



POLLINATORS, HERBIVORES, AND PLANT NEIGHBORHOOD EFFECTS

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ABSTRACT

Pollinator and herbivore interactions with individual plants can be strongly influenced by the densities and frequencies of other plants in local neighborhoods. The importance of these neighborhood effects is not yet clear, due in part to a profound disconnect between studies of pollinator and herbivore neighborhood effects. Considering these effects jointly is critical for understanding the role of plant spatial heterogeneity because plant fitness is often affected by pollinators, herbivores, and their interactions. We bring together these two types of neighborhood effects, describing the pathways through which these insects mediate neighborhood effects, and comparing their implementation in mathematical models. We find that ideas from

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each field can improve work in the other. For example, pollinator theory should broaden consideration of how pollinator traits influence responses to plant neighborhoods, while herbivore theory should consider adaptive foraging and connect herbivore neighborhood effects to plant fitness. We discuss approaches to theory that integrate pollinator and herbivore effects, particularly considering the nested spatial and temporal scales of these insects' responses to neighborhoods. Ultimately, models will need to combine neighborhood effects from the diverse species that affect plants with direct plant interactions to determine the importance of spatial structure for plant performance and evolution.

INTRODUCTION

THEORETICAL and empirical work has demonstrated that local plant spatial structure can influence the outcome of plant competition and the evolution of plant traits (Harper 1977; Stoll and Weiner 2000) because plant neighbors can strongly influence each other's fitness. Both pollinators and herbivores can also influence plant population growth and evolution, and the strength of these consumer interactions with individual plants can also be influenced by plants growing nearby (e.g., Waddington and Holden 1979; Underwood et al. 2014). For example, neighborhood effects on pollination may influence the evolution of floral traits (e.g., Caruso 2002; Thomson et al. 2019) or neighborhood effects on herbivory may alter the outcome of plant competition (e.g., Kim and Underwood 2015), creating feedbacks between current and future composition of plant neighborhoods (Stastny and Agrawal 2014; Underwood et al. 2014). Because of the great variety of potential mechanisms for neighborhood effects, researchers have hypothesized everything from positive to negative effects

on plant fitness (Table 1). In contrast to plant competition, which occurs primarily at the scale of immediate neighbors, per capita herbivory and pollination rates can change with plant density and frequency in neighborhoods at spatial scales well beyond immediate neighbors (Antonovics and Levin 1980; Barbosa et al. 2009; Mitchell et al. 2009; Underwood et al. 2014). Due to the logistical difficulty of measuring population dynamics and evolution in the field, empirical studies of neighborhood processes have focused mainly on per capita interaction strengths, such as pollinator-mediated selection (e.g., Gigord et al. 2001) or herbivory rates (Barbosa et al. 2009), while the population-level consequences of herbivore and pollinator neighborhood effects have primarily been addressed with mathematical models.

In this paper we compare pollinator- and herbivore-mediated neighborhood effects as a step toward addressing the question of when plant spatial structure matters for plant population dynamics and evolution. Our focus on pollinators and herbivores is motivated by the fact that these groups typically

TABLE 1
Effect of neighboring plants on focal plant species or genotype

Insect type	Positive (+)	Negative (-)
Herbivore	1. Associational resistance (effect of heterospecific neighbors)	2. Associational susceptibility (effect of heterospecific neighbors)
	3. Resource dilution (effect of conspecific neighbors)	4. Resource concentration (effect of conspecific neighbors)
Pollinator	5. Magnet plants (effect of heterospecific neighbors)	6. Interspecific pollen transfer (effect of heterospecific neighbors)
	7. Pollinator facilitation (effect of heterospecific or conspecific neighbors)	

Although pollinators have positive effects on plant fitness and herbivores have negative effects on plant fitness, neighborhood effects mediated by pollinators and herbivores have been hypothesized to be both positive and negative, depending on the particular mechanisms involved. Here we list some examples of named hypotheses for positive and negative effects: 1. Tahvanainen and Root (1972); 2. Letourneau (1995); 3. Cromartie (1975); 4. Root (1973); 5. Thomson (1978); 6. Levin and Anderson (1970); 7. Schemske (1981). Additional mechanisms have been considered in the literature (see Barbosa et al. 2009, Mitchell et al. 2009, and Underwood et al. 2014 for reviews).

have contrasting fitness effects (primarily positive versus primarily negative), while at the same time responding to and affecting plants through the same basic steps: plants influence pollinator or herbivore numbers or behavior, and herbivores and pollinators may influence plant-per-capita fitness. For example, the density or frequency of a neighboring plant species might influence future densities of a focal plant species by affecting how often herbivores find and damage the focal plant (Barbosa et al. 2009) or how frequently its flowers receive appropriate pollen (Morales and Traveset 2008). Progress toward integrating pollinator and herbivore neighborhood effects in models has been limited because studies of pollination, herbivory, and other processes (such as plant competition) typically engage different researcher communities, resulting in separate development of theory. We argue that further theoretical and empirical work would benefit from crosstalk and integration among the fields. In particular, we need to understand how differences in pollinator and herbivore biology, such as mobility, diet breadth, or ability to learn, may translate to differences in the strength, direction, or scale of their neighborhood effects.

Recognizing commonalities and differences in the mechanisms that create pollinator and herbivore neighborhood effects will help build a more general understanding of the consequences of plant spatial structure, and is of practical as well as fundamental importance. Agriculture and silviculture both manipulate plant neighborhoods as a form of pest control (Cook et al. 2007), and agriculture uses plant neighborhoods to increase crop pollination (e.g., Blaauw and Isaacs 2014). Even though many empirical studies find neighborhood effects on individual-level damage or pollination rates for agricultural species, our understanding of how and when these translate to increased yield at larger scales is limited. Similarly, impacts of invasive plants on native plants can be mediated by pollinator or herbivore responses to local plant densities or frequencies (Brown et al. 2002; Flanagan et al. 2010; Dietzsch et al. 2011; Bruckman and Campbell 2016), but we do not have a full understanding of when

these effects are likely to be positive or negative (Charlebois and Sargent 2017).

In this review, we compare neighborhood effects mediated by insect herbivores and pollinators, while keeping in mind that other types of organisms (e.g., pathogens: Smithson and Lenne 1996; soil organisms: Bever et al. 1997; mammals: Rautio et al. 2012 and Champagne et al. 2018; and birds: Nottebrock et al. 2017) can also mediate plant-plant interactions and should be considered in future work. To be precise, when we refer to “pollinators” we mean insects that deliver enough pollen to plants to be considered mutualists in most situations, and by “herbivores” we mean insects that have primarily negative effects on plants through consumption of plant tissue. We first lay out the similarities and differences in the pathways through which insect pollinators and herbivores mediate effects of plant neighborhoods on plant fitness, drawing on the empirical literature for examples. We then focus on the treatment of these pathways in models of pollinator and herbivore neighborhood effects and, finally, consider what these differences suggest for future work in each field and for the ultimate goal of integrating different types of neighborhood effects.

EFFECTS OF PLANT SPATIAL STRUCTURE ON POLLINATOR AND HERBIVORE INTERACTIONS WITH PLANTS: SIMILARITIES AND DIFFERENCES

Insect herbivore and pollinator interactions with plant neighborhoods could influence plant populations through similar pathways (Figures 1A and 1B), where individual insect responses to local plant density and frequency are influenced by fixed traits, plastic traits, and features of the environment that change based on plant neighborhood composition. Examples of relatively fixed traits that can affect insect movement include constitutive defenses, floral traits such as color or architecture, or insect abilities to perceive visual versus olfactory cues (e.g., Holt 1984; Pfister and Hay 1988; Hambäck et al. 2003). Examples of insect traits that change with plant neighborhoods include preference hierarchies that change with plant frequency (e.g.,

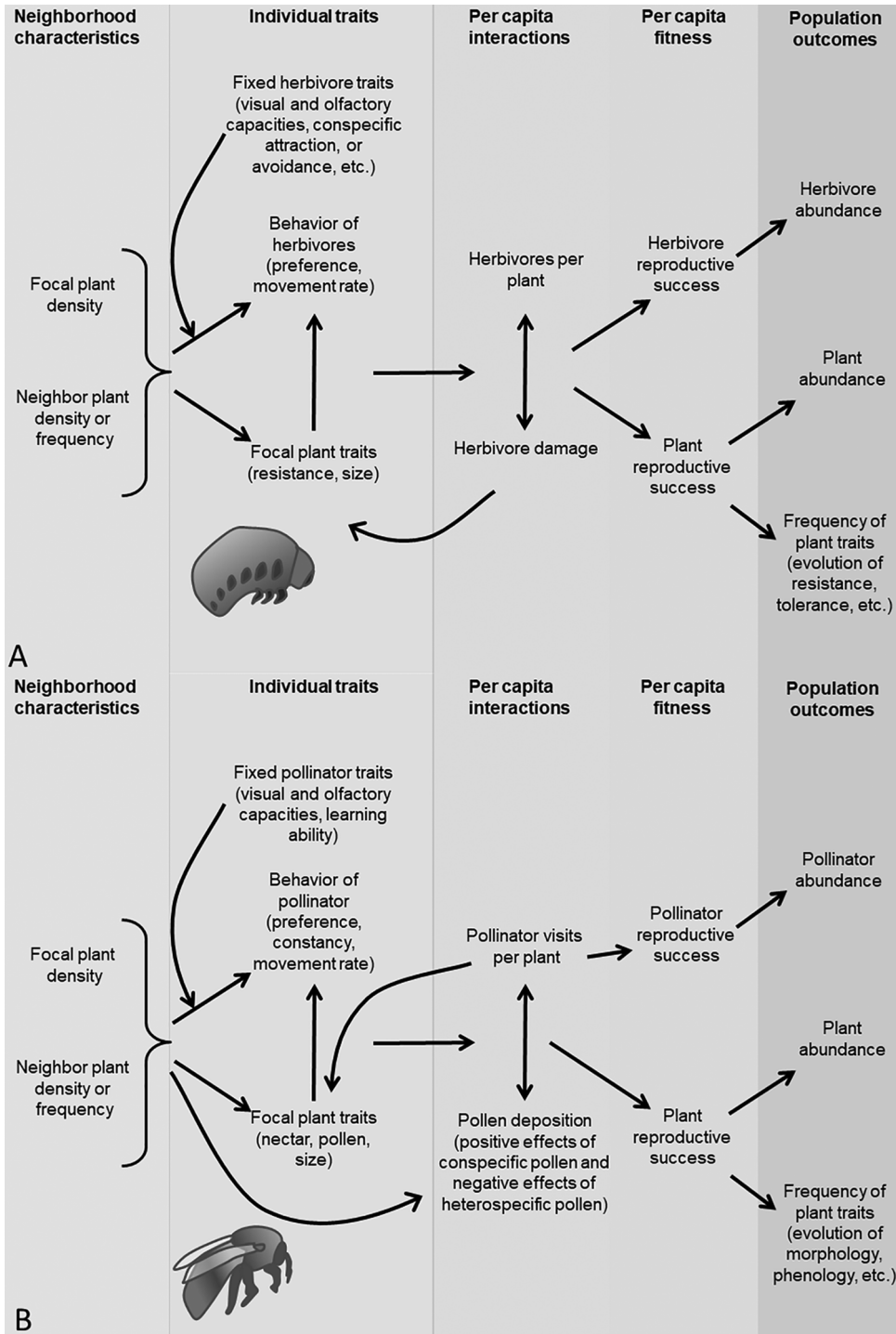


FIGURE 1. PATHWAYS FOR NEIGHBORHOOD EFFECTS

Potential mechanisms for plant neighborhood effects on insect and plant population processes, as estimated through per capita effects mediated by herbivores (A) and by pollinators (B). Plant neighborhoods are

Smithson and Macnair 1996; Hersch and Roy 2007), and movement behaviors that change with plant density (Morris 1993; Altizer et al. 1998). Plant neighborhoods can also change plant traits, including defenses, nutrient composition, floral display, and reward investment (e.g., Koricheva et al. 1998; Cipollini and Bergelson 2001; Burkle and Irwin 2010), and neighbors can influence the microclimate on or near a plant (Kim 2017). There can also be feedbacks between plant-insect interactions and plant traits, such as when damage by herbivores induces plant resistance (Karban and Baldwin 1997) or when pollinators deplete nectar or pollen and thus influence resources for other pollinators (e.g., Schaffer et al. 1983). These effects of plant neighborhoods result in changes in per capita interactions, such as numbers of insects or visits per plant, damage levels, or pollination rates; per capita interactions may change population-level outcomes, including plant population size or genetic composition and pollinator and herbivore population size (e.g., Gigord et al. 2001).

Despite these broad similarities, there are several key differences in how pollinators and herbivores are expected to mediate effects of plant neighborhoods on plant fitness. Most obviously, pollinators increase plant fitness, so many flowers have traits to attract pollinators, whereas herbivores generally decrease plant fitness and many plants have traits that reduce interactions with herbivores. Flowers typically provide conspicuous visual cues, so we expect pollinators to respond strongly to them (with the caveat that floral scents have until recently been less widely studied than floral display). In contrast, herbivores have long been known to rely on volatile compounds at long ranges and other cues at short ranges (e.g., Schoon-

hoven et al. 2005). Although many herbivores also use visual cues and pollinators also use olfactory cues (e.g., Larue et al. 2016; Lawson et al. 2017), we expect pollinators to more commonly rely on visual cues than herbivores. Because of differences in how visual and olfactory cues are perceived at a distance, visually and olfactorily guided insects should differ in their response to plant neighborhoods (Hambäck and Beckerman 2003; Hambäck and Englund 2005; Hambäck et al. 2014).

Traits related to diet breadth and learning may also differ between pollinators and herbivores and influence their responses to local plant density and frequency. Although there is variation in diet breadth for both groups, the proportion of specialists tends to be higher among herbivores than among pollinating insects (Fontaine et al. 2009). This implies that plant neighborhoods commonly include alternative resources for pollinators (although even generalists can be functional specialists at times), while containing mainly nonhosts for herbivores. Pollinators might therefore respond to the total resources provided by the plant community, while herbivores may be more strongly influenced by the identity of particular plants. Pollinators are also more likely to use learning to adjust their foraging (Bernays 2001; Jones and Agrawal 2017), resulting in a larger potential for change in their responses to plants within a season. For instance, pollinators often exhibit floral fidelity or constancy (Thomson 1981a), which is the tendency of a pollinator to make repeated visits to the same type of plant (species or morph) within a foraging bout and thereby to be a facultative specialist. Pollinator preferences and floral fidelity could be influenced by plant neighborhoods, for example, if pollinators are most faithful to the most frequent plant species (see Schmid

described in terms of the densities and frequencies of “focal” and “neighbor” plants. As the majority of empirical studies of insect-mediated neighborhood effects focus on interactions between plant species, “focal” plants would most often be some plant species of particular interest, while “neighbor” plants would be species other than the focal species. However, it is important to bear in mind that neighborhoods could alternately be described in terms of distributions of plant phenotypes or genotypes. Densities may be best measured in terms of individuals or biomass, depending on the natural history of the species. Mechanisms may directly cause neighborhood effects or modify the effect of another mechanism. See the online edition for a color version of this figure.

et al. 2016 for a discussion of this phenomenon in pollinating birds). Plant constancy and learning have rarely been investigated in herbivores, which are instead assumed in neighborhood models to have fixed preference hierarchies over short time scales (Wiklund 1974; Thompson 1993), although there is some evidence that larval experience with one plant may influence host plant preference in adults or across generations (referred to as Natal Habitat Preference Induction; Davis and Stamps 2004) or Hopkins' Host Selection Principle (Hopkins 1917; e.g., Lhomme et al. 2018).

Pollinators are on average more mobile than herbivores, in terms of both frequency and distance of moves among plants, due to the need to visit multiple flowers and plants to gather sufficient resources (pollen or nectar). On the other hand, insect herbivores can often complete development on a single plant. Although pollinators are usually capable of flight, insect herbivores often interact most strongly with plants while in the larval stage, with their location largely determined by adult oviposition. Thus, we expect pollinators to mediate neighborhood effects at larger spatial scales than herbivores, although the mobility of both insect herbivores and pollinators varies greatly among species. As few studies have attempted to measure scales of insect-mediated neighborhood effects (e.g., Thomson 1981b; Johnson et al. 2003; Lachmuth et al. 2018), it is not clear in general how neighborhood effects change with scale or how they differ between types of insects; previous studies mostly consider only one or a few spatial scales. It might seem that neighborhood effects should be strongest at the smallest possible spatial scales (i.e., immediate neighbors) and decline in strength with distance from a focal plant, but some studies have found that neighborhood effects are actually stronger at larger scales (Johnson et al. 2003; N. Underwood and B. D. Inouye, unpublished data), and can even reverse sign between scales (Hegland 2014; Charlebois and Sargent 2017). Future studies should quantify plant communities and collect data on interaction strengths of plants with pollinators and herbivores over a range of spatial scales. Spatially explicit data on responses

such as pollination rates, damage rates, and plant fitness could be used to characterize neighborhood effects at multiple scales in natural or experimental populations, given sufficient variation in neighborhood composition. To our knowledge, no study has yet compared the scale of neighborhood effects for pollinators and herbivores in the same system.

Differences in mobility also affect how pollinators and herbivores interact with plant resources. For pollinators, plant resources (pollen and nectar) are dynamic at the same time scale as foraging decisions. Every visit by a pollinator depletes pollen and/or nectar, making individual flowers less profitable for subsequent visits, yet nectar (and sometimes pollen) can also replenish. Although herbivores can also influence the quantity and quality of their resource (Morris 1997), for example, through induced resistance, this seldom happens at the time scale of foraging decisions. As a result of experiences with multiple flowers in a short time, or repeated visits along a trapline (Ohashi and Thomson 2009), pollinators can have dynamic foraging choices, either increasing or decreasing constancy and preference for particular flower types and thus the strength of frequency dependence in plant performance. Herbivores are less likely to be able to use familiarity with individual plants in their foraging as they move among plants less often. Many herbivores respond to the plant neighborhood when ovipositing, but then larvae move little or not at all among plants, making their feeding behavior less responsive to rapid changes in neighborhood properties. Some generalist and highly mobile herbivores (e.g., grasshoppers and whiteflies) could be exceptions to this pattern (Bernays et al. 1994).

Finally, a major difference between herbivory and pollination is that for plants that require outcrossed pollen, the value of a pollinator visit depends critically on which plants the pollinator has visited recently, whereas the order of visits to plants is largely irrelevant for the fitness impacts of herbivore damage. Pollen from a conspecific can lead to seed production, but heterospecific pollen may be of no value or can have a negative effect through stigma clogging (Waser and

Fugate 1986; Galen et al. 1989), allelopathy (Morales and Traveset 2008), or pollen discounting (Holsinger et al. 1984). The average value of pollen arriving at a particular flower can thus depend on the frequency of different plant species or morphs in the population. As a plant type becomes more frequent in its neighborhood, even random pollinator movements are more likely to confer effective pollination, causing positive frequency dependence in plant fitness (indicated by the arrow in Figure 1B directly linking plant neighborhood characteristics to pollen deposition, bypassing pollinator behavior; Levin and Anderson 1970).

There are potentially important pathways that are not included in Figure 1 because they have so far received little attention in models of neighborhood effects; they should be considered in future work. Feedbacks between current densities and frequencies of plants and the composition of future plant neighborhoods have not yet been fully demonstrated, but there is evidence that they are likely (Stastny and Agrawal 2014). It has also often been suggested that neighborhood effects can be mediated by predators (the “enemies” hypothesis) when predator abundance or effectiveness change with plant density or frequency (Elton 1958; Stiling et al. 2003). Pollinators and herbivores can also respond to plant diversity rather than the presence or frequency of particular plants (e.g., Bernays 1999; Hegland and Boeke 2006). Finally, insect population densities could influence how individual insects respond to plant neighborhoods (e.g., Thomson et al. 1987; Brosi and Briggs 2013); although some models of pollinator neighborhood effects consider the influence of variation in total pollinator density (e.g., Kunin and Iwasa 1996; Hanoteaux et al. 2013), studies of herbivore neighborhood effects have generally not considered the potential effect of average herbivore density on herbivore behavior (but see Merwin et al. 2017 for an empirical example). For herbivores with rapid generations and that move among nearby plants (i.e., aphids), herbivore loads on individual plants can be influenced by plant neighborhood effects on herbivore population dynamics (Underwood 2004, 2009).

THEORY FOR POLLINATOR AND HERBIVORE NEIGHBORHOOD EFFECTS

General ecological theory describes how variation in plant density and frequency can influence population dynamics and species persistence; negative density dependence affects equilibrium population size and the coexistence of competing species, negative frequency dependence (i.e., per capita performance declining with frequency) contributes to the coexistence of competing species (Barabás et al. 2018) or genotypes (Lively and Howard 1994), and positive frequency dependence destabilizes systems and contributes to exclusion of rare species unless there is persistent spatial patterning in a landscape (Molofsky et al. 2001). Models specifically addressing the contribution of insect-mediated neighborhood effects to plant population dynamics and evolution build upon general theory by including some reference to spatial structure, specifying how plant composition (density and/or frequency) in physical neighborhoods interacts with insect traits to influence interaction intensities with plants. In this section, we describe general ecological theory that has contributed important ideas to neighborhood models, outline the basic components of neighborhood models, and review key papers in the historical development of neighborhood models for plant-herbivore and plant-pollinator systems. These models have addressed a variety of questions, collectively providing a growing library of approaches. In Table 2 we summarize the basic features (structure, response variables, and mechanisms of neighborhood effects) of all insect-mediated neighborhood models of which we are aware. Network models were not included in this review primarily because none have yet addressed insect-mediated neighborhood effects, but also because network models are not the best tool for connecting individual-level traits or fitness with population-level consequences.

FOUNDATIONAL IDEAS FROM NONNEIGHBORHOOD MODELS

Several studies have provided crucial insights and mathematical building blocks for

TABLE 2
*A summary of the key features of mathematical and simulation models
of insect-mediated neighborhood effects*

Model	Structure		Primary response variables	Mechanisms generating neighborhood effects				Mechanisms modifying neighborhood effects		
	1	2	3	4	5	6	7	8	9	10
	Consumer type	Neighborhood structure	Primary response variables	Requirement for intraspecific pollen	Resource dynamics	Adaptive foraging	Unspecified behavioral response to neighborhood	Constancy	Preference	Pollen carryover
Levin and Anderson (1970)	P	Well mixed	Plant frequency	•			•	•	•	
Straw (1972)	P	Well mixed	Plant frequency	•			•	•		
Bobisud and Neuhaus (1975)	P	Well mixed	Per capita effects	•			•	•		
Waser (1978)	P	Explicit	Plant density	•	•					•
Fowler and Levin (1984)	P	Well mixed	Plant density	•				•		
Goulson (1994)	P	Well mixed	Per capita effects	•	•	•		•	•	
Kunin and Iwasa (1996)	P	Well mixed	Plant frequency	•	•				•	
Ishii and Higashi (2001)	P	Well mixed	Plant density	•						•
Feldman et al. (2004)	P	Implicit	Plant density	•			•			•
Sargent and Otto (2006)	P	Well mixed	Genotype frequency	•						
Rodriguez-Gironés and Santamaría (2007)	P	Explicit	Plant frequency	•	•				•	
Montgomery (2009)	P	Well mixed	Per capita effects	•				•		•
Tachiki et al. (2010)	P	Implicit	Per capita effects	•			•			
Hanoteaux et al. (2013)	P	Explicit	Plant density	•	•		•	•	•	
Song and Feldman (2014)	P	Well mixed	Plant density	•					•	•
Mesgaran et al. (2017)	P	Implicit	Plant density	•	•		•			
Qu et al. (2017)	P	Explicit	Plant density	•	•				•	•
Benadi and Gegeer (2018)	P	Explicit	Per capita effects	•	•	•			•	•
Turchin (1991)	H	Explicit	Per capita effects				•			
Tuomi and Augner (1993)	H	Well mixed	Genotype frequency				•		•	
Tuomi et al. (1994)	H	Well mixed	Genotype frequency				•		•	
Leimar and Tuomi (1998)	H	Well mixed	Genotype frequency			•			•	
Orrock et al. (2010b)	H	Implicit	Plant density		•	•			•	
Orrock et al. (2010a)	H	Explicit	Plant density		•	•			•	
Hambäck et al. (2014)	H	Implicit	Per capita effects				•		•	

Models address either herbivores (Consumer type = H) or pollinators (Consumer type = P), are spatially explicit, spatially implicit, or represent single well-mixed populations, and target effects on a range of plant variables. The key mechanisms included in models are separated between those that directly cause neighborhood effects and those that modify those effects. See the text for additional column heading explanations.

constructing models of neighborhood effects. The general insight that density and frequency dependence are important for population dynamics and evolution comes from a large body of theory that has no defined spatial structure; it assumes that all individuals interact with all others (“well-mixed” populations) and population regulation occurs at the same spatial scale for all species. Models of apparent competition or facilitation, which describe how consumer population growth mediates indirect interactions between two resource species (Holt 1977; Kuang and Chesson 2010), clearly resemble insect-mediated neighborhood effects between plants. However, these are poor matches for neighborhood effects via most insect herbivores and pollinators because of the assumptions that consumers and resources have population dynamics at the same temporal and spatial scales, that interactions are random (species are well mixed), and that plant populations are limited by only a single consumer species. Due to their mobility, insects (particularly pollinators) will often have population dynamics regulated at a spatial scale well beyond a local plant neighborhood, and few plant populations rely on a single pollinator species for reproduction, or are only damaged by a single herbivore species.

Nonneighborhood models have contributed mathematical machinery for representing the consumer movement that allows for insect-mediated neighborhood effects. Optimal foraging models introduced the idea that consumers change behavior based on resource abundances when foraging within patches of heterogeneous resources (e.g., Holt and Kotler 1987), a framework that may be appropriate for insects such as bees that can have good spatial memories. For other insects, a more appropriate behavioral framework is area-restricted search. Kareiva (1982) and Turchin (1991) showed that plants can affect insect movement parameters such as step length and turning angles, thus influencing herbivore distributions. Area-restricted search models do not specify a neighborhood structure, yet they describe how host plant density affects herbivore densities when within-patch processes dominate distributions. Hambäck and Englund (2005) initiated

a set of models where the emphasis was on the probability of finding resource patches in relation to patch properties (size and geometry), instead of on responses after entering a patch. These models focused on the effect of density of a single plant type, and their main innovation was to model insect densities as resource-dependent scaling of patch finding and leaving. This led to the insight that responses to plant cues will depend on the search mode of the insect (visual or olfactory; see also Capman et al. 1990).

NEIGHBORHOOD MODELS: BASIC COMPONENTS

The spatial structure necessary to model local neighborhood effects can be included in models of interactions between insects and plants in three general ways (Table 2, column 2). At one extreme are models of well-mixed plant populations that imply a local neighborhood by explicitly modeling only plant population dynamics or evolution, making insect population regulation occur outside the scale of the plant population. These models differ from apparent competition by assuming that individual pollinators or herbivores arrive from an external pool and then move among all plants. This assumption implies a relatively small spatial scale for the plant populations, i.e., a single type of plant neighborhood that is the same for all plants. Neighborhood effects can be included phenomenologically in this type of model, without specifying their spatial extent.

At the other extreme are spatially explicit models where individual plants and insects have specific locations and only interact with nearby individuals, thus individual plants can have unique neighborhoods (e.g., Orrock et al. 2010a; Benadi and Gegeer 2018). This approach is more akin to work on plant competition and facilitation that has acknowledged the importance of local neighborhoods for decades (Harper 1977), and has focused on spatially explicit plant neighborhoods (reviewed in Stoll and Weiner 2000). In between well-mixed and spatially explicit models are spatially implicit models that consider interactions at the scale of neighborhoods, but allow neighborhoods within a

larger population to contain different densities or frequencies of species and/or model movement of insects among neighborhoods (e.g., Feldman et al. 2004; Tachiki et al. 2010).

The type of spatial structure influences the scales of interaction that a model can address. Models lacking spatial structure (implying the existence of the neighborhood only by leaving out insect population dynamics) consider the behavior of consumers within the neighborhood, but cannot include neighborhood effects on the number of consumers arriving to the neighborhood. Models with spatial structure (implicit or explicit) may consider how the plant neighborhood influences the rates at which consumers find and remain within neighborhoods (immigration and emigration), thus affecting the density of interacting consumers. Models that address insect immigration and emigration often use the terminology “patch,” referring to some visible area of higher density of a focal plant or set of plants; a patch could contain multiple scales of neighborhoods.

Models have so far included seven basic types of mechanisms for insect-mediated neighborhood effects (in italics below): four that generate (Table 2, columns 4–7) and three that modify (Table 2, columns 8–10) neighborhood effects. The requirement for *intraspecific pollen transfer* creates positive frequency dependence for plant fitness (Levin and Anderson 1970) because random pollinator movements are more likely to be between individuals of the same species when a species is more common. This frequency dependence contributes to the exclusion of rare species. *Dynamic changes in resources* provided by a plant, such as pollen or nectar, can also generate neighborhood effects that are not observed in models with fixed resource availabilities (e.g., Waser 1978). *Adaptive foraging* can create nonlinear density dependence (Goulson 1994) or other types of neighborhood effects (Leimar and Toumi 1998). Some models assume *unspecified behavioral responses to plant neighborhoods* by simply including a mathematical function relating per capita interactions and plant density or frequency; these relationships can have a range of functional forms (e.g., Hanoteaux et al. 2013; Hambäck et al. 2014). *Pollinator*

constancy alleviates the positive frequency dependence created by a need for intraspecific pollen transfer by increasing the proportion of consecutive visits to the same plant type even when a plant type is rare. Constancy can also weaken density dependence if pollinators continue to visit a single plant type even when it is rare (e.g., Hanoteaux et al. 2013). *Preference* can similarly alter the strength of neighborhood effects by changing the “effective frequency” of plant types; preferred plants are visited at a higher rate, effectively acting as if they were more frequent in a neighborhood. When assumed to have a constant value, the effect of consumer preference is a simple linear modification of the strength of other mechanisms that generate neighborhood effects, whereas constancy creates a nonlinear modification of neighborhood effects because it concerns pairs of consecutive visits to plant types (compare Figures 1 and 2 in Levin and Anderson 1970). Like constancy, *pollen carryover* reduces the strength of positive frequency dependence generated by the need for intraspecific pollen because nonconsecutive visits can still result in pollination (e.g., Waser 1978; Feldman et al. 2004).

THE DEVELOPMENT OF NEIGHBORHOOD MODELS FOR POLLINATORS AND HERBIVORES

Pollination biologists have noted for over 100 years that competition for pollen between nearby plants should influence plant abundances and evolution (reviewed in Mitchell et al. 2009; Charlebois and Sargent 2017), but formal mathematical models of pollinator-mediated neighborhood effects began with the key work by Levin and Anderson (1970). They analyzed effects of pollinators on plant coexistence and included not only the odds of intraspecific pollen transfer, but also the idea of pollinator constancy. Levin and Anderson (1970) established a pattern for subsequent models of pollinator neighborhood effects by introducing the connection between intraspecific pollen transfer and positive frequency dependence, and asking whether additional mechanisms can prevent the exclusion of rare species or affect floral trait evolution. Levin and Anderson

(1970) also explored the effects of preference for one plant over another, a type of behavior that occurs for both pollinators and herbivores.

Levin and Anderson's analytical model of pollinator effects was transferred into a spatially explicit simulation context by Waser (1978). Waser's model repeated prior results that positive frequency dependence due to interspecific pollen transfer can rapidly cause exclusion of rare plant species. Waser did not include preference or constancy, but introduced another pollinator-specific mechanism: pollen carryover beyond consecutive visits. Waser (1978) was also the first to add dynamic effects of pollinator visits on the resources they collect. In this model pollen can be depleted and stigma surfaces can be filled, so that resource dynamics amplify the negative effects of interspecific pollen transfer on plant fitness. Kunin and Iwasa (1996) considered the dynamics of pollinator visits and nectar resources, which (unlike stigma surfaces) can be replenished on a fast time scale (see also Goulson 1994). By including adaptive foraging responses to nectar quantity, Kunin and Iwasa (1996) found density and frequency dependence in pollinator preference for different plant types, which caused complex forms of density and frequency dependence in plant fitness. They also found, not surprisingly, that the risk of interspecific pollen transfer, and thus the strength of frequency dependence in plant fitness, is reduced when pollinators specialize on a rarer plant. Models drawing on the same four basic types of neighborhood effects have also considered how neighborhood effects influence the evolution of floral traits; these models suggest that pollinator neighborhood effects should influence the evolution of floral specialization through both floral traits and flowering phenology (e.g., Sargent and Otto 2006; Rodríguez-Gironés and Santamaría 2007). Although most pollination models focus on interactions between two rewarding plant species, Qu et al. (2017) considered effects of rewarding species on the pollination of a nonrewarding (deceptive) species.

Spatially implicit and explicit models of pollinator neighborhood effects became more common in the 2000s. Feldman et al. (2004)

used a spatially implicit patch model to consider what happens when pollinator abundance responds to total flower density in a patch. In addition to the established positive frequency dependence of intraspecific pollen receipt, Feldman et al. found that sigmoidal responses of pollinator abundance to total flowers increased pollination of rare species, making plant coexistence more likely because other flowers can facilitate pollination of rare types. Tachiki et al. (2010) similarly found that plant facilitation was possible when pollinators respond to total flower density, or when pollinator density is an accelerating function of total patch attractiveness. This idea that pollinator responses to neighborhood flower density could result in facilitation between plants was further explored by Mesgaran et al. (2017), again in a model with implicit spatial structure. The main innovation in Mesgaran et al. (2017) was to separate the effects of plant competition for abiotic resources from competition for pollinators, by including a plant's attractiveness to pollinators separately from its density. This is an important step toward integrating competition and neighborhood effects to determine net positive or negative effect on plant performance. Hanoteaux et al. (2013) used a spatially explicit individual-based simulation model to point out that the distribution of neighborhood types can also affect regional population dynamics. In this model, intraspecific spatial aggregation of a less attractive plant (i.e., when present it is overrepresented) can facilitate its own pollination, particularly if pollinators make short moves between plants and have small fields of perception and thus fail to notice more attractive plants outside an aggregation of less attractive plants.

Two final factors considered in models of pollinator neighborhood effects are interactions among multiple pollinator types and pollinator density. For example, foraging behavior by generalist pollinators may be altered by the presence of specialists because this changes the expected rewards from different flower types (Kunin and Iwasa 1996; Valdovinos et al. 2013). A generalist pollinator might effectively have constancy for a single flower type by avoiding flowers heavily

visited by specialist pollinators (Song and Feldman 2014). This type of competition-induced niche shift, which can affect pollination success, has been observed in bumble bees (Inouye 1978; Brosi and Briggs 2013). Several models also show that regional pollinator density should modify neighborhood effects on pollination or plant fitness (e.g., Kunin and Iwasa 1996; Feldman et al. 2004; Tachiki et al. 2010).

The development of theory for herbivore neighborhood effects has taken a different path. Early influential verbal theory for plant neighborhood effects came from Root's work on plant patches, where he coined the terms "associational resistance" (Tahvanainen and Root 1972) and the "resource concentration hypothesis" (Root 1973). Although there is a long history of empirical work on herbivore neighborhood effects, motivated by observations of lower herbivore density and damage in mixed plant communities or larger plant patches, and by interest in using plant mixtures to reduce damage by crop pests (e.g., Andow 1991; Smithson and Lenne 1996), the development of formal mathematical structures lagged. Because of the positive frequency dependence created by intraspecific pollen receipt, many researchers modeling pollinator neighborhood effects have focused on the conundrum presented by the long-term persistence of rare plant species. Rather than long-term persistence, most studies of herbivore neighborhood effects have emphasized the short-term effects of plant density on damage or herbivore loads. This is despite the fact that insect herbivores can affect plant population dynamics (e.g., Kim et al. 2013; Schultz et al. 2017).

Because work on herbivore-mediated neighborhood effects has emphasized the role of short-term behavioral responses, a logical starting point for models was area-restricted search (summarized above in the section titled Foundational Ideas From Nonneighborhood Models). Hambäck et al. (2014) extended this approach to directly involve the neighborhood effects that arise from mixed plant communities containing different total plant densities and frequencies, where patch finding, host switching within patches, and patch leaving depend on the scaling of plant

cues and on consumer preferences. This model and Hambäck and Englund (2005) both indicate that the strength and even the sign of the effects of plant density and frequency in a neighborhood depend on how insects perceive plants and plant patches; to our knowledge these are the only models to consider how insect perception influences neighborhood effects. In addition to models describing how neighborhood effects on herbivores per plant arise from insect search behavior, models have addressed the evolutionary and ecological consequences of herbivore neighborhood effects for plant populations. Models by Tuomi and colleagues (Tuomi and Augner 1993; Tuomi et al. 1994) showed that frequency dependence in herbivore attack rates on plants with different levels of resistance influences the evolution of plant resistance. Among the few studies of herbivore neighborhood effects that consider population dynamics, two by Orrock et al. (2010a,b) used spatially implicit models to show that the spatial scale of consumer behavior relative to the spatial area over which plants compete can affect the outcome of plant competition.

FUTURE DIRECTIONS

Given the broad similarities between pollinator- and herbivore-mediated neighborhood effects, it is striking how little contact there has been between these fields, either empirically or theoretically. Models of pollinator and herbivore neighborhood effects essentially never reference each other; only one model (Feldman et al. 2004) cites theory developed for the other type of consumer. Similarly, although many empirical studies document neighborhood effects on pollinators or herbivores, almost no studies have measured these two effects together (but see Andersson et al. 2016), even though herbivores and pollinators can jointly affect plant fitness (e.g., Strauss 1997; McCall and Irwin 2006). Theory for both types of neighborhood effects would be improved by drawing on the differing strengths of both fields. A range of theoretical approaches have been used, including game theory, adaptive dynamics models, coupled differential equations,

and spatially explicit simulations. In general, models of neighbor effects suggest that local density and frequency dependence in consumer–resource interactions should be common and influence population and evolutionary dynamics, but models so far have not addressed nonlinear and spatially explicit frequency dependence in neighborhood effects. Ultimately, integrating pollinator and herbivore effects (as well as those of other organisms that affect plant fitness) into more general models of neighborhood effects will be necessary for a more complete understanding of the function of spatial structure in plant communities.

EXTENDING MODELS FOR HERBIVORES AND POLLINATORS

Connecting neighborhood effects to plant fitness is a logical starting point for the extension of herbivore neighborhood models. Although it is often suggested that herbivore neighborhood effects should influence plant populations (e.g., Atsatt and O’Dowd 1976; Thomas 1986; Pfister and Hay 1988; Russell and Louda 2005), most herbivore models stop at per capita interactions (Figure 1A; Table 2). The focus of pollination neighborhood models on population outcomes is a reminder that herbivore neighborhood models could be extended to include effects on plant fitness, plant population size, and plant genetic or community structure.

Herbivore neighborhood models can also be improved by including two mechanisms for neighborhood effects that pollinator models have found to be important: dynamic foraging behaviors/learning and effects of consumer density. Pollinator neighborhood models show that adaptive foraging, constancy, and variable preference hierarchies can generate or modify neighborhood effects in a way that should also be relevant for herbivores. Indeed, generalist herbivores, some of which have strong effects in natural and agricultural communities, can show flexible foraging behaviors similar to those of pollinators. For example, grasshoppers can shift plant choices to obtain a nutritionally balanced diet (Bernays et al. 1994), implying plant neighborhoods may influence their preferences and

thus patterns of damage to plants. Pollinator neighborhood models have also shown that pollinator density can have both evolutionary and ecological consequences, for example, the evolution of mixed foraging strategies in pollinators and specialization in plant visitation are more likely with higher pollinator density (Kunin and Iwasa 1996; Muchhala et al. 2010), and pollinator density can alter effects of floral resource dynamics (e.g., Wasser 1978; Hanoteaux et al. 2013). Herbivore neighborhood models have not yet considered the influence of insect density, despite the fact that herbivore densities can vary greatly among seasons or years in the field and have been shown empirically to affect neighborhood effects (Merwin et al. 2017).

New pollinator neighborhood models can similarly be informed by the herbivore neighborhood models that focus on how movements in and out of neighborhoods (or patches) determine herbivore densities. Pollinator models mostly focus on the movement of pollinators or pollen *within* a neighborhood, although pollination rates are functions of both the number of pollinators arriving in an area *and* how they move after arrival. Mathematical expressions for herbivore immigration to a patch and distribution among plants within a patch (Hambäck et al. 2014) could be expanded to include pollinator behavior and pollen transfer. Moreover, empirical work and verbal theory for herbivores often focuses on negative effects of neighboring plants on the ability of an herbivore to locate its host (i.e., “masking” or “repellency”; e.g., Hay 1986; Hambäck et al. 2000), but similar negative effects of plant neighbors have not yet been examined for pollinators, although odors from multiple plants can make flower finding difficult for pollinators (e.g., Riffell et al. 2014). Finally, pollination models have not yet considered how traits such as body size, mobility, tongue length, or height of foraging flights may alter neighborhood effects, although these traits are known to affect flower visitation patterns.

Surprisingly few studies, whether for pollinators or herbivores, have considered how broad differences in consumer traits or natural history predict the functional forms (i.e., shape of frequency or density-dependence)

and scales of neighborhood effects (but see Hambäck et al. 2014). Most neighborhood models assume a single suite of consumer traits and explore the neighborhood effects entailed by that one set of assumptions. Similarly, few studies determine the consequences of alternative model assumptions about the form of neighborhood effects for population outcomes. Feldman et al. (2004) compared two pollinator responses to plant density (sigmoid versus saturating); only sigmoid responses led to facilitation of one plant species by the other. Tachiki et al. (2010) compared linear, sigmoid, and saturating functions for the number of pollinator visits as a function of plant density, likewise finding that pollinator visits must be an accelerating function of total plant density (over at least some range of densities) in order for plants to facilitate each other. Increasing our ability to predict the influence of both pollinator and herbivore neighborhood effects will require models that compare alternative assumptions about species' traits and the type of neighborhood effects, as opposed to varying parameter values for a single functional form.

Finally, we suggest that researchers consider how pollinators and herbivores respond to continuous distributions of phenotypic diversity rather than discrete types. Pollinator and herbivore neighborhood models have generally treated neighborhoods as containing distinct species or genotypes, and field studies of diversity effects often focus on numbers of species or genotypes, although pollinators and herbivores must in fact respond to the distribution of plant phenotypes (Hughes et al. 2008). Outside of agricultural systems, plant communities are typically diverse; both pollinators and herbivores can respond to the diversity of a neighborhood (Bernays 1999; Hegland and Boeke 2006), at the genotype level as well as among species (reviewed in Hughes et al. 2008). One herbivore model (Leimar and Tuomi 1998) showed that using a continuous distribution of resistance values could lead to different predictions about herbivore neighborhood effects than similar models that treated herbivore resistance as a binary trait (Tuomi and Augner 1993). Work on pathogens has also shown that considering a distribution of trait variation can lead

to different dynamics than treating resistance and virulence as binary traits (Dwyer et al. 1997), and has addressed effects of multi-host communities on interaction patterns (Truitt et al. 2019). These pathogen models may be good starting points for models that explore effects of plant diversity on neighborhood effects.

INTEGRATING ACROSS SCALES AND TYPES OF NEIGHBORHOOD EFFECTS

A first step toward embracing the full diversity of neighborhood effects would be to model joint neighborhood effects mediated by insect pollinators and herbivores. We see three potentially fruitful approaches to building such integrative models. For any of these approaches the logical response variable would be plant fitness, which integrates per capita effects of different consumers, although one would have to make assumptions about the relative effects of herbivore damage and pollination on fitness. It may seem that pollination would always have larger effects, but for some plants vegetative growth and spread will have large effects on fitness, and for others there may not be pollen limitation. A first approach would be to start with an "herbivore-style" model, which focuses on how insects arrive at local neighborhoods (patches) with differing composition. One could include both visual (presumably pollinator) and olfactory (presumably herbivores) searchers, with visual searchers having positive fitness effects and olfactory searchers having negative effects. This approach would allow asking if pollinator and herbivore effects on fitness might vary simply based on their perceptual differences, and what their net effects on fitness would be. A second approach would be to start with a more "pollination-style" model of insects moving within a patch, but allow some insects to be pollinators (with positive frequency-dependent fitness effects) and some to be herbivores (with negative fitness effects). This would allow asking about the interaction of frequency-dependent and independent consumers. Finally, one could take a more general approach and have insects responding to plants at nested spatial scales, with some responding at larger scales and

others at smaller scales. Both consumers could be allowed density and frequency dependence, and one could ask what happens when negative neighborhood effects happen at a smaller spatial scale than positive ones (as may occur for pollinators; Charlebois and Sargent 2017).

Most neighborhood models have not dealt directly with the issue of spatial scale (but see Orrock et al. 2010a,b), a gap also found in empirical work (reviewed in Braun and Lortie 2019). Scale is critical for understanding the role of neighborhood effects because plant-insect systems vary widely in patterns and scales of plant aggregation, and neighborhood effects through plant competition, herbivory, and pollination likely occur at a range of spatial scales simultaneously (plant competition with immediate neighbors and insect-mediated effects at a range of scales). Pollination models that have allowed an aggregated plant spatial structure (Levin and Anderson 1970; Waser 1978; Hanoteaux et al. 2013) are a first step toward grappling with spatial scale, but positive effects of intraspecific aggregation on pollination success may be offset by negative effects of aggregation on intraspecific competition or by herbivore responses to plant aggregations. These analyses are also restricted to considering processes either in or outside of aggregations, yet real variation in plant neighborhood composition is likely to be continuous. A major step for future work would be to develop models including neighborhood effects at multiple spatial scales, as dictated by the mobilities and behaviors of different groups of insects. One promising approach to incorporating multiple scales is to use agent-based models. Other computationally intensive methods are being developed by researchers working on protein interactions within and among cells; these methods may also be adapted to represent interacting populations of species within and among patches (e.g., Yu and Bagheri 2016).

Future work should also take into account the variety of temporal scales of neighborhood effects, as the plant resources for pollinators and herbivores vary over a range of time scales. The availability of host plant species for an herbivore may be relatively constant over a season compared to the floral

neighborhood for pollinators, which could change rapidly as different plants come in and out of bloom. Although both leaf tissue and floral resources (nectar and pollen) can be rapidly depleted, floral resources typically renew faster than leaves can regrow. Plant-induced defenses, which are known to influence herbivore distributions across plants (Underwood et al. 2005), may change on the order of days (Underwood 1998) or across years (Haukioja 1991). Thus, neighborhood effects can occur at multiple temporal scales, just as they can occur at multiple spatial scales. Because of the spatial memory of bees, neighborhoods at one time can even influence plant-pollinator interactions days later (e.g., Ogilvie and Thompson 2016), suggesting that considering only immediate neighbors at a single time will underestimate total neighborhood effects. Even though empirical work should take temporal variation into account, models representing temperate systems with a single reproductive season per year might ignore within-season changes in effective neighborhood composition by focusing on neighborhood effects on annual fitness components (growth, survival, reproduction). For systems with more continuous reproduction, modelers will likely need to use numerical approaches that allow interactions to respond to temporal variation at multiple time scales (i.e., Holt and Barfield 2003; Yu and Bagheri 2016).

Finally, it is important to acknowledge that insect pollinators and herbivores are not the only guilds that interact with plant neighborhoods and affect plant fitness. Describing net effects of spatial neighborhoods will require accounting for multiple taxa that may react to neighborhoods differently and occupy different trophic levels. Seed predators and florivores are particularly interesting cases because they affect plant sexual reproduction and are likely to respond to both floral and vegetative neighborhoods. Pathogens, some of which are vectored by insect pollinators and herbivores, can also clearly affect plant populations and have transmission rates that depend on local plant density and diversity (e.g., Biere and Honders 1998). Although there are many spatial models of host-pathogen dynamics, we are not aware of any that

have been used to explore effects of local neighborhood structure. Soil microbial communities can also potentially mediate neighborhood effects, although the spatial scale of these effects is perhaps more similar to the spatial scale of plant competitive interactions. Local density- and frequency-dependent effects of plant-soil feedbacks have been modeled before (e.g., Molofsky 1994; Molofsky et al. 2001); the cellular automaton framework applied in these models may be useful for future work on other types of neighborhood effects. Mammalian herbivores are known to be affected by plant neighborhoods (e.g., Champagne et al. 2018) and, in contrast to models for insect herbivores, at least one model of mammalian herbivore neighborhood effects does take into account effects of herbivore density and flexible foraging behavior (Ishii and Crawley 2011). Vertebrate herbivores may have behavioral flexibility in common with insect pollinators, but models for more behaviorally flexible vertebrate predators will need to take into account not just additional flexibility but also the very different spatial scale at which vertebrates forage relative to insect herbivores. For example, due to an assumption that multiple plant types are eaten in a single “bite,” the Ishii and Crawley (2011) model cannot easily be adapted to insect herbivores. Finally, predators and parasitoids can use cues from plant neighborhoods when searching for insect prey (Vet and Dicke 1992) and may alter neighborhood effects generated by insect pollinators, herbivores, or seed predators.

CONCLUSIONS

Taken together, models of pollinator and herbivore neighborhood effects have considered many paths through which local plant density and frequency can influence per capita interactions of insects with plants. These models demonstrate that a variety of mechanisms potentially generate density- and fre-

quency-dependence in plant fitness at the neighborhood scale, which should scale up to influence population processes such as trait evolution and population dynamics. Although studies of herbivore and pollinator neighborhood effects can each benefit from being aware of work in the other field, the most important goal for future work would be to integrate multiple types of neighborhood effects. This is consistent with recent calls for better integration of work on pollination and herbivory in other contexts such as network theory (Sauve et al. 2016) and the evolution of plant defenses (Lucas-Barbosa 2016). Future models should consider the net neighborhood effects from pollinators and herbivores together, since both types of insects affect plant fitness but in different ways (Andersson et al. 2016), and because insects affect each other through interactions with plants (e.g., Brody 1992; Strauss 1997; Herrera 2000; Sletvold et al. 2015). Empirical studies have found both additive (Sletvold et al. 2015) and nonadditive effects (Herrera 2000) of pollination and herbivory, but we lack both empirical and theoretical understanding of whether neighborhood effects mediated by these two types of consumers might be additive or not. With our growing knowledge of plant-mediated interactions between pollination and herbivory, and expanding methods for analysis for spatially implicit and explicit mathematical models, we have the resources to build a more synthetic understanding of when and how neighborhood effects are important factors in plant ecology and evolution.

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REFERENCES

- Altizer S. M., Thrall P. H., Antonovics J. 1998. Vector behavior and the transmission of anther-smut infection in *Silene alba*. *American Midland Naturalist* 139: 147–163.

- Andersson P., Ehrlén J., Hambäck P. A. 2016. Plant patch structure influences plant fitness via antagonistic and mutualistic interactions but in different directions. *Oecologia* 180:1175–1182.
- Andow D. A. 1991. Vegetational diversity and arthropod population response. *Annual Review of Entomology* 36:561–586.
- Antonovics J., Levin D. A. 1980. The ecological and genetic consequences of density-dependent regulation in plants. *Annual Review of Ecology and Systematics* 11:411–452.
- Atsatt P. R., O'Dowd D. J. 1976. Plant defense guilds. *Science* 193:24–29.
- Barabás G., D'Andrea R., Stump S. M. 2018. Chesson's coexistence theory. *Ecological Monographs* 88:277–303.
- Barbosa P., Hines J., Kaplan I., Martinson H., Szczepaniec A., Szendrei Z. 2009. Associational resistance and associational susceptibility: having right or wrong neighbors. *Annual Review of Ecology, Evolution, and Systematics* 40:1–20.
- Benadi G., Gegeer R. J. 2018. Adaptive foraging of pollinators can promote pollination of a rare plant species. *American Naturalist* 192:E81–E92.
- Bernays E. A. 1999. When host choice is a problem for a generalist herbivore: experiments with the whitefly *Bemisia tabaci*. *Ecological Entomology* 24:260–267.
- Bernays E. A. 2001. Neural limitations in phytophagous insects: implications for diet breadth and evolution of host affiliation. *Annual Review of Entomology* 46:703–727.
- Bernays E. A., Bright K. L., Gonzalez N., Angel J. 1994. Dietary mixing in a generalist herbivore: tests of two hypotheses. *Ecology* 75:1997–2006.
- Bever J. D., Westover K. M., Antonovics J. 1997. Incorporating the soil community into plant population dynamics: the utility of the feedback approach. *Journal of Ecology* 85:561–573.
- Biere A., Honders S. C. 1998. Anther smut transmission in *Silene latifolia* and *Silene dioica*: impact of host traits, disease frequency, and host density. *International Journal of Plant Sciences* 159:228–235.
- Blaauw B. R., Isaacs R. 2014. Flower plantings increase wild bee abundance and the pollination services provided to a pollination-dependent crop. *Journal of Applied Ecology* 51:890–898.
- Bobisud L. E., Neuhaus R. J. 1975. Pollinator constancy and survival of rare species. *Oecologia* 21:263–272.
- Braun J., Lortie C. J. 2019. Finding the bees knees: a conceptual framework and systematic review of the mechanisms of pollinator-mediated facilitation. *Perspectives in Plant Ecology, Evolution and Systematics* 36:33–40.
- Brody A. K. 1992. Oviposition choices by a pre-dispersal seed predator (*Hylemya sp.*). I. Correspondence with hummingbird pollinators, and the role of plant size, density and floral morphology. *Oecologia* 91:56–62.
- Brosi B. J., Briggs H. M. 2013. Single pollinator species losses reduce floral fidelity and plant reproductive function. *Proceedings of the National Academy of Sciences of the United States of America* 110:13044–13048.
- Brown B. J., Mitchell R. J., Graham S. A. 2002. Competition for pollination between an invasive species (purple loostripe) and a native congener. *Ecology* 83:2328–2336.
- Bruckman D., Campbell D. R. 2016. Pollination of a native plant changes with distance and density of invasive plants in a simulated biological invasion. *American Journal of Botany* 103:1458–1465.
- Burkle L. A., Irwin R. E. 2010. Beyond biomass: measuring the effects of community-level nitrogen enrichment on floral traits, pollinator visitation and plant reproduction. *Journal of Ecology* 98:705–717.
- Capman W. C., Batzli G. O., Simms L. E. 1990. Responses of the common sooty wing skipper to patches of host plants. *Ecology* 71:1430–1440.
- Caruso C. M. 2002. Influence of plant abundance on pollination and selection on floral traits of *Ipomopsis aggregata*. *Ecology* 83:241–254.
- Champagne E., Moore B. D., Côté S. D., Tremblay J.-P. 2018. Spatial correlations between browsing on balsam fir by white-tailed deer and the nutritional value of neighboring winter forage. *Ecology and Evolution* 8:2812–2823.
- Charlebois J. A., Sargent R. D. 2017. No consistent pollinator-mediated impacts of alien plants on natives. *Ecology Letters* 20:1479–1490.
- Cipollini D. F., Bergelson J. 2001. Plant density and nutrient availability constrain constitutive and wound-induced expression of trypsin inhibitors in *Brassica napus*. *Journal of Chemical Ecology* 27:593–610.
- Cook S. M., Khan Z. R., Pickett J. A. 2007. The use of push-pull strategies in integrated pest management. *Annual Review of Entomology* 52:375–400.
- Cromartie W. J., Jr. 1975. The effect of stand size and vegetational background on the colonization of cruciferous plants by herbivorous insects. *Journal of Applied Ecology* 12:517–533.
- Davis J. M., Stamps J. A. 2004. The effect of natal experience on habitat preferences. *Trends in Ecology and Evolution* 19:411–416.
- Dietzsch A. C., Stanley D. A., Stout J. C. 2011. Relative abundance of an invasive alien plant affects native pollination processes. *Oecologia* 167:469–479.
- Dwyer G., Elkinton J. S., Buonaccorsi J. P. 1997. Host heterogeneity in susceptibility and disease dynamics: tests of a mathematical model. *American Naturalist* 150:685–707.
- Elton C. S. 1958. *The Ecology of Invasions By Plants and Animals*. London (United Kingdom): Methuen and Company.
- Feldman T. S., Morris W. F., Wilson W. G. 2004. When can two plant species facilitate each other's pollination? *Oikos* 105:197–207.
- Flanagan R. J., Mitchell R. J., and Karron J. D. 2010. Increased relative abundance of an invasive competitor

- for pollination, *Lythrum salicaria*, reduces seed number in *Mimulus ringens*. *Oecologia* 164:445–454.
- Fontaine C., Thébault E., Dajoz I. 2009. Are insect pollinators more generalist than insect herbivores? *Proceedings of the Royal Society B: Biological Sciences* 276:3027–3033.
- Fowler N. L., Levin D. A. 1984. Ecological constraints on the establishment of a novel polyploid in competition with its diploid progenitor. *American Naturalist* 124:703–711.
- Galen C., Gregory T., Galloway L. F. 1989. Costs of self-pollination in a self-incompatible plant, *Polemonium viscosum*. *American Journal of Botany* 76:1675–1680.
- Gigord L. D. B., Macnair M. R., Smithson A. 2001. Negative frequency-dependent selection maintains a dramatic flower color polymorphism in the rewardless orchid *Dactylorhiza sambucina* (L.) Soð. *Proceedings of the National Academy of Sciences of the United States of America* 98:6253–6255.
- Goulson D. 1994. A model to predict the influence of insect flower constancy on interspecific competition between insect pollinated plants. *Journal of Theoretical Biology* 168:309–314.
- Hambäck P. A., Beckerman A. P. 2003. Herbivory and plant resource competition: a review of two interacting interactions. *Oikos* 101:26–37.
- Hambäck P. A., Englund G. 2005. Patch area, population density and the scaling of migration rates: the resource concentration hypothesis revisited. *Ecology Letters* 8:1057–1065.
- Hambäck P. A., Ågren J., Ericson L. 2000. Associational resistance: insect damage to purple loosestrife reduced in thickets of sweet gale. *Ecology* 81:1784–1794.
- Hambäck P. A., Pettersson J., Ericson L. 2003. Are associational refuges species specific? *Functional Ecology* 17:87–93.
- Hambäck P. A., Inouye B. D., Andersson P., Underwood N. 2014. Effects of plant neighborhoods on plant-herbivore interactions: resource dilution and associational effects. *Ecology* 95:1370–1383.
- Hanoteaux S., Tielbörger K., Seifan M. 2013. Effects of spatial patterns on the pollination success of a less attractive species. *Oikos* 122:867–880.
- Harper J. L. 1977. *Population Biology of Plants*. London (United Kingdom): Academic Press.
- Haukioja E. 1991. Induction of defenses in trees. *Annual Review of Entomology* 36:25–42.
- Hay M. E. 1986. Associational plant defenses and the maintenance of species diversity: turning competitors into accomplices. *American Naturalist* 128:617–641.
- Hegland S. J. 2014. Floral neighbourhood effects on pollination success in red clover are scale-dependent. *Functional Ecology* 28:561–568.
- Hegland S. J., Boeke L. 2006. Relationships between the density and diversity of floral resources and flower visitor activity in a temperate grassland community. *Ecological Entomology* 31:532–538.
- Herrera C. M. 2000. Measuring the effects of pollinators and herbivores: evidence for non-additivity in a perennial herb. *Ecology* 81:2170–2176.
- Hersch E. I., Roy B. A. 2007. Context-dependent pollinator behavior: an explanation for patterns of hybridization among three species of indian paintbrush. *Evolution* 61:111–124.
- Holsinger K. E., Feldman M. W., Christiansen F. B. 1984. The evolution of self-fertilization in plants: a population genetic model. *American Naturalist* 124:446–453.
- Holt R. D. 1977. Predation, apparent competition, and the structure of prey communities. *Theoretical Population Biology* 12:197–229.
- Holt R. D. 1984. Spatial heterogeneity, indirect interactions, and the coexistence of prey species. *American Naturalist* 124:377–406.
- Holt R. D., Barfield M. 2003. Impacts of temporal variation on apparent competition and coexistence in open ecosystems. *Oikos* 101:49–58.
- Holt R. D., Kotler B. P. 1987. Short-term apparent competition. *American Naturalist* 130:412–430.
- Hopkins A. D. 1917. A discussion of C. G. Hewitt's paper on "Insect Behaviour." *Journal of Economic Entomology* 10:92–93.
- Hughes A. R., Inouye B. D., Johnson M. T. J., Underwood N., Vellend M. 2008. Ecological consequences of genetic diversity. *Ecology Letters* 11:609–623.
- Inouye D. W. 1978. Resource partitioning in bumblebees: experimental studies of foraging behavior. *Ecology* 59:672–678.
- Ishii R., Crawley M. J. 2011. Herbivore-induced coexistence of competing plant species. *Journal of Theoretical Biology* 268:50–61.
- Ishii R., Higashi M. 2001. Coexistence induced by pollen limitation in flowering-plant species. *Proceedings of the Royal Society B: Biological Sciences* 268:579–585.
- Johnson S. D., Peter C. I., Nilsson L. A., Ågren J. 2003. Pollination success in a deceptive orchid is enhanced by co-occurring rewarding magnet plants. *Ecology* 84:2919–2927.
- Jones P. L., Agrawal A. A. 2017. Learning in insect pollinators and herbivores. *Annual Review of Entomology* 62:53–71.
- Karban R., Baldwin I. T. 1997. *Induced Responses to Herbivory*. Chicago (Illinois): University of Chicago Press.
- Kareiva P. 1982. Experimental and mathematical analyses of herbivore movement: quantifying the influence of plant spacing and quality on foraging discrimination. *Ecological Monographs* 52:261–282.
- Kim T. N. 2017. How plant neighborhood composition influences herbivory: testing four mechanisms of associational resistance and susceptibility. *PLOS ONE* 12:e0176499.
- Kim T. N., Underwood N. 2015. Plant neighborhood effects on herbivory: damage is both density and frequency dependent. *Ecology* 96:1431–1437.

- Kim T. N., Underwood N., Inouye B. D. 2013. Insect herbivores change the outcome of plant competition through both inter- and intraspecific processes. *Ecology* 94:1753–1763.
- Koricheva J., Larsson S., Haukioja E. 1998. Insect performance on experimentally stressed woody plants: a meta-analysis. *Annual Review of Entomology* 43:195–216.
- Kuang J. J., Chesson P. 2010. Interacting coexistence mechanisms in annual plant communities: frequency-dependent predation and the storage effect. *Theoretical Population Biology* 77:56–70.
- Kunin W., Iwasa Y. 1996. Pollinator foraging strategies in mixed floral arrays: density effects and floral constancy. *Theoretical Population Biology* 49:232–263.
- Lachmuth S., Henrichmann C., Horn J., Pagel J., Schurr F. M. 2018. Neighbourhood effects on plant reproduction: an experimental–analytical framework and its application to the invasive *Senecio inaequidens*. *Journal of Ecology* 106:761–773.
- Larue A.-A. C., Raguso R. A., Junker R. R. 2016. Experimental manipulation of floral scent bouquets restructures flower–visitor interactions in the field. *Journal of Animal Ecology* 85:396–408.
- Lawson D. A., Whitney H. M., Rands S. A. 2017. Colour as a backup for scent in the presence of olfactory noise: testing the efficacy backup hypothesis using bumblebees (*Bombus terrestris*). *Royal Society Open Science* 4:170996.
- Leimar O., Tuomi J. 1998. Synergistic selection and graded traits. *Evolutionary Ecology* 12:59–71.
- Letourneau D. K. 1995. Associational susceptibility: effects of cropping pattern and fertilizer on Malawian bean fly levels. *Ecological Applications* 5:823–829.
- Levin D. A., Anderson W. W. 1970. Competition for pollinators between simultaneously flowering species. *American Naturalist* 104:455–467.
- Lhomme P., Carrasco D., Larsson M., Hansson B., Anderson P. 2018. A context-dependent induction of natal habitat preference in a generalist herbivorous insect. *Behavioral Ecology* 29:360–367.
- Lively C. M., Howard R. S. 1994. Selection by parasites for clonal diversity and mixed mating. *Philosophical Transactions of the Royal Society B: Biological Sciences* 346:271–281.
- Lucas-Barbosa D. 2016. Integrating studies on plant–pollinator and plant–herbivore interactions. *Trends in Plant Science* 21:125–133.
- McCall A. C., Irwin R. E. 2006. Florivory: the intersection of pollination and herbivory. *Ecology Letters* 9:1351–1365.
- Merwin A. C., Underwood N., Inouye B. D. 2017. Increased consumer density reduces the strength of neighborhood effects in a model system. *Ecology* 98:2904–2913.
- Mesgaran M. B., Bouhours J., Lewis M. A., Cousens R. D. 2017. How to be a good neighbour: facilitation and competition between two co-flowering species. *Journal of Theoretical Biology* 422:72–83.
- Mitchell R. J., Flanagan R. J., Brown B. J., Waser N. M., Karron J. D. 2009. New frontiers in competition for pollination. *Annals of Botany* 103:1403–1413.
- Molofsky J. 1994. Population dynamics and pattern formation in theoretical populations. *Ecology* 75:30–39.
- Molofsky J., Bever J. D., Antonovics J. 2001. Coexistence under positive frequency dependence. *Proceedings of the Royal Society B: Biological Sciences* 268:273–277.
- Montgomery B. R. 2009. Do pollen carryover and pollinator constancy mitigate effects of competition for pollination? *Oikos* 118:1084–1092.
- Morales C. L., Traveset A. 2008. Interspecific pollen transfer: magnitude, prevalence and consequences for plant fitness. *Critical Reviews in Plant Sciences* 27:221–238.
- Morris W. F. 1993. Predicting the consequence of plant spacing and biased movement for pollen dispersal by honey bees. *Ecology* 74:493–500.
- Morris W. F. 1997. Disentangling effects of induced plant defenses and food quantity on herbivores by fitting nonlinear models. *American Naturalist* 150:299–327.
- Muchhala N., Brown Z., Armbruster W. S., Potts M. D. 2010. Competition drives specialization in pollination systems through costs to male fitness. *American Naturalist* 176:732–743.
- Nottebrock H., Schmid B., Mayer K., Devaux C., Esler K. J., Böhning-Gaese K., Schleuning M., Pagel J., Schurr F. M. 2017. Sugar landscapes and pollinator-mediated interactions in plant communities. *Ecography* 40:1129–1138.
- Ogilvie J. E., Thomson J. D. 2016. Site fidelity by bees drives pollination facilitation in sequentially blooming plant species. *Ecology* 97:1442–1451.
- Ohashi K., Thomson J. D. 2009. Trapline foraging by pollinators: its ontogeny, economics and possible consequences for plants. *Annals of Botany* 103:1365–1378.
- Orrock J. L., Baskett M. L., Holt R. D. 2010a. Spatial interplay of plant competition and consumer foraging mediate plant coexistence and drive the invasion ratchet. *Proceedings of the Royal Society B: Biological Sciences* 277:3307–3315.
- Orrock J. L., Holt R. D., Baskett M. L. 2010b. Refuge-mediated apparent competition in plant–consumer interactions. *Ecology Letters* 13:11–20.
- Pfister C. A., Hay M. E. 1988. Associational plant refuges: convergent patterns in marine and terrestrial communities result from different mechanisms. *Oecologia* 77:118–129.
- Qu H., Seifan T., Seifan M. 2017. Effects of plant and pollinator traits on the maintenance of a food deceptive species within a plant community. *Oikos* 126:1815–1826.
- Rautio P., Bergvall U. A., Tuomi J., Kesti K., Leimar O. 2012. Food selection by herbivores and neighbourhood effects in the evolution of plant defences. *Annales Zoologici Fennici* 49:45–57.

- Riffell J. A., Shlizerman E., Sanders E., Abrell L., Medina B., Hinterwirth A. J., Kutz J. N. 2014. Flower discrimination by pollinators in a dynamic chemical environment. *Science* 344:1515–1518.
- Rodríguez-Gironés M. A., Santamaría L. 2007. Resource competition, character displacement, and the evolution of deep corolla tubes. *American Naturalist* 170: 455–464.
- Root R. B. 1973. Organization of a plant-arthropod association in simple and diverse habitats: the fauna of collards (*Brassica oleracea*). *Ecological Monographs* 43:95–124.
- Russell F. L., Louda S. M. 2005. Indirect interaction between two native thistles mediated by an invasive exotic floral herbivore. *Oecologia* 146:373–384.
- Sargent R. D., Otto S. P. 2006. The role of local species abundance in the evolution of pollinator attraction in flowering plants. *American Naturalist* 167:67–80.
- Sauve A. M. C., Thébault E., Pocock M. J. O., Fontaine C. 2016. How plants connect pollination and herbivory networks and their contribution to community stability. *Ecology* 97:908–917.
- Schaffer W. M., Zeh D. W., Buchmann S. L., Kleinhans S., Schaffer M. V., Antrim J. 1983. Competition for nectar between introduced honey bees and native North American bees and ants. *Ecology* 64:564–577.
- Schemske D. W. 1981. Floral convergence and pollinator sharing in two bee-pollinated tropical herbs. *Ecology* 62:946–954.
- Schmid B., Nottebrock H., Esler K. J., Pagel J., Böhning-Gaese K., Schurr F. M., Mueller T., Schleuning M. 2016. A bird pollinator shows positive frequency dependence and constancy of species choice in natural plant communities. *Ecology* 97:3110–3118.
- Schoonhoven L. M., van Loon J. J. A., Dicke M. 2005. *Insect-Plant Biology*. Second Edition. Oxford (United Kingdom): Oxford University Press.
- Schultz E. L., Eckberg J. O., Berg S. S., Louda S. M., Miller T. E. X. 2017. Native insect herbivory overwhelms context dependence to limit complex invasion dynamics of exotic weeds. *Ecology Letters* 20:1374–1384.
- Sletvold N., Moritz K. K., Ågren J. 2015. Additive effects of pollinators and herbivores result in both conflicting and reinforcing selection on floral traits. *Ecology* 96:214–221.
- Smithson A., Macnair M. R. 1996. Frequency-dependent selection by pollinators: mechanisms and consequences with regard to behaviour of bumblebees *Bombus terrestris* (L.) (Hymenoptera: Apidae). *Journal of Evolutionary Biology* 9:571–588.
- Smithson J. B., Lenné J. M. 1996. Varietal mixtures: a viable strategy for sustainable productivity in subsistence agriculture. *Annals of Applied Biology* 128: 127–158.
- Song Z., Feldman M. W. 2014. Adaptive foraging behaviour of individual pollinators and the coexistence of co-flowering plants. *Proceedings of the Royal Society B: Biological Sciences* 281:20132437.
- Stastny M., Agrawal A. A. 2014. Love they neighbor? Reciprocal impacts between plant community structure and insect herbivory in co-occurring Asteraceae. *Ecology* 95:2904–2914.
- Stiling P., Rossi A. M., Cattell M. V. 2003. Associational resistance mediated by natural enemies. *Ecological Entomology* 28:587–592.
- Stoll P., Weiner J. 2000. A neighborhood view of interactions among individual plants. Pages 11–27 in *The Geometry of Ecological Interactions: Simplifying Spatial Complexity*, edited by U. Dieckmann, R. Law, and J. A. J. Metz. Cambridge (United Kingdom): Cambridge University Press.
- Strauss S. Y. 1997. Floral characters link herbivores, pollinators, and plant fitness. *Ecology* 78:1640–1645.
- Straw R. M. 1972. A Markov model for pollinator constancy and competition. *American Naturalist* 106:597–620.
- Tachiki Y., Iwasa Y., Satake A. 2010. Pollinator coupling can induce synchronized flowering in different plant species. *Journal of Theoretical Biology* 267: 153–163.
- Tahvanainen J. O., Root R. B. 1972. The influence of vegetational diversity on the population ecology of a specialized herbivore, *Phyllotreta cruciferae* (Coleoptera: Chrysomelidae). *Oecologia* 10:321–346.
- Thomas C. D. 1986. Butterfly larvae reduce host plant survival in vicinity of alternative host species. *Oecologia* 70:113–117.
- Thompson J. N. 1993. Preference hierarchies and the origin of geographic specialization in host use in swallowtail butterflies. *Evolution* 47:1585–1594.
- Thomson J. D. 1978. Effects of stand composition on insect visitation in two-species mixtures of *Hieracium*. *American Midland Naturalist* 100:431–440.
- Thomson J. D. 1981a. Field measures of flower constancy in bumblebees. *American Midland Naturalist* 105:377–380.
- Thomson J. D. 1981b. Spatial and temporal components of resource assessment by flower-feeding insects. *Journal of Animal Ecology* 50:49–59.
- Thomson J. D., Peterson S. C., Harder L. D. 1987. Response of traplining bumble bees to competition experiments: shifts in feeding location and efficiency. *Oecologia* 71:295–300.
- Thomson J. D., Fung H. F., Ogilvie J. E. 2019. Effects of spatial patterning of co-flowering plant species on pollination quantity and purity. *Annals of Botany* 123:303–310.
- Truitt L. L., McArt S. H., Vaughn A. H., Ellner S. P. 2019. Trait-based modeling of multihost pathogen transmission: plant-pollinator networks. *American Naturalist* 193:E149–E167.
- Tuomi J., Augner M. 1993. Synergistic selection of unpalatability in plants. *Evolution* 47:668–672.

- Tuomi J., Augner M., Nilsson P. 1994. A dilemma of plant defences: is it really worth killing the herbivore? *Journal of Theoretical Biology* 170:427–430.
- Turchin P. 1991. Translating foraging movements in heterogeneous environments into the spatial distribution of foragers. *Ecology* 72:1253–1266.
- Underwood N. 1998. The timing of induced resistance and induced susceptibility in the soybean-Mexican bean beetle system. *Oecologia* 114:376–381.
- Underwood N. 2004. Variance and skew of the distribution of plant quality influence herbivore population dynamics. *Ecology* 85:686–693.
- Underwood N. 2009. Effect of genetic variation in plant quality on the population dynamics of a herbivorous insect. *Journal of Animal Ecology* 78:839–847.
- Underwood N., Anderson K., Inouye B. D. 2005. Induced vs. constitutive resistance and the spatial distribution of insect herbivores among plants. *Ecology* 86:594–602.
- Underwood N., Inouye B. D., Hambäck P. A. 2014. A conceptual framework for associational effects: when do neighbors matter and how would we know? *Quarterly Review of Biology* 89:1–19.
- Valdovinos F. S., Moisset de Espanés P., Flores J. D., Ramos-Jiliberto R. 2013. Adaptive foraging allows the maintenance of biodiversity of pollination networks. *Oikos* 122:907–917.
- Vet L. E. M., Dicke M. 1992. Ecology of infochemical use by natural enemies in a tritrophic context. *Annual Review of Entomology* 37:141–172.
- Waddington K. D., Holden L. R. 1979. Optimal foraging: on flower selection by bees. *American Naturalist* 114:179–196.
- Waser N. M. 1978. Interspecific pollen transfer and competition between co-occurring plant species. *Oecologia* 36:223–236.
- Waser N. M., Fugate M. L. 1986. Pollen precedence and stigma closure: a mechanism of competition for pollination between *Delphinium nelsonii* and *Ipomopsis aggregata*. *Oecologia* 70:573–577.
- Wiklund C. 1974. Oviposition preferences in *Papilio machaon* in relation to the host plants of the larvae. *Entomologia Experimentalis et Applicata* 17:189–198.
- Yu J. S., Bagheri N. 2016. Multi-class and multi-scale models of complex biological phenomena. *Current Opinion in Biotechnology* 39:167–173.

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