

POLLINATOR NICHE BREADTH AND NATURAL ENEMIES

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Fundamental to ecology is understanding what mechanisms contribute to niche breadth (Colwell and Futuyma 1971, Futuyma and Moreno 1988, Odling-Smee et al. 2003). Patterns of specialization and generalization (or niche breadth) in pollinators has received increasing attention, perhaps in part because mutualistic interactions are critical to patterns and processes of biological systems, including the provision of ecosystem services (Kremen 2005) and the maintenance of biodiversity (Bascompte et al. 2006). At geographical scales physiological tolerance limits the niche of an organism (Futuyma and Moreno 1988). Within the geographical range limits of a species, behavior may be of primary importance in determination of a species ecological niche (Futuyma and Moreno 1988). Just as plant secondary chemistry plays a significant role in determining behavior and plant host range in phytophagous insects (Bernays 1989), so do floral morphology, phenology and nectar chemistry play significant roles in determining pollinator visitation (Santamaría and Rodríguez-Gironés 2007). However, just as natural enemies of herbivores influence plant-herbivore dynamics (e.g., trophic cascades; Shurin et al. 2002, Borer et al. 2005), natural enemies of pollinators can have important consequences for plant-pollinator dynamics (Knight et al. 2005, Knight et al. 2006). An important contribution towards evaluating the consequences of natural enemies of pollinators for plants and pollinators is evaluating the magnitude of natural enemy influence on pollinator niche breadth.

To gain insight to the potential role of pollinator enemies in pollinator niche breadth, we can draw on the rich literature on mechanisms underlying patterns of specialization and generalization of insect herbivores (reviewed in Jaenike 1990). For example, plant secondary chemistry was previously thought to solely regulate insect herbivores. Recently other mechanisms contributing to insect herbivore dynamics have been explored, including natural enemies of herbivores. In similar fashion, pollination ecologists have historically assumed that plant-pollinator interactions are largely driven by trait- and phenological matching. That is, patterns in plant-pollinator interactions are simply the result of two trophic levels (plants and pollinators) interacting. However, plant-pollinator interactions are embedded within a community of organisms, and consideration of alternative community members in general has

lead to new insights (Irwin et al. 2004). For example, Whitney & Stanton (2004) revealed that a fruit color polymorphism in *Acacia ligulata* (Fabaceae) is influenced not only by presumed selective agents (seed dispersers), but also by seed predators. Given the diversity of natural enemies of pollinators (Stephen et al. 1969), natural enemies of pollinators may influence pollinator traits (e.g., plant host breadth) at least in some cases.

There are two ways that natural enemies can negatively influence pollinators: consumption and threat of attack. Even if consumption of pollinators at flower patches is rare, the threat of attack (Trussell et al. 2006) by these enemies may be enough to influence visitation rates or what plant species pollinators visit. Recent work by Dukas (2005) has revealed that consumptive effects can have large consequences for pollinators. A 50 km² area encompassing a single bumble bee wolf (*Philanthus bicinctus*; Hymenoptera: Sphecidae) had lower bumble bee density than comparable areas without *P. bicinctus*. In addition, fruit set in monkshood (*Aconitum*; Ranunculaceae) was significantly lower in areas with than without *P. bicinctus*. Although *P. bicinctus* largely influenced bumblebees via consumptive effects (predation), non-consumptive effects (threat of attack; Lima and Dill 1990 for a review) can have important consequences for pollinator visitation and pollination outcome for plants. Thus, natural enemies of pollinators influence pollinators via direct effects ('the effect of one species on another that does not involve another species, i.e., they would occur if the species pair was in isolation; Wootton 2002) and plants via indirect effects ('effects of one species on another that only arise in the presence of other species'; Wootton 2002). In predator-herbivore-plant interactions 50% of indirect effects that occur between predators and plants can be accounted for by predators altering herbivore behavior (i.e., threat of attack), rather than directly reducing herbivore density (i.e., consumption; Preisser et al. 2005). As the study of herbivory has advanced via inclusion of natural enemies of herbivores, pollination ecology may gain from incorporating natural enemies of pollinators.

Natural enemies of pollinators may respond to the architecture (or other characteristics) of plants at which pollinators forage. Interestingly, a number of studies have shown that natural

enemies of herbivorous insects strongly respond to vegetation architecture (Neuvonen 1999, Gingras et al. 2002), suggesting that there may be differential ability due to plant architecture for predators and parasites of herbivores to find their prey. Similarly, if natural enemies of pollinators respond to variation in plant traits (e.g., architecture, size) they may have the ability to influence host plant selection by pollinators, and possibly niche breadth of pollinators.

Here, I examine the prevalence of natural enemy pressure on pollinators, and patterns of occurrence of pollinator natural enemies in relation to plant attributes. The following specific questions will be addressed. First, do predators of pollinators have significant effects on foraging pollinators and on plant reproduction (via predation on, or deterrence of, pollinators)? Second, do parasites of pollinators have significant effects on pollinators? Third, can plant characteristics explain the species richness of pollinator natural enemies occurring with different plant taxa?

Natural history

Plants. Although there are major trends and differences within and among biomes, many angiosperms rely on animal pollinators to transfer pollen, facilitating plant reproduction. Animal pollinated plants have a wide variety of architectural forms and sizes, and vary widely in diversity, abundance patterns, and distribution. With specific importance to plant-pollinator interactions is the architecture of flowers and inflorescences (although density effects, among others, are important here, available data do not allow such analyses). Inflorescence structure, as well as vegetative architecture, growth form, and other plant attributes are not independent of plant phylogenetic history – thus independent phylogenetic contrasts are an ideal test of architectural differences. Nonetheless, initial analyses presented below are a necessary first step.

Pollinators. Plant pollinators are diverse, and include bees, wasps, and ants (Hymenoptera), flies (Diptera), beetles (Coleoptera), butterflies and moths (Lepidoptera), earwigs (Dermaptera), cockroaches (Dictyoptera), bugs (Hemiptera), thrips, (Thysanoptera), birds, bats, rodents, reptiles and others (Proctor et al. 1996). However, with ~17,000 species, all of which are pollinators, bees are the major pollinators of flowering plants. Thus, this paper is

concerned largely with the interactions between bees and their natural enemies. Pollinators forage for nectar and pollen rewards (rarely oil (e.g., Malphigiaceae) and scents (e.g., Orchidaceae); Proctor et al. 1996), with significant variation in reward collection due to many factors. For example, bees collect both pollen and nectar, while butterflies only collect nectar from flowers; both affect plant pollination via incidental pollen deposition on stigmas. A major factor that sets many pollinators apart, with respect to their susceptibility to natural enemies, is food storage. Ants store vast amounts of food, and thus are susceptible to many natural enemies, but are rarely pollinators and thus are not of major concern here. Flies, beetles, butterflies, moths, and others do not store food. Lastly, bees (and some wasps, esp. Masaridae [pollen wasps]) collect and store pollen and nectar, and often exhibit nesting in the same location each year, resulting in attraction of many natural enemies (Weislo and Cane 1996).

Natural enemies of pollinators. Just as pollinators are extremely diverse, so too are the natural enemies of pollinators. Natural enemies range from extremely specific (e.g., parasitic bees, e.g., *Nomada* spp.) to extremely generalist (e.g., lizards). Many natural enemies of pollinators also feed on plants where they find their pollinator hosts, which likely creates dynamics different from the case where natural enemies do not also feed on plants. These enemies can also be pollinators in many cases. Examples of natural enemies that feed on plants in addition to attacking pollinators are: Bombyliidae (attack: bees, wasps, beetles, flies, moths, butterflies), Conopidae (attack: almost entirely bees; Smith and Peterson 1987), Syrphidae (attack: ants, Homoptera, Thysanoptera, Coleoptera, Lepidoptera; Vockeroth and Thompson 1987) (Diptera), Meloidae (attack: bees and wasps; Erickson et al. 1976), Cleridae (attack: bark beetles, bees and aculeate wasps, grasshoppers), Rhipiphoridae (attack: bees and wasps) (Coleoptera), parasitic bees (attack: bees) (Hymenoptera). Some natural enemies of pollinators that largely do not feed on plants in addition to pollinators are: predacious wasps (e.g., Sphecidae), flies (e.g., Asilidae), and spiders (e.g., Thomisidae). Because bees are so diverse and are largely pollinators, a synopsis, tabulated from Stephen et al. (1969), of the known natural enemies of bees is presented in Table 1.

Effects of natural enemies on pollinators: predators and parasites

One way to describe niche breadth is the idea of specialization and generalization with respect to number of species the focal species interacts with. Authors addressing specialization-generalization patterns in nature stress there is unlikely to be a single factor of paramount importance that determines the degree of specialization (citation?). In the plant-herbivore and aquatic literature a discussion has arisen stressing the role of predation/parasitism in structuring specialization-generalization patterns (Jeffries and Lawton 1984, Bernays and Graham 1988, Berdegue et al. 1996, Heard et al. 2006; but see Jaenike 1990, who stresses the importance of genetically based tradeoffs in phytophagous insect offspring performance on different plant hosts), instead of competition for limiting resources and differential response to host defense molding niches. This discussion, framed as one of enemy free space (EFS: 'ways of living that reduce or eliminate a species' vulnerability to one or more species of natural enemies'; Jeffries and Lawton 1984), prompted Berdegue et al. (1996) to state that 'EFS has emerged in the literature as a significant niche-moulding factor'. Indeed, increasing attention has been given to testing for the existence and magnitude of EFS in nature. However, a recent vote-counting review (Heard et al. 2006) of 38 plant-herbivore EFS studies suggested that there is some evidence for EFS, but that EFS should be thought of as a force that is geographically and temporally variable, rather than constant in space and time. Enemy free space is a real phenomenon, but the importance of the effect, and the extent to which it operates, is still a matter of dispute (Heard et al. 2006). The role of natural enemies in shaping pollinator niche breadth has not been explored (but was alluded to by Wcislo and Cane 1996, and Dukas 2001).

Two distinctly different kinds of pollinator natural enemies are predators and parasites. I will first consider predators. I conducted a meta-analysis of studies that measured pollinator performance with and without a predator present to determine the effect of predators on pollinators. Although most of the data come from one source (Knight et al. 2006), additional sources are listed in Appendix Table 1. I calculated the effect size as the log response ratio ($\ln R$)

for each study to facilitate comparison among studies and calculation of a mean effect size across studies. The log response ratio ($\ln R$) is defined as $\ln R = \bar{X}^P / \bar{X}^{NP}$, where \bar{X} is the mean of a given response variable (e.g., pollinator visitation rate), and P and NP denote predator and no (or reduced) predator treatments, respectively. Data were collected for pollinator visitation rate (number of pollinators visiting flowers of a plant species per unit time), proportion of flowers visited, number of ovipositions per fruit (yucca moths), and plant reproduction (seeds per fruit, fruit set, etc.). A negative mean effect size indicates that natural enemies of predators have the ability to negatively affect pollinators or plant reproduction. A positive mean effect size would indicate that natural enemies of pollinators positively influence pollinators or plant reproduction. I calculated mean effect sizes, with 95% bias-corrected confidence intervals for each category using MetaWin 2.0 (Rosenberg et al. 2000).

Of three pollinator response variables and one plant reproduction variable, only two variables (pollinator visitation rate and plant reproduction) had large enough sample sizes to draw general conclusions (Fig. 1). Mean effect size for pollinator visitation rate was -0.62 ($n = 15$; Fig. 1), which suggests an even bigger effect of predators on pollinators than previously reported (-0.34; Knight et al. 2006). Thus, natural enemies can exert significant negative effects on pollinators. Proportion of flowers visited and number of ovipositions per fruit are presented (Fig. 1), but had very low sample sizes and are not discussed further. Plant reproduction had a mean effect size of -0.36 ($n = 12$; Fig. 1), larger than previously reported (-0.22; Knight et al. 2006), indicating that negative effects of natural enemies of pollinators can extend to plant reproduction. Interestingly, generalists predators like those included in this meta-analysis also predate on plant antagonists (herbivores). Thus, the affect of predators on plants is due to predation on plant mutualists (pollinators) as well as plant antagonists (herbivore).

If EFS is an important factor influencing niche breadth in pollinators, mortality due to specialist natural enemies should be greater in specialist relative to generalist pollinators (Lawton 1986, Bernays 1988, 1989). Specialist bees, by definition, are more predictable with respect to plants that they visit relative to generalist bees, making specialists bees more profitable for a

specialist natural enemy. In contrast, mortality due to generalist natural enemies should be greater in generalist relative to specialists pollinators. Generalist bees visit many plants and thus deal with many more predators than specialist bees; specialist bees, unlike generalist bees, may be able to learn to avoid often conspicuous predators because they visit similar plants with similar morphology. If these predictions are true, then specialist enemies should drive pollinators to become generalists, and generalist enemies should drive pollinators to become specialists (Fig. 2). However, generalist pollinators (e.g., honey bees) are likely to be more abundant than specialist pollinators, due to the fact that generalist pollinators can have extended activity periods and geographical ranges due to lack of a limiting resource (i.e., specialist plant hosts for specialists bees). Thus, abundant pollinators may have more natural enemies overall.

Bees are an especially conspicuous and important pollinator group (Proctor et al. 1996). Two ways in which pollinating bees are influenced by natural enemy pressure are while foraging at flowers and while in nests. A diverse array of parasites, parasitoids, and predators attack bees at nests and exploit stored food reserves in bee nests (Appendix Table 1; Wcislo 1996). The effect of natural enemies of bees that attack at nests are well known relative to those of enemies that attack foraging bees. This is due largely to the ease of studying enemies of bees in nests; artificial trap nests (made by drilling holes in wood) allow easy determination of rates of parasitism and identity of parasites. Thus, there are numerous reports of parasitic natural enemies of bees. I searched the literature for papers that documented rates of cell parasitism in bees. Data largely come from one source (Wcislo 1996, Table A1), but other literature were included. The data presented are almost entirely for solitary bee species. This is justified because ~15,000 of the present ~17,000 species of bees are solitary (Wcislo and Cane 1996). I compared the mean parasitism rate of oligolectic (specialist; collection of pollen from a single plant species, genus, or tribe) to polylectic (generalist; collection of pollen from more than one plant family) bees with a non-parametric (Wilcoxon) two-sample test (SAS 2004) due to lack of normality and heteroscedacity of residuals.

Overall, mean (\pm SE) percent cell parasitism was slightly higher in specialist bees (\bar{X} =

26.2 \pm 3.9) than in generalist bees (\bar{X} = 23.8 \pm 4.7) (Fig. 2), but there is no statistically significant difference (two-sample Wilcoxon test, X^2 = 0.83, df = 1, P = 0.36). Interestingly, the coefficient of variation in parasitism rates was much higher in generalist bees (CV = 108.6) than specialist bees (CV = 78.6), suggesting that bee specialization may cause higher mean mortality, but less variation (esp. extending into the right tail of the distribution). On average, irrespective of level of foraging specialization, one-quarter of bee offspring are killed due to parasites. The natural enemies in the studies included are not all known, precluding any further analyses. However, of those that are known, some of the natural enemies are those that feed on plants themselves. In sum, natural enemies can affect bee offspring survival, and possibly lead to differential pressures on bees with different foraging strategies (specialists vs generalists). Experiments controlling for bee and plant phylogeny using congeneric specialist and generalist bees would be required to rigorously evaluate this hypothesis.

Can plant characteristics influence bee natural enemy diversity?

At first glance it may seem that enemies that attack foraging bees (predators) are the natural enemies most likely to influence plant selection by pollinators, and possibly drive community level interaction patterns. However, parasites that attach to foraging pollinators (e.g., meloid beetles), parasites that find and oviposit on/into pollinator hosts while pollinators are foraging (e.g., conopid flies), and parasites that oviposit eggs into/around nests, might have equal ability to affect host plant selection by pollinators. For example, if plant species A is associated with greater density of parasites that attach to bees than plant species B, individual pollinators that visit plant species A may suffer greater mortality than individual pollinators visiting plant species B. This is despite absence of a predator attack which would reinforce the risk ('threat of attack') associated with a predator and/or location of attack. Just as plant attributes affect herbivore communities (Neuvonen 1999), and host-finding by parasitoids of herbivores (Gingras et al. 2002), plants may influence the ability of natural enemies of bees to attack and consume bees.

Some characteristics of plants likely to affect the distribution of natural enemies of pollinators are: geographic distribution, abundance, phenology, and architecture. Geographic distribution and abundance of plants likely affects patterns of pollinator natural enemy distribution at large scales. At smaller scales plant architecture may be important. Plant architecture is well-known to be important to plants through effects on herbivore feeding (e.g., Rudgers and Whitney 2006). Architecture can also influence insect herbivore host finding by predators, parasites, and parasitoids, influencing herbivore survival and plant damage (Grevstad and Klepetka 1992, Gingras et al. 2002, Riihimaki et al. 2006). In addition, plant architectural traits are known to be heritable (Bailey et al. 2004), with some evidence suggesting that herbivores (Schat and Blossey 2005) and predators (Louda 1982) can influence plant architecture. However, the role of plant architecture in determining distribution of the natural enemies of pollinators has not been addressed.

I used North American host plant occurrence data for Nemognathine (Coleoptera: Meloidae) beetles from Erickson et al. (1976). I quantified the number of beetle taxa (including subspecies) associated with each of 153 plant taxa. Next, I recorded the following plant variables where available: number of species in plant genus, maximum plant height, plant growth form, flower color, and inflorescence architecture (Hickman 1993, Committee) 2003). Inflorescence architecture in the family Asteraceae was problematic because each flower head is an inflorescence in itself. Therefore, I attempted to fit inflorescence architecture for the family into categories (e.g., raceme, panicle) fitting most other plants. Thus, a single Asteraceae flower head is simply considered a single ‘flower’ in my analyses. I did not include plants that were only identified to genus. Due to much missing information, data were not subjected to statistical analysis.

Nemognathine meloid beetles are associated with 85 plant species across 17 plant families. Of the 68 plant species for which flower color could be found, nearly half (~45%) of plant species had yellow flowers. Thirty-five percent of plants were annuals, whereas ~59% were perennial. Forty-one percent of plants were herbaceous perennials, with ~27% annuals, ~20%

shrubs, and ~8% sub-shrubs. The most common inflorescence architecture was solitary flowers (or solitary flower heads in Asteraceae; ~40%), cymes (~19%), and racemes (~18%).

The vast majority (73% or 61 species) of plant-beetle associations involved members of the Asteraceae. Although only two plant species (*Larrea divericata* and *L. tridentata*) in the family were considered, Zygophyllaceae hosted the highest average number of beetle species (Fig. 3). The highest number of beetle species overall was associated with *Helianthus annuus* (Asteraceae). A combination of red and yellow flower color was associated with the highest number of beetle species, with purple and yellow hosting the second and third highest diversity of beetles (Fig. 3). Inflorescence architecture types with the greatest diversity of beetles was solitary flowers (or flower heads in Asteraceae), with racemes with the least number of beetle species (Fig. 3). Perennial herbs hosted the highest diversity of beetles, but was not much different than shrubs (Fig. 3); only one tree species was included in the database, so that inferences regarding the tree growth form are not possible. Annual plants hosted slightly higher beetle diversity than perennials (Fig. 3). As transformations could not fix non-normality and heteroscedacity in residuals, data were not subjected to statistic analyses. However, during exploratory data analyses, there was a trend for number of beetle species to increase with maximum plant size (and was even more apparent in a model taking into account annual vs perennial life history).

Spiders are common natural enemies of pollinators, and their niche use patterns have been studied in detail relative to other natural enemies of pollinators. Many studies have documented the role of vegetation architecture in determining spider niche breadth (Riechert 1976, Hatley and Macmahon 1980, Robinson 1981, Gunnarsson 1990, Kevan and Greco 2001, Schmitz and Suttle 2001, de Souza and Martins 2004, Romero and Vasconcellos-Neto 2004b, de Souza and Martins 2005, Romero and Vasconcellos-Neto 2005). Spider abundance and diversity generally increases with increasing foliage density and the composition of spiders changes among plant species. Spider guilds respond in relatively predictable ways to vegetation architecture, resulting in a non-random natural enemy mosaic which pollinators forage in.

276 Interestingly, Louda's (1982) work suggests that spiders may even influence inflorescence
277 architecture via predation on plant enemies and deterrence/predation of plant mutualists. Thus,
278 not only does plant architecture influence spider niche breadth, but spiders may sometimes drive
279 variation in plant architecture through differential predation on plant antagonists and mutualists.

280 Contrary to spiders, the role of plant attributes in shaping niche breadth and host finding
281 behavior of other natural enemies of pollinators have not been documented in such detail.
282 However, work addressing parasites and parasitoids of plant herbivores may lend insight. For
283 example, Gingras et al. (2002) found that the rate of parasitism for a wasp on lepidopteran larvae
284 is predicted reasonably well using the variable of plant connectivity (abundance of connections
285 among plant parts). The analysis of meloid beetle plant association presented herein is one of the
286 few to analyze the association of pollinator natural enemies (other than spiders) in relation to
287 plant attributes. Although patterns were found in the data, due to the very coarse nature of the
288 data collected, and the simplistic response variable (beetle occurrence records), interpretation of
289 data is difficult and easily affected by beetle collector bias. A major drawback to the meloid
290 beetle dataset is that it does not include abundance data. Occurrence data do not allow insights
291 into the differential potential impact on pollinators due to different densities/abundances of
292 natural enemies. Some work has quantified the magnitude of natural enemy pressure on
293 pollinators (parasitic wasps, bees, and flies; Tylianakis et al. 2007) and abundance of pollinator
294 natural enemies on plant species (Conopidae, Freeman 1966, Bombyliidae, Toft 1983). For
295 instance, Tylianakis et al. (2007) quantified bee and wasp parasitism rates within a community,
296 rather than simply describing which parasite-bee/wasp interactions occur (present or absent). In
297 order to assess the role of natural enemies of pollinators, quantitative data on plant-pollinator
298 interactions needs to be collected along with data on pollinator-natural enemy interactions. In
299 addition, quantifying vegetation and plant species specific attributes (e.g., inflorescence
300 architecture) along with pollinator natural enemy abundance patterns may lend valuable insight.

301 An essential prerequisite for natural enemies to be able to influence pollinator niche
302 breadth is differential success in prey capture among plants. If natural enemies experience

differential prey capture of pollinators, due to plant architecture for example, pollinators will be faced with a mosaic of varying threats. Plant architecture is known to influence the ability of herbivores to damage plants (Neuvonen 1999), as well as the host-finding ability of herbivore predators (Riihimäki et al. 2006). A number of studies have documented varying prey capture or deterrence in flower dwelling spiders and ants (Louda 1982, Fritz and Morse 1985, Schmalhofer 2001, Muñoz and Arroyo 2004, Junker et al. 2007), or the effect of generalist predators (largely spiders) on plant reproduction (e.g., Ott et al. 1998, Romero and Vasconcellos-Neto 2004a). In a study of a single crab spider species, Fritz & Morse (1985) found that spiders attacked three times more (larger) bumblebees than (smaller) honeybees, but successfully captured seven times more honeybees than bumblebees. Likewise, the negative effects of natural enemies on pollinator visitation differed whether bird or lizard predators were present, and whether the pollinator was a butterfly, fly, or bee (Muñoz and Arroyo 2004). Thus, there is differential capture success of pollinators by predators, and for parasites/parasitoids (discussed earlier). Schmalhofer (2001) found that a crab spider (*Misumenoides*) experienced greater hunting success on *Bidens* than *Solidago* (both Asteraceae), and greater success in large than small patches, which may reflect well-known pattern of increasing pollinator visitation with increasing floral display (Ohashi and Yahara 2001). Furthermore, size of captured pollinators was significantly greater than size of pollinators visiting flower patches, suggesting that body size (as well as predator:prey body size ratio) is an important variable in determining predator effects on pollinators.

Species-area relationships are well-documented patterns in nature, and relate to the issue at hand. In some exploratory analyses with the meloid-plant data, number of meloid beetle species per plant species increased with plant size. Other reports document similar trends with other pollinator natural enemies. Hatley and MacMahon (1980) conducted a detailed analysis of spider communities in response to vegetation attributes in the Great Basin Desert of Utah. They found that the diversity and numerical abundance of spiders was most strongly correlated with vegetation height. Density of individuals in the guild of spiders including Misumeminae (crab spiders that often predate on pollinators) was correlated most strongly with foliage density, while

density in the guild including jumping spiders (Salticidae; who predate on pollinators) was most strongly correlated with vegetation volume, diversity, and vegetation height (in decreasing importance). If pollinator communities are significantly effected by natural enemies, the increase in abundance/diversity of natural enemies with increasing vegetation height and/or volume, and differential abundance of plant species at varying scales will likely influence pollinator communities. For example, as pollinator visitation is well known to increase with increasing floral display (Ohashi and Yahara 2001), natural enemies of pollinators may respond via increased abundance (and/or diversity) with increasing floral display size.

Conclusion

Plant-pollinator interactions have been an intense area of study over many decades (Proctor et al. 1996), and their importance in nature is increasingly recognized (Kremen 2005). Most theories attempting to explain the interactions among plants and pollinators involve only factors related to the interactions between plants and pollinators, and ignore other factors, such as predation on pollinators (Knight et al. 2005) and endophyte influence on plants (Lehtonen et al. 2005). For instance, recent research exploring patterns of specialization and generalization in mutualistic communities only discuss traits of plants and pollinators as important in determining their interactions with one another (Blüthgen et al. 2007, Santamaría and Rodríguez-Gironés 2007). Recent work with aquatic food webs suggest that intermediate trophic levels (e.g., equivalent to pollinators in terrestrial systems), not lower trophic levels as previously assumed, are the most susceptible to natural enemies (Lafferty et al. 2006). Perhaps a more in depth look at natural enemies, their effect on plant-pollinator interactions, and factors determining natural enemy distribution and abundance, is warranted. I have shown that natural enemies of pollinators can significantly influence pollinator visitation rate, and that plant reproduction is negatively affected indirectly via predation on pollinators (Fig. 1). Bee parasitism rates reached nearly one out of every four offspring (Fig. 2). Although parasitism rates on generalist versus specialist bees did not significantly differ, specialist bees experienced slightly higher parasitism rates than generalist

bees. An analysis of common natural enemies of bees (nemognathine beetles) revealed no pattern in species richness of beetle taxa to plant characteristics. However, although species richness may not differ, abundance of beetles may likely vary with plant characteristics.

Natural enemies of pollinators have the potential to significantly influence plant-pollinator interactions, although the extent to which natural enemies respond to plants to provide a mosaic of differential enemy pressure for pollinators is unclear. Experiments measuring niche breadth in pollinators in the presence and absence of natural enemies may lend great insight into questions posed herein. Given the importance of pollination services and plants for human and global welfare, and the current decline of native and non-native (honey bees) pollinators, understanding alternative mechanisms that influence plant-pollinator interactions seems timely.

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Figure 1. Summary of meta-analysis examining the effect of natural enemies on pollinators and plant reproduction. (A) Results from Knight et al. (2006) of pollinator visitation rate and plant reproduction (with 95% bootstrap confidence intervals). (B) Expanded dataset collected during this study (w/o confidence intervals) with additional variables. Pollinator visitation rate is the number of pollinator visiting flowers of a plant species per unit time. N = number of individual cases (some from within individual studies). Effect size is the log response ratio, $\ln R = \bar{X}^P / \bar{X}^{NP}$; see text for explanation. GET RID OF “(B)” AND “N=”, AND REDO ANALYSES IN METAWIN, THEN ADD 95% CI’S HERE AS WELL....

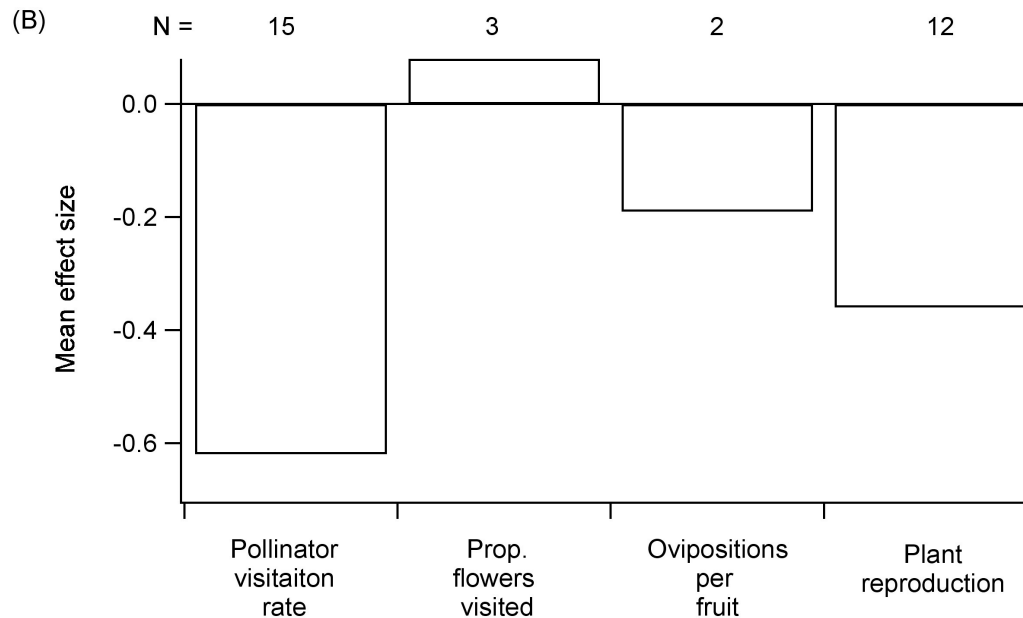


Fig. 2

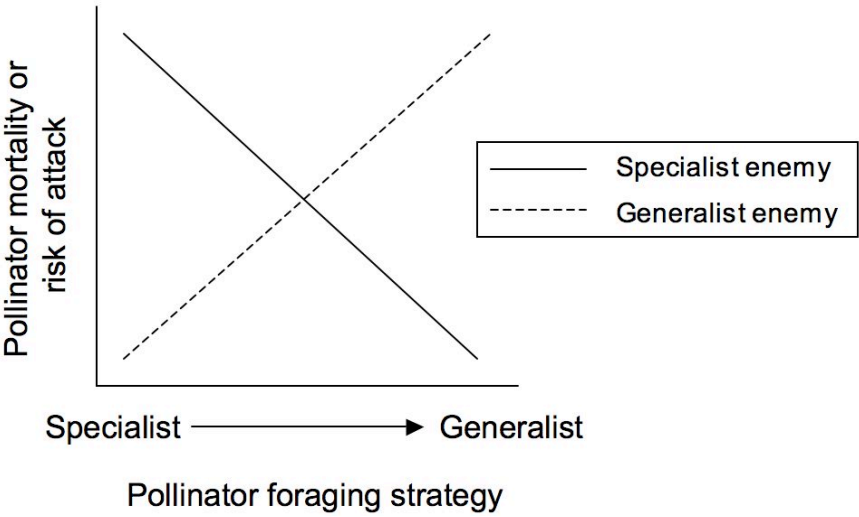


Figure 3. Percent bee cell parasitism (% of individual offspring killed) by various natural enemies for generalist (polylectic) vs specialist (oligolectic) bees. Natural enemies include those that find bee hosts at forage plants or at nests, but all attack bees in nests (not killing or attacking bee hosts at forage plants). Data largely from Weislo (1996). Replicates are individual bee species across many studies. In some cases multiple records of the same bee species are included, but are from different studies, or different years in the same study.

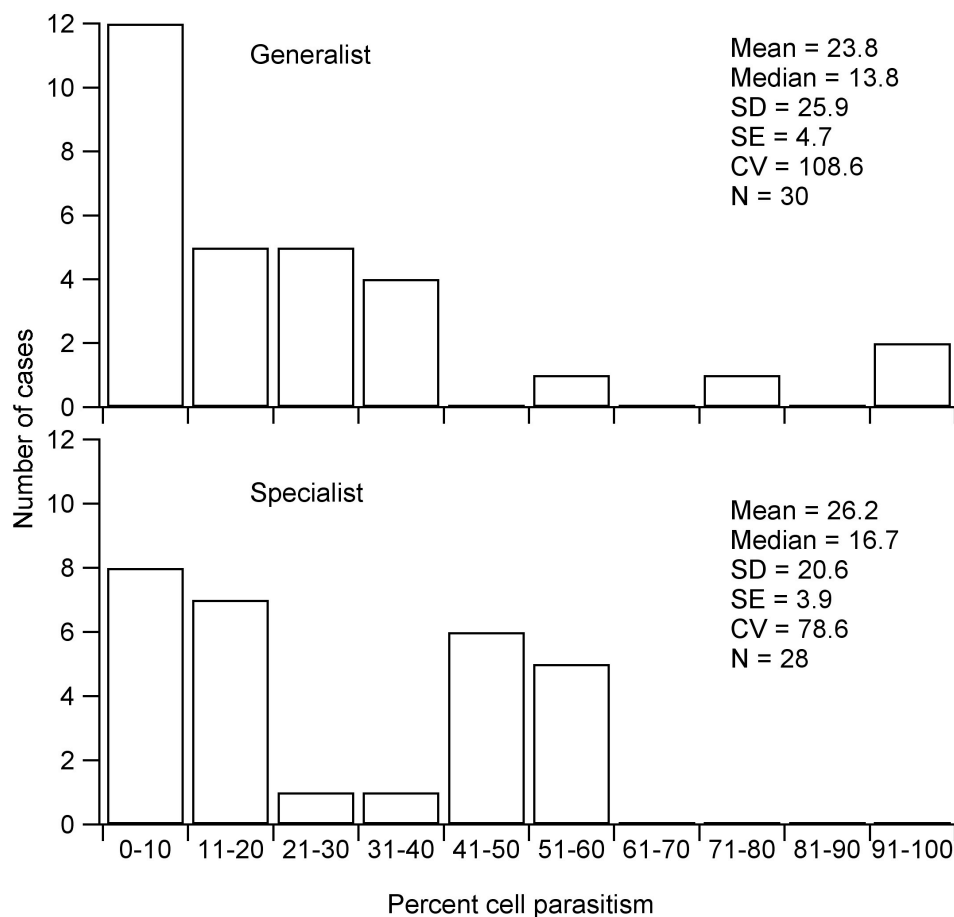


Figure 4. Variation in diversity of meloid beetle species (parasites of bees) among plant species. Individual plant species are replicates in this analysis. Data from Erickson et al. (1976). Many bars in figures below have sample sizes of one, thus no error estimate available. Ann/per, plant species that can be either annual or perennial, depending on conditions. Zyg:Zygophyllaceae, Ast:Asteraceae, Cap:Capparaceae, Pol:Polemoniaceae, Cel:Celastraceae, Chen:Chenopodiaceae, Euph:Euphorbiaceae, Fab:Fabaceae, Fra:Frankeniaceae, Lam:Lamiaceae, Loas:Loasaceae, Malv:Malvaceae, Pap:Papaveraceae, Poa:Poaceae, Port:Portulaceae, Ros:Rosaceae, Sol:Solanaceae, y:yellow, r:red, p:purple, w:white, b:blue, o:orange.

