experimental branches from the 2008 – 2019 predator exclusion experiments, and caterpillars opportunistically collected from non-experimental branches were combined. The total number of parasitized caterpillars, the number parasitized by each of the two major parasitoid taxa, and the number of unparasitized caterpillars were summed for each caterpillar and host-plant species combination to create the robust parasitism dataset used in the present study.

Predator Effect Sizes

Effect sizes are useful for quantifying the magnitude of an experimental treatment effect. In ecological studies, especially meta-analyses, one of the most commonly used methods to calculate effect sizes is the log response ratio (LRR) (Hedges et al. 1999). This method is especially useful to compare and combine datasets using similar treatments or projects spanning multiple years with changes in design (Lajeunesse et al. 2015). It quantifies the results of an experiment by the log-proportional change between the means of a treatment and control group. In this study it is calculated as the natural log of mean density on exclusion branches (X_T) divided by mean density on control branches (X_C) across all years and site for each caterpillar and hostplant combination.

$$LRR = \ln\left(X_T / X_C\right)$$

Sampling error plays a large role in introducing variability to experimental outcomes, so the variance of response ratios is a central feature. The variance utilizes sample sizes (N), here it is the number of branches sampled of that hostplant and treatment) and standard deviation (SD) to help quantify the sampling variability in the response ratio (Lajeunesse et al. 2015).

$$var(LRR) = \frac{(SD_T)^2}{N_T X_T^2} + \frac{(SD_C)^2}{N_C X_C^2}$$

Recent studies that utilize log response ratios implement the inverse of variance as weights to account for the sampling variability in effect sizes (Lajeunesse et al. 2015, Albert et al. 2021, Hong et al. 2021). The inverse of the variance is used as a weight in most of our models so that caterpillar and host-plant species combinations with high variance (either due to low sample sizes or large standard deviations) receive lower weights in the model. We also employed a bias-correction of LRRs and variance described in Lajeunesse et al. 2015 to try and further account for low sample sizes.

$$LRR^{\Delta} = LRR + 1/2\left[\frac{(SD_T)^2}{N_T X_T^2} + \frac{(SD_C)^2}{N_C X_C^2}\right]$$

$$var(LRR^{\Delta}) = var(LRR) + 1/2\left[\frac{(SD_T)^4}{N_T^2 X_T^4} + \frac{(SD_C)^4}{N_C^2 X_C^4}\right]$$

These bias-corrected LRRs were calculated for both bird and ant predation and are used as continuous predictor variables in the generalized linear models.

Statistical Analysis

The analysis utilized nine related generalized linear models to test the predictions of the enemy-free space for parasitoids hypothesis. These models included the probability of parasitism as a response variable (the ratio of parasitized caterpillars versus unparasitized caterpillars) and the effect size of predation as a predictor variable, along with the independent variables of caterpillar species and host-plant species as fixed effects. The nine models represented distinct variations on this basic structure (*Table 4*).

Table 4: Outlines the 9 different models and their respective response and predictor variables.

Response Variables			Predictor Variables	
All Parasitism	Tachinid Parasitism	Hymenopteran Parasitism	Risk of Predation	Fixed Effects
Model 1	**Model 2**	**Model 3**	Bird	Caterpillar Species and Host-plant
Model 4	**Model 5**	**Model 6**	Ant	Caterpillar Species and Host-plant
Model 7	**Model 8**	**Model 9**	Bird, Ant	Caterpillar Species and Host-plant

All of the models followed the same general equation using a logit link function and assuming a quasibinomial error distribution, with models 7 – 9 including two LRR terms:

$$Probability\ of\ Parasitism \sim LRR + Host\ Plant + Caterpillar\ Species$$

Models containing risk of both bird and ant predation were included because we are interested in the effects of ant and bird predation in combination, and how accounting for both predator taxa may increase the predictive powers of our models.

Additionally, our analysis attempted to balance including as many caterpillar and host-plant species combinations, with limiting those observations to combinations that only had suitable sample sizes. The inclusion of all nine models includes as much of the community as we can in the first six, and the last three are restricted to the caterpillar and host-plant species combinations with the most predation data where we can see the effect of predation from both taxa. Models 1 – 6 were weighted by the inverse of variance for the given risk of predation included as a predictor variable. The models with both bird and ant risk as predictor variables (Models 7 – 9) were weighted by the inverse of the sum of variance for both bird and ant risk. The fixed effects of host-plant and caterpillar species were included to account for known sources of variation in the probability of parasitism and reduce noise in the model fitting process. All models were tested for autocorrelation using the stats package (R Core Development Team) and none showed signs of autocorrelation.

An analysis of deviance was performed on all models to show the reduction in residual deviance provided by each predictor term in the model. It is a method to compare the contribution of each predictor variable to the model fit by comparing the deviance explained by each predictor term showing the reduction in residual deviance provided by each predictor term (Nelder and Wedderburn 1972, but see https://www.rdocumentation.org/packages/stats/versions/3.6.2/topics/anova.glm). These values are reported instead of model coefficients for the fixed effects of caterpillar species and host-plant species. These fixed effects are known to have an effect on probability of parasitism, and by comparing the reduction in deviance from all terms in the model we can statistically test each terms contribution to model fit.

RESULTS

Overall Parasitism Rate

In our full dataset consisting of 6,448 reared caterpillars, 18.9% of caterpillars collected were parasitized. This 18.9% breaks down between the two main taxa with tachinid flies being responsible for 9.26% and wasps for 8.48% of this mortality. Some parasitoids either did not emerge or were unable to be identified, and these unknown individuals make up the remaining 1.16% of parasitized caterpillars. In the subset of data restricted to caterpillar and host-plant species combinations that meet our sample size cut-offs, 4,629 reared caterpillars resulted in 15.5% of these caterpillars being parasitized (5.62% from tachinid flies, 8.19% from wasps, 1.69% from unidentified parasitoids).

Effect of Bird Predation on Probability of Parasitism

The models using bird predation alone as the predation predictor variable show the predicted trend of a negative association between bird predation risk and probability of parasitism (*Figure 2, Table 5*). Although this trend is significant for hymenopteran parasitism (β = -0.41, 95% CI = -0.77 – 0.03, p = 0.042), it is not significant for total parasitism (β = -0.23, 95% CI = -0.56 – 0.11, p = 0.178) and marginally non-significant for tachinid parasitism (β = -0.72, 95% CI = -1.57 – 0.12, p = 0.088). For all three models, bird predation risk reduced residual deviance by a significant amount, but the fixed effects of host-plant species and caterpillar species reduced deviance by roughly 10 to 20 times as much (*Table 8*).

Effect of Ant Predation on Probability of Parasitism

Contrary to predictions of the enemy-free space hypothesis, Models 4 – 6, which use risk of ant predation as the only predation predictor variable (*Figure 3, Table 6*), show a non-significant positive relationship for risk of ant predation and total parasitism ($\beta = 0.24$, 95% CI = -0.55 – 1.08, $p = 0.557$) as well as tachinid parasitism ($\beta = 1.28$, 95% CI = -0.34 – 2.97, $p = 0.127$). The relationship between risk of ant predation and hymenopteran parasitism is also non-significant, but it is a negative relationship ($\beta = -0.16$, 95% CI = -0.96 – 0.66, $p = 0.691$). In all three models, the risk of ant predation reduced deviance by a marginal amount with only a significant effect when total parasitism is the response variable. Only caterpillar species and host-plant significantly reduced residual deviance across these three models (*Table 9*).

Effect of Both Predator Groups on Probability of Parasitism

In the models using both the risk of bird predation and risk of ant predation as independent predictors (Models 7-9, *Figures 4 & 5, Table 7*), total parasitism has a non-significant negative relationship with the risk of bird predation ($\beta = -0.42$, 95% CI = -0.95 – 0.12, $p = 0.124$) and a non-significant positive relationship with the risk of ant predation ($\beta = 0.42$, 95% CI = -0.33 – 1.18, $p = 0.274$). Notably, the probability of tachinid parasitism is significantly negatively associated with the risk of bird predation ($\beta = -1.45$, 95% CI = -2.04 – -0.87, $p < 0.001$) and significantly positively associated with the risk of ant predation (β = 1.31, 95% CI = 0.52 – 2.13, p = 0.001). Hymenopteran parasitism showed a similar qualitative pattern, but neither bird predation risk (β = -0.28, 95% CI = -0.80 – 0.24, p = 0.287) nor ant predation risk (β = 0.01, 95% CI = -0.73 – 0.76, p = 0.977) were significant effects. For all three models, both bird and ant predation risk reduced residual deviance by a significant amount, but the fixed effects of host-plant and caterpillar species further reduced deviance by multiple orders of magnitude (*Table 10*).

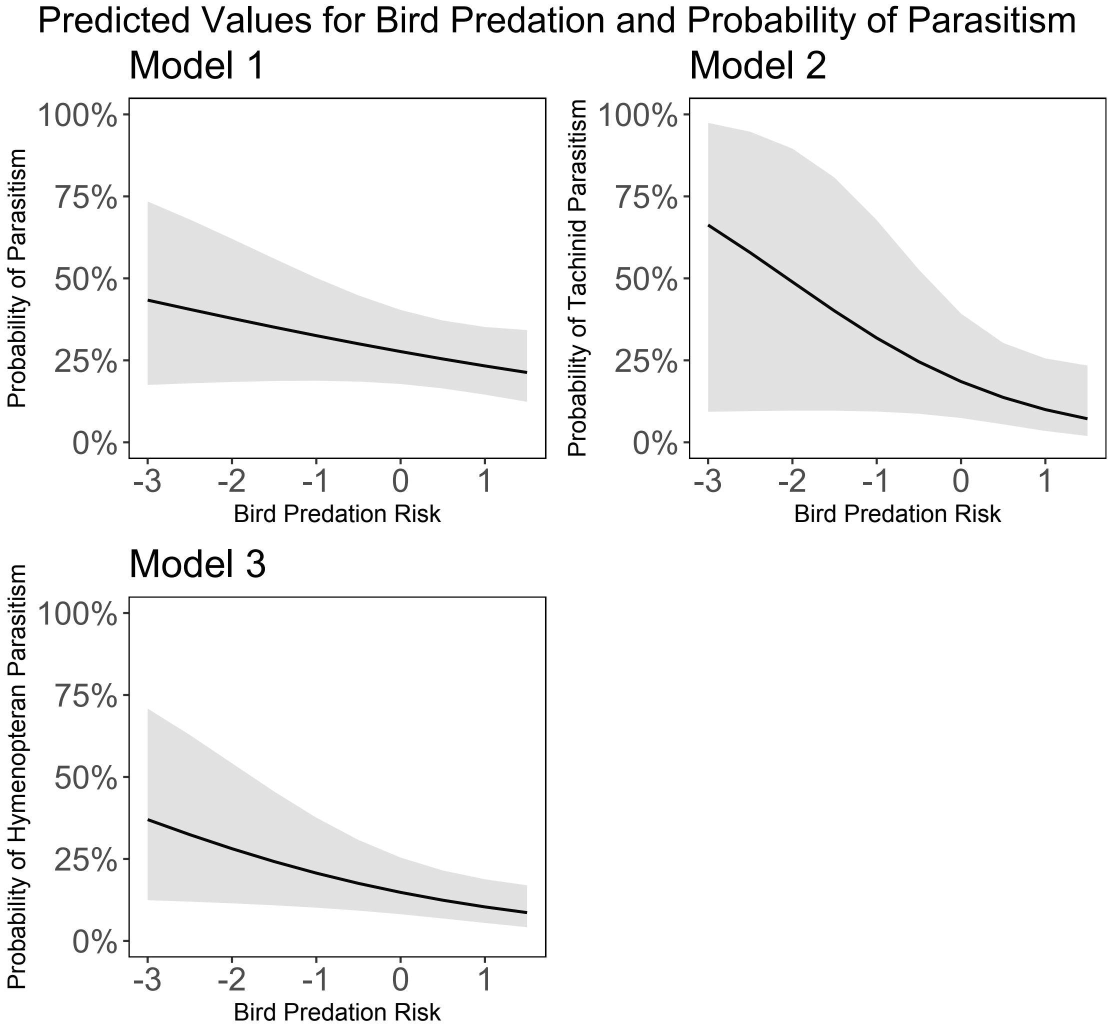


Figure 2: Predicted values of probability of parasitism based on bird predation risk as a predictor in Models 1 – 3. The black curves show how the predicted probability of parasitism changes based on the risk of bird predation (LRR_{Birds}) of a caterpillar and hostplant species combination. The gray areas denote the 95% confidence interval around these predicted values.

Table 5: Regression results for Models 1 – 3 that follow the general equation of: Probability of parasitism ~ LRR_{birds} + fixed effects. CI is the 95% confidence interval.

	All Parasitism: Model 1			**Tachinid Parasitism: Model 2**			**Hymenopteran Parasitism: Model 3**		
Predictors	*Log-Odds*	*CI*	*p*	*Log-Odds*	*CI*	*p*	*Log-Odds*	*CI*	*p*
Bird Predation Risk	-0.23	-0.56 – 0.11	0.178	-0.72	-1.57 – 0.12	0.088	-0.41	-0.77 – -0.03	**0.032**
Observations	52			52			52		

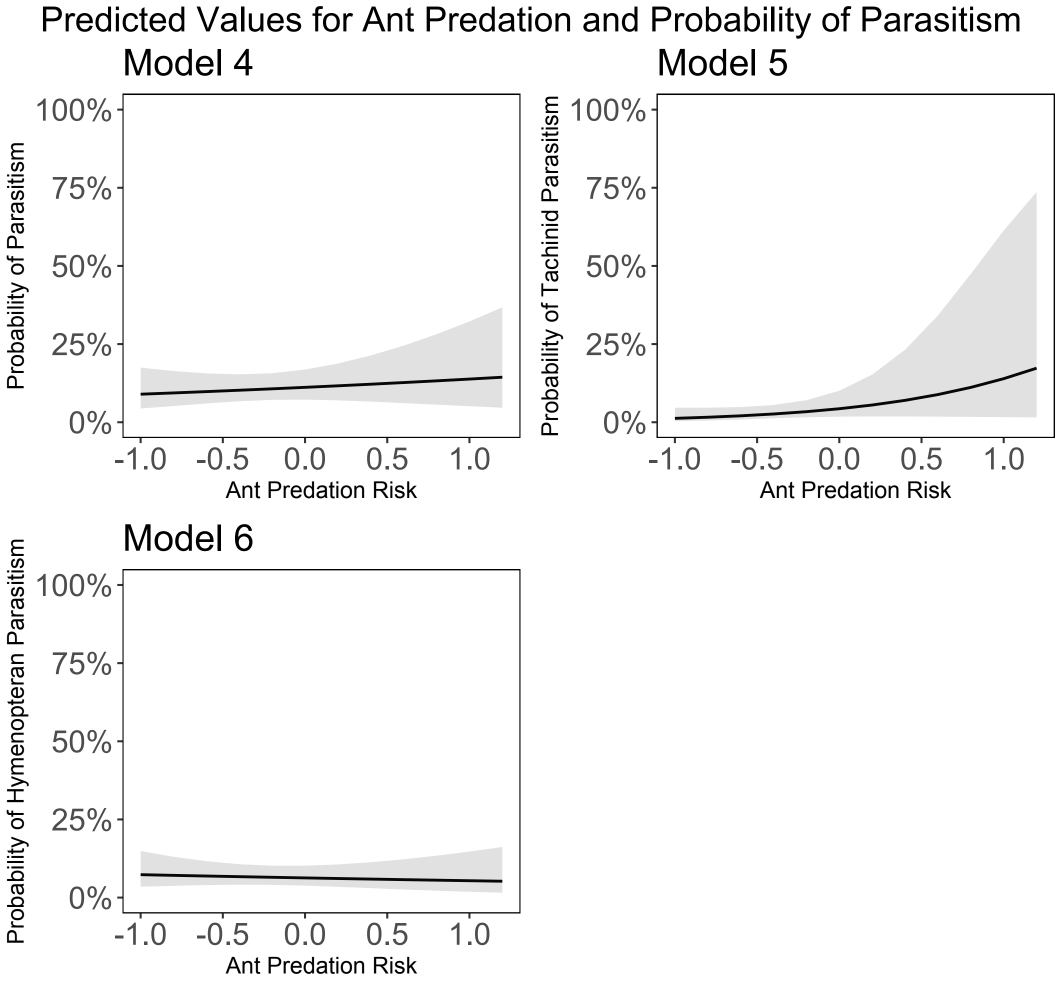


Figure 3: Predicted values for probability of parasitism based on ant predation risk as a predictor in Models 4 – 6. The black curves show how the predicted probability of parasitism changes based on the risk of ant predation (LRR_{Ants}) of a caterpillar and hostplant species combination. The gray areas denote the 95% confidence interval around these predicted values.

Table 6: Regression results for Models 4 – 6 that follow the general equation of: Probability of parasitism ~ LRR_{ants} + fixed effects. CI is the 95% confidence interval.

	All Parasitism: Model 4			**Tachinid Parasitism: Model 5**			**Hymenopteran Parasitism: Model 6**		
Predictors	*Log-Odds*	*CI*	*p*	*Log-Odds*	*CI*	*p*	*Log-Odds*	*CI*	*p*
Ant Predation Risk	0.24	-0.55 – 1.08	0.557	1.28	-0.34 – 2.97	0.127	-0.16	-0.96 – 0.66	0.691
Observations	46			46			46		

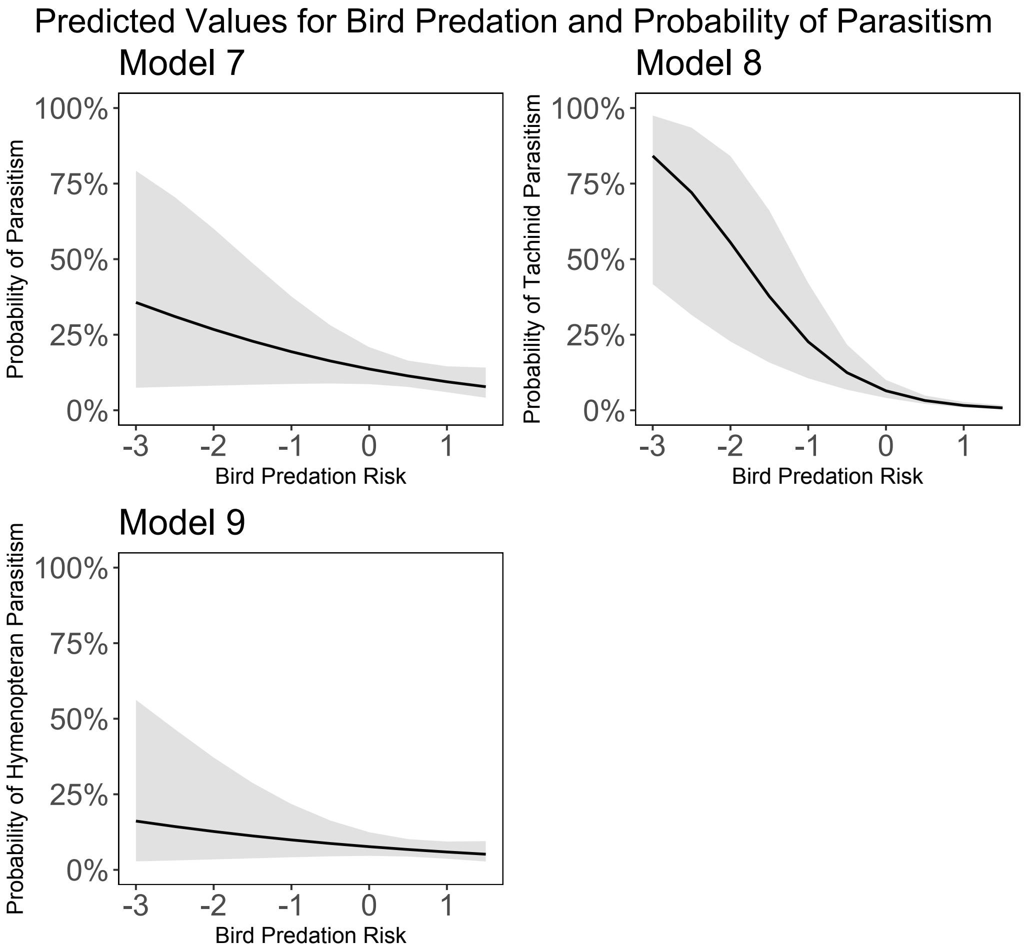


Figure 4: Predicted values for probability of parasitism based on bird predation risk as a predictor in Models 7 – 9. The black curves show how the predicted probability of parasitism changes based on the risk of bird predation (LRR_{Birds}) of a caterpillar and hostplant species combination. The gray areas denote the 95% confidence interval around these predicted values.

Table 7: Regression results for Models 7 – 9 that follow the general equation of: Probability of parasitism ~ LRR_{birds} + LRR_{ants} + fixed effects. CI is the 95% confidence interval.

	All Parasitism: Model 7			**Tachinid Parasitism: Model 8**			**Hymenopteran Parasitism: Model 9**		
Predictors	*Log-Odds*	*CI*	*p*	*Log-Odds*	*CI*	*p*	*Log-Odds*	*CI*	*p*
Bird Predation Risk	-0.42	-0.95 – 0.12	0.124	-1.45	-2.04 – -0.87	**<0.001**	-0.28	-0.80 – 0.24	0.287
Ant Predation Risk	0.42	-0.33 – 1.18	0.274	1.31	0.52 – 2.13	**0.001**	0.01	-0.73 – 0.76	0.977
Observations	39			39			39		

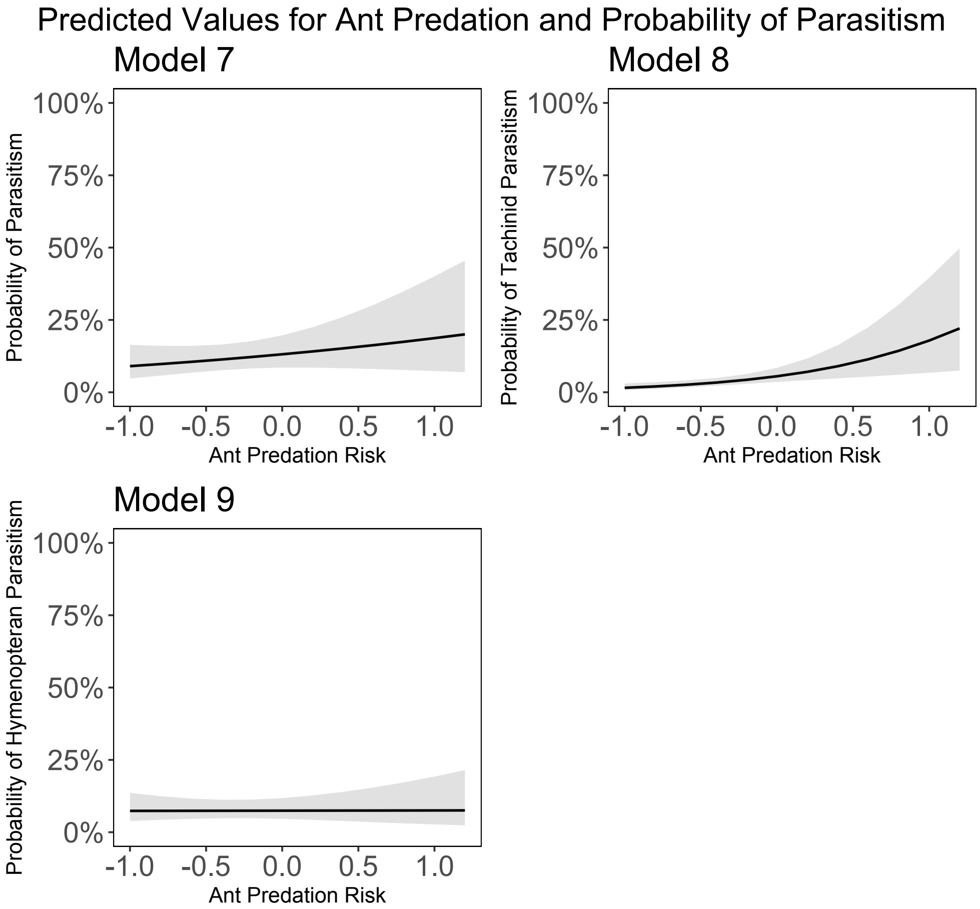
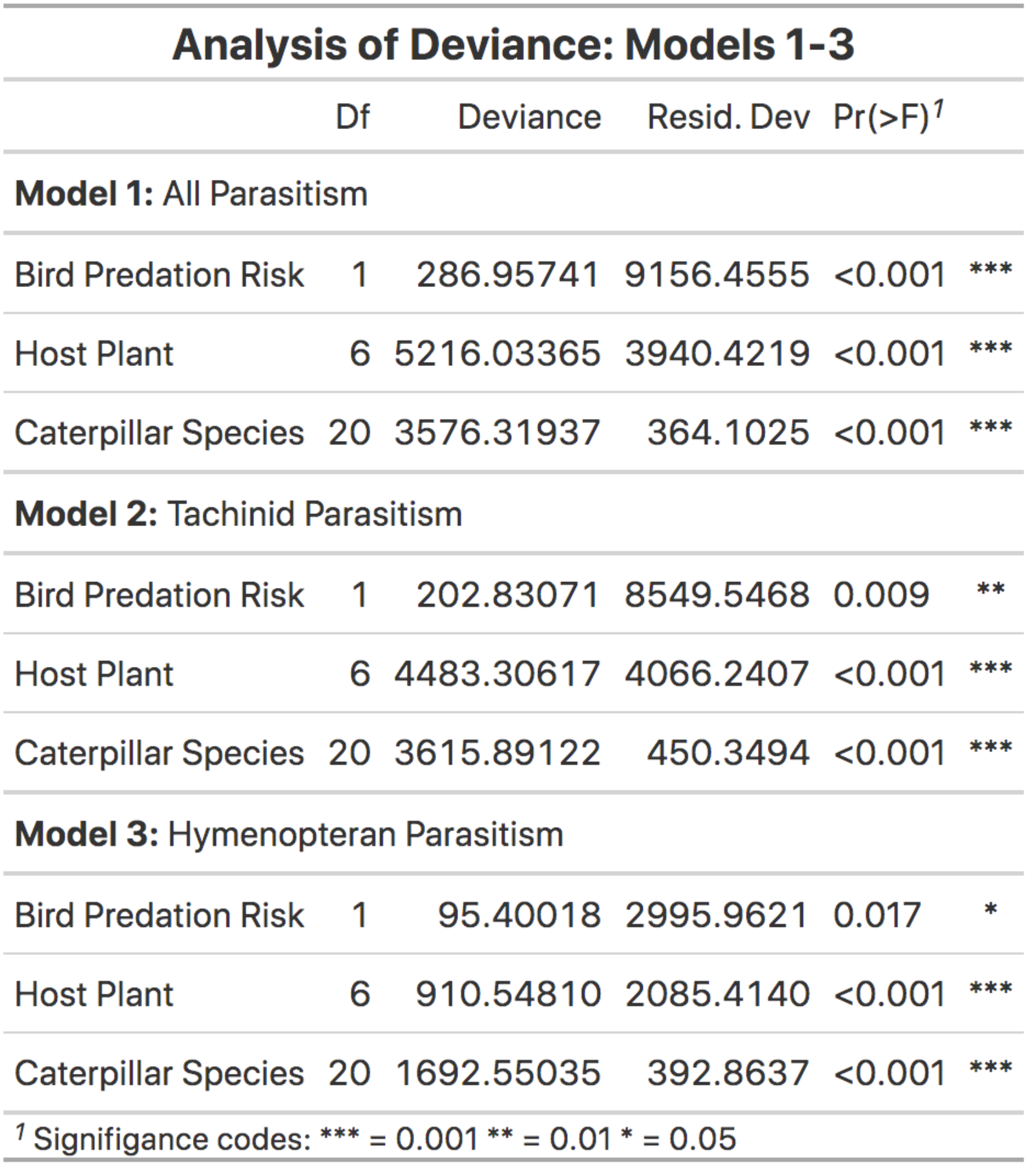


Figure 5: Predicted values for probability of parasitism based on ant predation risk as a predictor in Models 7 – 9. The black curves show how the predicted probability of parasitism changes based on the risk of ant predation (LRR_{Ants}) of a caterpillar and hostplant species combination. The gray areas denote the 95% confidence interval around these predicted values.

Table 8: Analysis of deviance for Models 1 – 3.



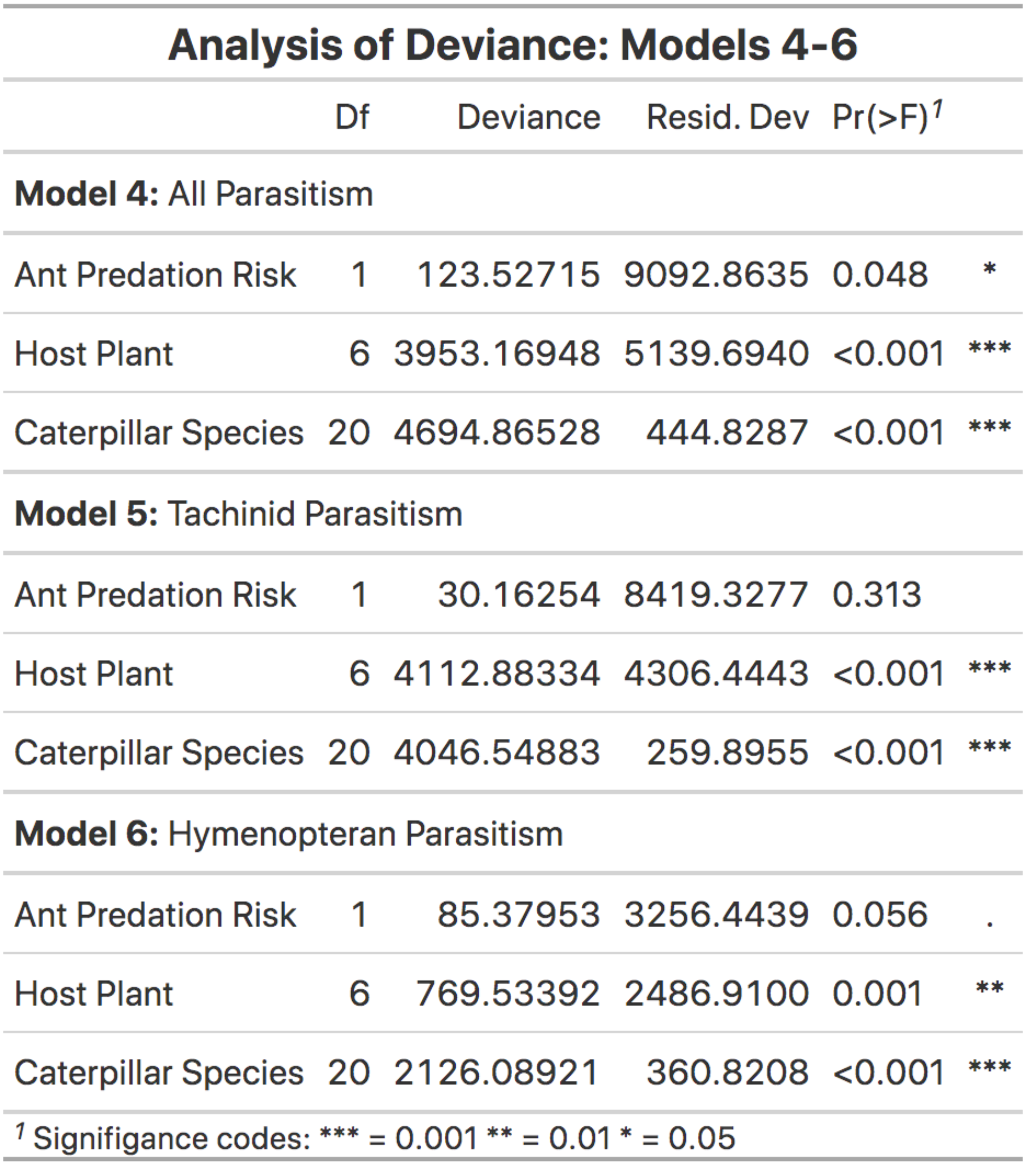
Analysis of Deviance: Models 1-3

	Df	Deviance	Resid. Dev	Pr(>F)[1]	
Model 1: All Parasitism					
Bird Predation Risk	1	286.95741	9156.4555	<0.001	***
Host Plant	6	5216.03365	3940.4219	<0.001	***
Caterpillar Species	20	3576.31937	364.1025	<0.001	***
Model 2: Tachinid Parasitism					
Bird Predation Risk	1	202.83071	8549.5468	0.009	**
Host Plant	6	4483.30617	4066.2407	<0.001	***
Caterpillar Species	20	3615.89122	450.3494	<0.001	***
Model 3: Hymenopteran Parasitism					
Bird Predation Risk	1	95.40018	2995.9621	0.017	*
Host Plant	6	910.54810	2085.4140	<0.001	***
Caterpillar Species	20	1692.55035	392.8637	<0.001	***

[1] Signifigance codes: *** = 0.001 ** = 0.01 * = 0.05

Df is the degrees of freedom of each predictor variable, Deviance is the total amount of deviance reduced when that term is added to the model, Resid. Dev is the residual deviance remaining after adding the terms sequentially, Pr(>F) is the p-value from the F-test performed on the reduction in deviance from each term.

Table 9: Analysis of deviance for Models 4 – 6.



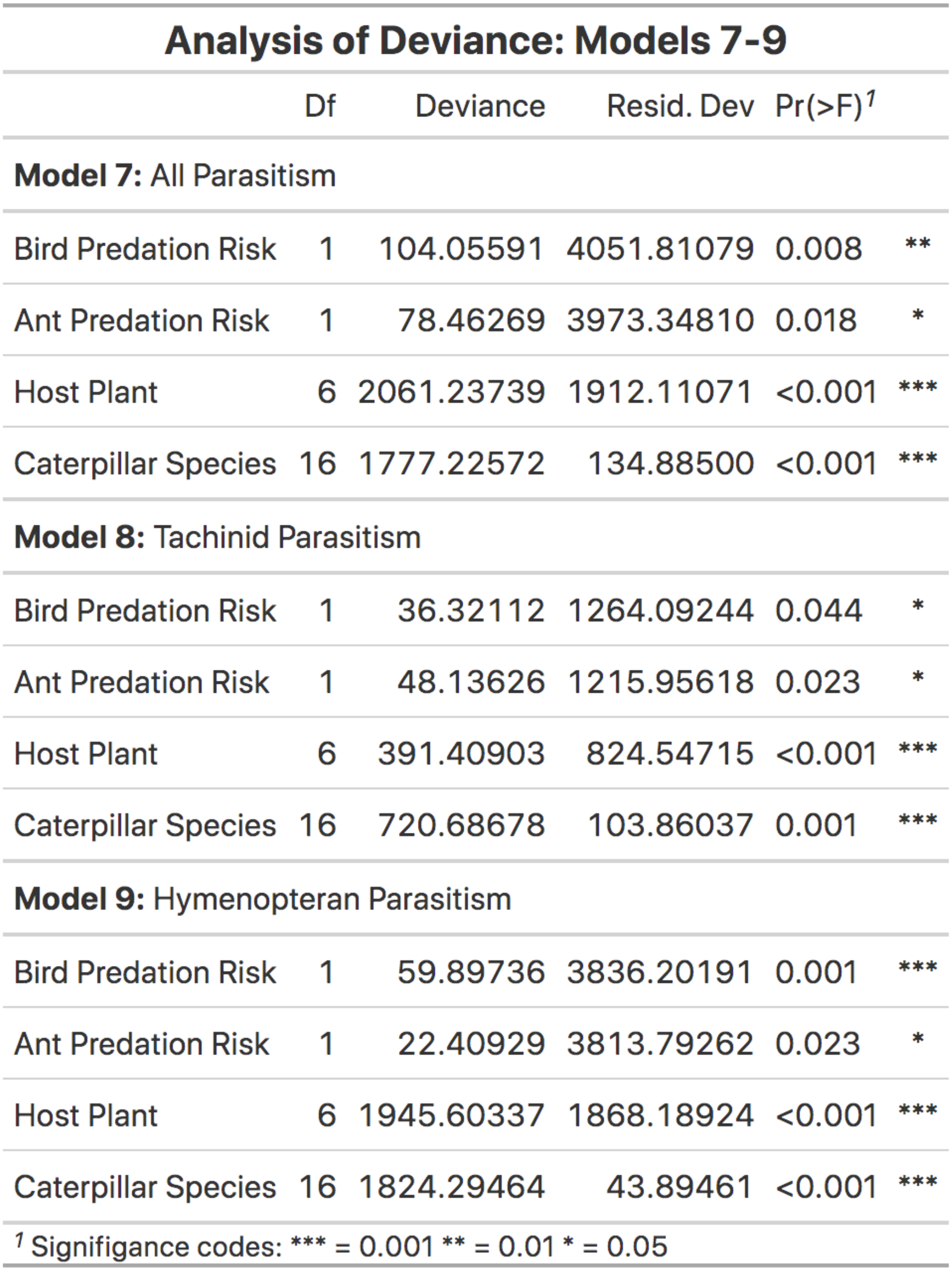
Analysis of Deviance: Models 4-6

	Df	Deviance	Resid. Dev	Pr(>F)[1]	
Model 4: All Parasitism					
Ant Predation Risk	1	123.52715	9092.8635	0.048	*
Host Plant	6	3953.16948	5139.6940	<0.001	***
Caterpillar Species	20	4694.86528	444.8287	<0.001	***
Model 5: Tachinid Parasitism					
Ant Predation Risk	1	30.16254	8419.3277	0.313	
Host Plant	6	4112.88334	4306.4443	<0.001	***
Caterpillar Species	20	4046.54883	259.8955	<0.001	***
Model 6: Hymenopteran Parasitism					
Ant Predation Risk	1	85.37953	3256.4439	0.056	.
Host Plant	6	769.53392	2486.9100	0.001	**
Caterpillar Species	20	2126.08921	360.8208	<0.001	***

[1] Signifigance codes: *** = 0.001 ** = 0.01 * = 0.05

Df is the degrees of freedom of each predictor variable, Deviance is the total amount of deviance reduced when that term is added to the model, Resid. Dev is the residual deviance remaining after adding the terms sequentially, Pr(>F) is the p-value from the F-test performed on the reduction in deviance from each term.

Table 10: Analysis of deviance for Models 7 – 9.



Analysis of Deviance: Models 7-9

	Df	Deviance	Resid. Dev	Pr(>F)[1]	
Model 7: All Parasitism					
Bird Predation Risk	1	104.05591	4051.81079	0.008	**
Ant Predation Risk	1	78.46269	3973.34810	0.018	*
Host Plant	6	2061.23739	1912.11071	<0.001	***
Caterpillar Species	16	1777.22572	134.88500	<0.001	***
Model 8: Tachinid Parasitism					
Bird Predation Risk	1	36.32112	1264.09244	0.044	*
Ant Predation Risk	1	48.13626	1215.95618	0.023	*
Host Plant	6	391.40903	824.54715	<0.001	***
Caterpillar Species	16	720.68678	103.86037	0.001	***
Model 9: Hymenopteran Parasitism					
Bird Predation Risk	1	59.89736	3836.20191	0.001	***
Ant Predation Risk	1	22.40929	3813.79262	0.023	*
Host Plant	6	1945.60337	1868.18924	<0.001	***
Caterpillar Species	16	1824.29464	43.89461	<0.001	***

[1] Signifigance codes: *** = 0.001 ** = 0.01 * = 0.05

Df is the degrees of freedom of each predictor variable, Deviance is the total amount of deviance reduced when that term is added to the model, Resid. Dev is the residual deviance remaining after adding the terms sequentially, Pr(>F) is the p-value from the F-test performed on the reduction in deviance from each term.

DISCUSSION

The results show support for the enemy-free space for parasitoids hypothesis through consistently negative relationships between the risk of bird predation and the probability of parasitism across caterpillar species on multiple host-plant species. While all measures of parasitism had negative relationships with the risk of bird predation, this was a significant relationship when hymenopteran and tachinid parasitism were response variables in separate models (Model 3, Model 8). These results suggest that parasitoids in this community generally avoid parasitizing caterpillar hosts at high risk of bird predation, but that hymenopteran and tachinid parasitoids acquire this enemy-free space in different ways. In contrast to bird predation risk, parasitism was not responsive to ant predation risk at all or as predicted by the enemy-free space hypothesis. The lack of an enemy-free space response of parasitoids to ant predation risk does not support predictions 1 and 3, but it is consistent with previous findings of the relatively weak predatory effects of ants on caterpillars in temperate forests worldwide (Roslin et al. 2017) as well as in this community (Singer et al. 2017).

These results also support the fourth prediction about probability of tachinid parasitism being more negatively associated with risk of bird predation than the probability of wasp parasitism. The effects of predation risk are similarly negative in direction, but weaker for hymenopteran parasitism, showing that tachinid host use is more heavily influenced by bird predation than is hymenopteran host use. This reduced response from wasps to risk of predation suggests that these two groups may be under different ecological pressures in terms of their host selection. We might not see the effect of predation on wasps because they have evolved other ways of gaining enemy-free space than avoiding high risk caterpillars. Parasitoid wasps can control host behavior to protect themselves from natural enemies (Brodeur and Vet 1994, Grosman et al. 2008, Harvey et al. 2008, Murphy et al. 2014), and may control host behavior to avoid predation from birds. The weak relationship between wasp parasitism and our coarse-grained measure of predation may occur because the effect sizes combine the various risks experienced by a caterpillar species across all individuals on a given host-plant species. Undoubtedly there are more nuanced factors than the host caterpillar species and its host plant that influence predation risk and are detectable by parasitoids via environmental cues. If we could measure and account for more predation risk factors or how the parasitoid influences host behavior to lower predation risk (Karban and English-Loeb 1997, Grosman et al. 2008), the probability of parasitism may show stronger enemy-free space effects.

The difference between the strength of the enemy-free space effect as well as the structure of best-fit models for parasitoid wasps and flies raises interesting questions about the ecological differences between these taxa. Enemy-free space for parasitoid wasps and flies is likely to differ in the timing of bird predation relative to parasitoid oviposition. Generalist predators may influence parasitoid host choice through predation of immature parasitoids within the host (i.e., post-oviposition predation), but predation may also shape the caterpillar community that is available to the adult female parasitoids prior to oviposition (i.e., pre-oviposition predation).

Because they tend to attack early instar caterpillars (Godfray 1994, Shaw 2006), parasitoid wasps are likely to oviposit before caterpillars face significant bird predation. However, because parasitoid flies frequently parasitize middle and late instar caterpillars (Stireman et al. 2006), their hosts may face more pre-oviposition predation. Therefore, enemy-free space for parasitoid wasps is expected to primarily involve avoidance of post-oviposition predation, and thus avoiding a set of caterpillar species and plant species combinations with the greatest bird predation risk when wasp larvae occupy them. In contrast, pre-oviposition and post-oviposition bird predation is expected to affect parasitoid flies by reducing the availability of some host environments and posing a risk of predation on immature tachinids in others. This difference between the parasitoid taxa in oviposition timing relative to size and risk of bird predation of the host may be a large driver in the stronger effects of bird predation on tachinid parasitism. Tachinid parasitoids face limiting effects of predators twice in the host selection process, before choice and during development, compared to wasps potentially only experiencing predation effects during immature development. This may also explain why the models accounting for both risks of predation show a stronger enemy-free space effect for probability of tachinid parasitism. Accounting for more of their host caterpillar's risk of predation strengthened the pattern because tachinids face more limiting effects from pre- and post-oviposition predation. In contrast, wasp parasitism showed the strongest enemy-free space effects when only accounting for bird predation because enemy-free space for wasps may mostly involve avoiding post-oviposition predation from birds. Even though this study only looks at generalist predators, more specialized natural enemies such as hyperparasitoids may be an equally, or more important force in selection for enemy-free space in primary parasitoids (Volkl 1992 and Kaneko 2003). Expansion of enemy-free space to higher trophic levels could explain variation in community dynamics that are currently unexplained by bottom-up processes alone and improve our understanding of selection processes on traits of higher trophic-level organisms.

These are some of the first results comparing top-down and bottom-up ecological effects on the patterns of parasitoid-host interactions. They provide insight as well as further questions about parasitoid host use. We expected the fixed effects of caterpillar species and host-plant species to have an influence on the probability of parasitism, as previous studies have shown that caterpillars in North American forests experience a differential risk of mortality from parasitoids across caterpillar species (Hawkins 1994, Farkas and Singer 2013) as well as across host-plant species (Barbosa et al. 2001, Lill et al. 2002, Farkas and Singer et al. 2013). Parasitoids are likely to be under selection to choose hosts that will not be killed before the parasitoid has completed its development (Lafferty and Kuris 2002), but the host's risk of predation does not entirely predict its probability of parasitism. Variation in parasitism relating to the caterpillar or host-plant species had a stronger predictive effect in our models than enemy-free space. These predictor variables encompass many more of the ecological interactions related to parasitoid host selection than the risk from predators. The influences of the various caterpillar and host-plant traits discussed in the Introduction, along with their interactions, have been boiled down to these two very broad predictor variables. When comparing the effects of whole trophic levels against risk from specific groups of predators, it is unsurprising that these broadly representational variables had a stronger effect on probability of parasitism. These caterpillar and plant traits also serve as the first determinants of host suitability and detectability, and in order for natural enemies to directly shape parasitoid host choice, the parasitoid must first respond to these traits of the lower trophic levels. These bottom-up effects would be expected to dominate because not finding or being able to use a host directly prevents reproduction. A parasitoid within a host with a high risk of predation will have a greater chance of survival than a parasitoid that has no host insect. The inclusion of these sources of variation as fixed effects does not address the mechanisms behind these bottom-up structuring forces of parasitoid host choice.

Previous work on parasitoid host choice has hypothesized many mechanisms that can contribute to variation in parasitism relating to caterpillar and host-plant traits (e.g., Hawkins 1994, Lill et al. 2002, Hunter 2003), with some of those mechanisms receiving study in the community studied here (Farkas and Singer 2013). Differences in parasitism due to caterpillar species is likely from differences in behavioral response to foraging adults as well as a caterpillar’s physiological defenses such as immune response. While not directly tested with respect to attacking parasitoids, notable differences in behavioral response to pinching with forceps exist within this community of caterpillars (Lichter-Marck et al. 2015), and these responses may be behind the positive relationship between ant predation and tachinid parasitism. Ant predation risk is largely predicted by the behavioral responsiveness of a caterpillar, and has been shown to be lower for species with higher frequency of behavioral response (Singer et al. 2019). Caterpillar responses such as biting, regurgitating, and dropping from the host plant protect these herbivores from ants, but are general responses that may also protect them from parasitoids (Greeney et al. 2012). Caterpillars with a low risk of ant predation may escape tachinid attack through similar mechanisms. Due to the variety of methods used by tachinid flies when attacking prey (i.e., some species oviposit on host integument while others oviposit near the host and larvae must search out the nearby host) that are less direct than typical wasp oviposition, some of these general behavioral responses could be effective in preventing tachinid attack (Gentry and Dyer 2002, Stireman et al. 2006, Shaw 2006). If these behavioral defenses work against both ant and tachinid attack, these caterpillar traits may explain the unexpected positive relationship between ant predation risk and probability of tachinid parasitism.

In a previous study in this system focused on variation in parasitism across host-plants, Farkas and Singer (2013) addressed how density-dependent foraging by parasitoids and host-plant quality do not explain variation in parasitism. They concluded that the differential parasitism across host-plant species is not solely due to variation in caterpillar density across hot-plant species coupled with density-dependent mortality from parasitoids (Farkas and Singer 2013). Lill et al. (2002) also found no relationship between risk of parasitism and abundance of a caterpillar species on a particular host-plant, suggesting that host-plant effects on parasitism are likely driven by additional mechanisms. Unlike other host-plant species, the chemical defenses of temperate trees are unlikely to influence parasitoid development in the hemocoel (Farkas and Singer 2013). Growth performance of caterpillars differed substantially across these host-plants (Singer et al. 2012), indicating that host-plant quality affects physiology of caterpillars; but Farkas and Singer (2013) finds this does not propagate up trophic levels as host-plant quality had no significant effect on parasitism.

Variation in volatile organic compounds released from the host-plants has received limited study but may be a powerful driver of parasitism host choice. Volatile organic compounds released from plants in response to herbivory are known to be used by parasitoids as foraging cues (Turlings and Erb 2018). These compounds vary immensely between plant species and within individuals of the same species, and many environmental factors can lead to varied concentrations and abundances of these compounds (Gouinguené and Turlings 2002, Hare 2011). When considering ecological effects on the release of volatile organic compounds such as herbivore-specific responses, differences between ontogenetic stages, and the effects of multiple herbivores on the suite of compounds, community-level patterns related to volatile organic compounds may be difficult to discern (Hare 2011). Variation in the abundance and concentration of compounds across host plants, environmental conditions, and ecological interactions likely to play a significant role in the strong bottom-effects on parasitoid host choice, but disentangling the importance of effects from so many sources will be a major challenge of future work.

CONCLUSIONS

This is one of the first studies to simultaneously consider bottom-up and top-down effects on parasitoid host choice. Parasitoids generally avoid caterpillar and host-plant species combinations with a high risk of bird predation, therefore enemy-free space from birds in conjunction with host-plant and caterpillar species-based effects drive parasitoid host choice in this temperate community. Enemy-free space, even as a partial factor structuring parasitoid communities, may have large implications for patterns in parasitism. Parasitoid communities may be structured around more nuanced differences in predation risk between host herbivores, such as microhabitat differences. Parasitoids have evolved to utilize enemy-free space, and the cues that inform them of these top-down risks likely originate in the lower trophic levels. Attempting to attribute patterns of parasitism at the community level to bottom-up versus top-down effect is not useful. The effects of natural enemies or traits of the hostplant and host caterpillar species alone are not structuring parasitoid communities, the web of these interacting effects is influencing parasitoid host ranges over evolutionary time. Our results emphasize an important point from Jeffries and Lawton (1984): absolute enemy-free space does not truly exist in natural communities. The negative relationship between risk of bird predation and probability of parasitism highlights a potential trade-off in mortality from birds versus parasitoids for these caterpillars.

Understanding community patterns of parasitism requires further understanding of the complex ecological and evolutionary factors influencing parasitoid host decisions. Communities are not simple; they are formed on the interactions of innumerable biotic and abiotic variables, and it can be incredibly difficult to properly model these interactions. The inclusion of multiple generalist predator taxa, parasitoid taxa, and a large range of caterpillar and hostplant combinations allowed for the detection of many patterns of parasitism in relation to the hosts risk of predation. These results show us the importance of considering multiple and varied ecological effects at once when looking to uncover community-level patterns.

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