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Effects of plant neighborhoods on plant–herbivore interactions: resource dilution and associational effects

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Abstract. Effects of neighboring plants on herbivore damage to a focal plant (associational effects) have been documented in many systems and can lead to either increased or decreased herbivore attack. Mechanistic models that explain the observed variety of herbivore responses to local plant community composition have, however, been lacking. We present a model of herbivore responses to patches that consist of two plant types, where herbivore densities on a focal plant are determined by a combination of patch-finding, within-patch redistribution, and patch-leaving. Our analyses show that the effect of plant neighborhood on herbivores depends both on how plant and herbivore traits combine to affect herbivore movement and on how experimental designs reveal the effects of plant density and plant relative frequency. Associational susceptibility should be the dominant pattern when herbivores have biased landing rates within patches. Other behavioral decision rules lead to mixed responses, but a common pattern is that in mixed patches, one plant type experiences associational resistance while the other plant experiences associational susceptibility. In some cases, the associational effect may shift sign along a gradient of plant frequency, suggesting that future empirical studies should include more than two plant frequencies to detect nonlinearities. Finally, we find that associational susceptibility should be commonly observed in experiments using replacement designs, whereas associational resistance will be the dominant pattern when using additive designs. Consequently, outcomes from one experimental design cannot be directly compared to studies with other designs. Our model can also be translated to other systems with foragers searching for multiple resource types.

Key words: associational effects; density dependence; experimental design; frequency dependence; herbivore search behavior; insect herbivores; neighbor effects; patch size; plant volatiles; resource concentration hypothesis.

Introduction

Neighboring plants can affect the strength of interactions between individual plants and their herbivores (Root 1973, Andow 1991, Hambäck and Beckerman 2003, Barbosa et al. 2009, Underwood et al. 2014), between herbivores and their natural enemies (Langellotto and Denno 2004, Bukovinszky et al. 2007), and between plants and their pollinators (Feldman 2008). The presence of specific plant neighbors can decrease or increase insect attraction to a focal plant species or genotype; these phenomena are referred to as associational resistance and associational susceptibility, respectively (Tahvanainen and Root 1972, Letourneau 1995). Associational effects are important in ecology because they have been hypothesized to affect plant and herbivore populations and communities (e.g., Agrawal et al. 2006), and are used as tools in crop and forest agriculture (Andow 1991). However, the presence and direction of associational effects are highly variable among studies, depending on the relative and absolute palatability of focal and neighbor plants (Andow 1991).

Understanding when to expect associational resistance vs. susceptibility (or any associational effect at all) requires understanding how particular mechanisms for associational effects generate distributions of insects and their effects on plants. Early hypotheses for how associational effects arise were verbal (Tahvanainen and Root 1972, Root 1973, Atsatt and O'Dowd 1976), but mathematical models are needed to generate quantitative predictions. Previous models based on either optimal foraging (Holt and Kotler 1987) or reaction–diffusion equations (Kareiva 1982, Turchin 1991) have considered a small subset of potential mechanisms for associational effects (i.e., variation in consumer emigration from patches in response to resources *within* patches), but many important mechanisms remain unexamined. In particular, previous models did not consider the role of patch-finding, whereas empirical studies suggest that patch-finding is more important than within-patch processes for deter-

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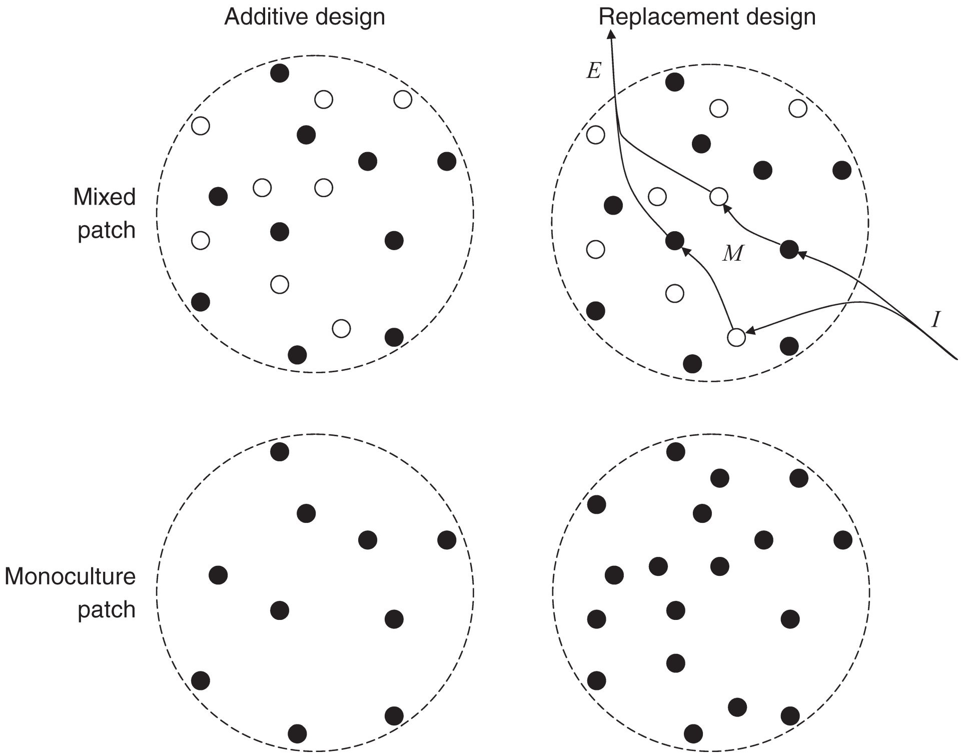

FIG. 1. Patch setup for models with mixed or monoculture patches, illustrating features of additive and replacement designs in the two columns. Additive designs hold the density of a focal plant type (solid circles) constant; replacement designs usually keep total density constant. Three movement types are considered in the models we present; into patches (I), out from patches (E) and between plant types within patches (M).

mining herbivore load (number of herbivores) in plant mixtures (Andow 1990). Because host-finding is often a multi-scale process, involving decisions at both plant and patch levels (Ioannou et al. 2009), it will be important to include processes at both scales in theory for associational effects. Additionally, theory needs to address the fact that herbivores using different plant cues will respond differently to plant neighborhoods. For example, an herbivore using olfactory cues to locate host plants may face a different dilemma than a seed predator using visual cues. Therefore, theory for associational effects should take into account both within- and among-patch search and selection processes and both plant and herbivore traits.

Consumer interactions with a focal plant could be affected by both the relative frequency of plant types in the neighborhood and plant density. Higher plant density could either increase herbivore loads (resource concentration effects; Root 1973) or decrease loads (resource dilution effects; Otway et al. 2005). In nature and experiments, focal plant density often covaries with non-focal neighbor plant frequency (Ioannou et al. 2009). Empirical studies of associational effects generally attribute effects of neighborhood composition to the frequency of non-focal plants, but these studies tend to rely on experimental designs that do not effectively separate frequency- and density-dependent effects. Additive designs hold focal plant density constant while plant neighbor density is manipulated; replacement designs hold total plant density constant while manipulating relative frequency of plants (Fig. 1). For the same system, these designs thus might lead to different (and incomplete) conclusions about associational effects (Inouye 2001; see also Ioannou et al. 2009). Characterizing frequency-dependent (associational) effects separately from density-dependent (concentration or dilution) effects is important both because it allows confirmation that a real associational effect is occurring, and because frequency and density effects have different consequences for the long-term dynamics of interactions between plants and herbivores.

We develop a novel quantitative framework for predicting how insect loads on a focal plant may be affected by focal and non-focal plant neighbors in patches that include a mixture of plants (species or genotypes) with different traits. Our model connects herbivore behavior (a product of both herbivore and plant traits) with herbivore distributions among plants. We focus on three processes that can generate density and frequency dependence in mixed plant communities: (1) how plants affect the number of herbivores arriving in a patch, (2) how herbivores distribute themselves among plant types within a patch, and (3) effects of patch composition on how long herbivores stay in the

TABLE 1. Parameters used in models.

Parameter or function	Description
H_m, H_n	Herbivore loads on plant types m and n
$\pi_m = v^a$, $\pi_n = 1 - v^a$	Probability of landing on plant types m and n in the patch
$p = i\sqrt{vT + d(1 - v)T}$	Maximum distance for detecting a patch
I	Rate of patch finding when $T = 1$
v	Relative frequency of plant type m
T	Total number of plant individuals in the patch
d	Detection distance of odors from plant type n relative to odors of type m at the same plant density
a	Relative rate at which an individual herbivore lands on plant type n
$F_m = f_m$, $F_n = f_n$	Rate of movement from plant types m and n in the patch
$E_m = \varepsilon_m T^{-k}$, $E_n = \varepsilon_n T^{-k}$	Rate of leaving the patch from plant types m and n ($k = 0$ implies that the leaving rate is independent of host plant number).
ε_m, ε_n	Absolute leaving rate from plant types m and n when $T = 1$
k	Scaling factor for the relationship between plant number and patch leaving rate

patch. The seeds for this theory can be found in previous attempts to predict density distributions of herbivores on a single host plant in relation to patch size or resource density within the patch (Hambäck and Englund 2005, Andersson et al. 2013) and in theories discussing optimal group sizes for reducing mortality risk (Foster and Treherne 1981, Cresswell and Quinn 2011, Ioannou et al. 2011).

Although our models are phrased in terms of herbivores and herbivory, the same framework can be used for other consumers searching for multiple prey types, e.g., pollinators visiting plants or parasitoids attacking insect hosts, and some of our general conclusions are relevant to studies of neighborhood effects on consumer–resource interactions in general. In the analysis, we address three questions: what are the separate roles of relative frequency and density of plants as drivers of herbivore load in mixed plant communities; how do processes at between- and within-patch scales interact to determine attack rates on different plants; and finally, how does the choice of experimental design for an empirical study affect conclusions about neighborhood effects?

THEORETICAL BACKGROUND

For simplicity, we model a patch that consists of two plant types, but our approach can be extended to more than two types. A patch is meant to describe a situation where herbivores perceive the collective characteristics of multiple plant individuals, such as when insects using olfactory cues respond to mixed volatile signals from multiple plant types. We phrase results in terms of patterns generated by herbivores searching for multiple host plant types, such as poly/oligophagous herbivores searching for multiple host plant species or monophagous herbivores searching for host genotypes that differ in traits affecting host-finding. However, results also apply to monophagous herbivores whose searching is affected by non-host plants. We focus on small- to intermediate-sized patches, similar to the size typically used in field experiments (e.g., Golden and Crist 1999), and a timescale such that the turnover of herbivore individuals due to movement is greater than turnover due to demographic processes. This means that population dynamics occur at a spatial scale larger than the patch and do not affect the distribution of herbivores within a patch. We assume that the density and relative frequency of plant types can vary independently, so the roles of frequency- and density-dependent effects can be separated. The remaining space in a patch may be thought of as empty or filled by plants to which the herbivores do not respond. We define plant types as differing in traits that affect host finding or acceptance by herbivores.

Our model distinguishes three processes that determine herbivore load: immigration (movements into the patch), movements between plants within the patch, and emigration (movements out of the patch); see Tables 1 and 2. Each process may be affected by how herbivores respond to plant traits as follows. First, one plant type may be easier to detect from a distance (i.e., more apparent; sensu Feeny 1976), so the proportion of plant types affects the rate of patch-finding. Second, the relative attractiveness of plant types may bias movements between types within a patch. Third, plant types may induce herbivore movements from the patch at different rates, so the proportion of types affects the overall leaving rate of herbivores. Using this framework, we explore how changes in the relative frequency and number of each plant type affect herbivore loads on each type. We will describe the assumptions underlying the three processes; equations are presented in Tables 1 and 2 and in Appendix A.

Immigration rates

The effect of immigration on the herbivore load on a focal plant type m can be decomposed into three parts (Table 2): [the number of herbivores arriving at the patch] × [the proportion of individuals landing on plant type m]/[the number of individuals of plant m over which the herbivores can be distributed]. Previous analyses suggest that the number of herbivores arriving at a patch depends on the cue used during patch-finding; thus we consider three sensory modalities: contact,

TABLE 2. Equations for the quantitative case of the model for two plant types; corresponding equations for the qualitative case are in Appendix A.

Function	Plant type *m*	Plant type *n*
Basic model	$\frac{dH_x}{dt} = I_x + M_x(H_m, H_n) - E_x H_x$	$\frac{dH_x}{dt} = I_x + M_x(H_m, H_n) - E_x H_x$
Immigration rate	$I_m = \frac{\pi_m p}{vT} = iv^a \frac{\sqrt{v + d(1-v)}}{v\sqrt{T}}$	$I_n = \frac{\pi_n p}{(1-v)T} = i(1-v^a)\frac{\sqrt{v + d(1-v)}}{(1-v)\sqrt{T}}$
Within patch movements and emigration†	$M_m - E_m H_m = -F_m H_m + \pi_m$ $\times (F_n - E_n) H_n D_{nm} + \pi_m$ $\times (F_m - E_m) H_m = -f_m H_m + v^a$ $\times \left(\left(f_n - \frac{\varepsilon_n}{T^k} \right) H_n \frac{1-v}{v} + \left(f_m - \frac{\varepsilon_m}{T^k} \right) H_m \right)$	$M_n - E_n H_n = -F_n H_n + \pi_n (F_n - E_n) H_n + \pi_n$ $\times (F_m - E_m) H_m D_{mn} = -f_n H_n + (1 - v^a)$ $\times \left(\left(f_n - \frac{\varepsilon_n}{T^k} \right) H_n + \left(f_m - \frac{\varepsilon_m}{T^k} \right) H_m \frac{v}{1-v} \right)$
Total model: mixed patches	$\frac{dH_m}{dt} = iv^a \frac{\sqrt{v + d(1-v)}}{v\sqrt{T}} - f_m H_m + v^a$ $\times \left(\left(f_n - \frac{\varepsilon_n}{T^k} \right) H_n \frac{1-v}{v} + \left(f_m - \frac{\varepsilon_m}{T^k} \right) H_m \right)$	$\frac{dH_n}{dt} = i \frac{(1-v^a)\sqrt{v + d(1-v)}}{(1-v)\sqrt{T}} - f_n H_n$ $+ (1 - v^a) \left(\left(f_n - \frac{\varepsilon_n}{T^k} \right) H_n + \left(f_m - \frac{\varepsilon_m}{T^k} \right) H_m \frac{v}{1-v} \right)$
Equilibrium loads: mixed patches	$\dot{H}_m = \frac{i f_n v^a \sqrt{v + d(1-v)} T^{k-1/2}}{\left(f_m \varepsilon_n (1 - v^a) + f_n \varepsilon_m v^a \right) v}$	$\dot{H}_n = \frac{i f_m (1 - v^a) \sqrt{v + d(1-v)} T^{k-1/2}}{\left(f_m \varepsilon_n (1 - v^a) + f_n \varepsilon_m v^a \right)(1-v)}$
Total model: monocultures	$\frac{dH_{m,\mathrm{mono}}}{dt} = i \frac{\sqrt{vT}}{vT} - \frac{\varepsilon_m}{(vT)^k} H_{m,\mathrm{mono}}$	$\frac{dH_{n,\mathrm{mono}}}{dt} = i \frac{\sqrt{d(1-v)T}}{(1-v)T} - \frac{\varepsilon_n}{\left((1-v)T \right)^k} H_{n,\mathrm{mono}}$
Equilibrium load: monocultures	$\dot{H}_{m,}\ \mathrm{mono} = \frac{i}{\varepsilon_m} \frac{(vT)^k}{\sqrt{vT}} = \frac{i}{\varepsilon_m} (vT)^{k-1/2}$	$\dot{H}_{n,\mathrm{mono}} = \frac{i}{\varepsilon_n} \frac{\left((1-v)T \right)^k \sqrt{d}}{\sqrt{(1-v)T}} = \frac{i\sqrt{d}}{\varepsilon_n} \left((1-v)T \right)^{k-1/2}$
Log response ratio: additive design	$\mathrm{LRA}_m = \log\left(\dot{H}_m(v) \right) - \log\left(\dot{H}_{m,\mathrm{mono}}(v) \right)$ $= \log \left(\frac{f_n \varepsilon_m v^a \sqrt{v + d(1-v)}}{\left(f_n \varepsilon_m v^a + f_m e_n (1 - v^a) \right) v^{k+1/2}} \right)$	$\mathrm{LRA}_n = \log\left(\dot{H}_n(v) \right) - \log\left(\dot{H}_{n,\mathrm{mono}}(v) \right)$ $= \log \left(\frac{f_m \varepsilon_n (1 - v^a) \sqrt{v + d(1-v)}}{(1-v)^{k+1/2} \sqrt{d} \left(f_m \varepsilon_n (1 - v^a) + f_n e_m v^a \right)} \right)$
Log response ratio: replacement design	$\mathrm{LRR}_m = \log\left(\dot{H}_m(v) \right) - \log\left(\dot{H}_m(v = 1) \right)$ $= \log \left(\frac{f_n \varepsilon_m v^{a-1} \sqrt{v + d(1-v)}}{f_n \varepsilon_m v^a + f_m e_n (1 - v^a)} \right)$	$\mathrm{LRR}_n = \log\left(\dot{H}_n(v) \right) - \log\left(\dot{H}_n(v = 0) \right)$ $= \log \left(\frac{f_m \varepsilon_n (1 - v^a) \sqrt{v + d(1-v)}}{(1-v) \sqrt{d} \left(f_m \varepsilon_n (1 - v^a) + f_n e_m v^a \right)} \right)$

Note: See Table 1 for parameter descriptions.

† $D_{nm} = 1/D_{mn} = (1 - v)/v$. Correlation factor for within patch movements when plant numbers of *m* and *n* are different.

olfactory, and visual search (Bukovinszky et al. 2005). Many insects use multiple cues to find a host (e.g., they start by following an odor cue, switch to visual cues to find a plant to land on, and then use taste to verify host plant identity; Schoonhoven et al. 2005), but arrival rates depend most strongly on the cue acting over the longest distance. Contact, olfactory, and visual searchers may respond differently to spatial heterogeneity due to different physical properties of their respective cues (Bukovinszky et al. 2005, Englund and Hambäck 2007). A patch for a visual forager may be the combined impression of a group of plants as they appear in the visual field, whereas a patch for an olfactory forager may be the combined odor plume from a set of neighboring plants. As a first approximation, based on both empirical and theoretical studies, we assume that

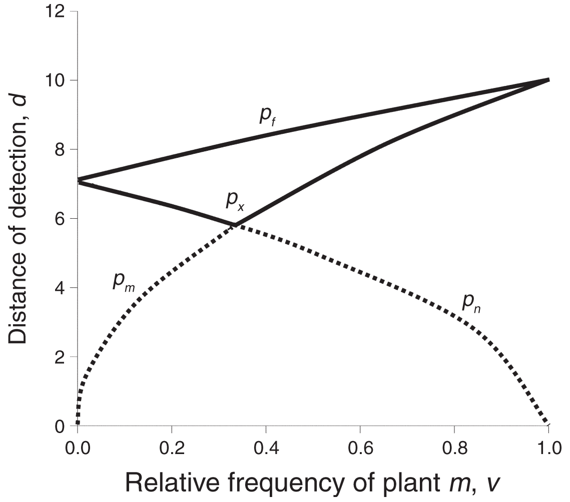

FIG. 2. Patch detection distances (d) for relative frequencies of two plant types m and n when insects detect the two plant types' odors through qualitatively different receptors (p_x) or when probability of detection is based on the combined odor concentration emitted from both types (p_f). For reference we also include the detection of either plant type alone (p_m and p_n). In this example, m is detected by herbivores from a longer distance ($d < 1$) and the total number of plants in the patch does not change with plant relative frequency.

the probability of visual foragers finding a patch depends on a power function of the area of the patch, whereas the probability of olfactory foragers finding a patch depends on a power function of the number of plants in the patch (Bowman et al. 2002, Englund and Hambäck 2007, Ioannou et al. 2011, Andersson et al. 2013). As patches all have the same diameter, but vary in plant density, the number of herbivores arriving at mixed and monoculture patches is the same for both visual and contact searchers.

Next we describe the scaling properties of olfactory search, as these are perhaps less intuitive than for visual searching. It is more straightforward to measure responses to odors than responses to what an insect is seeing, so an olfactory-based theory may be more amenable to empirical testing. Olfactory searchers first locate an odor plume emanating from a source, and then navigate upwind against the plume to locate the source. Locating a plume is typically the limiting step. Although pockets of high odor concentration can exist far from a source due to turbulence (Murlis et al. 1992, Riffell et al. 2008), the average odor concentration decreases roughly as a power relation of the distance from the source (Bossert and Wilson 1963, Andersson et al. 2013). If there is a threshold above which a forager is able to detect an odor, its maximum detection distance is proportional to the square root of the odor concentration at the source (Bossert and Wilson 1963). The exact scaling relationship depends on the vertical spread of the plume (Sutton 1953), but for real odor plumes, the deviation from a square-root relationship is small (Andersson et al. 2013). Because the probability of locating an odor plume is proportional to the square root of the odor concentration at the source, the probability p of finding a patch is also proportional to the square root of the number of odor sources (plants) when plant individuals have a common emittance rate (Table 1, Fig. 2).

The contrast between mixed and monoculture patches is likely to be different for visual and olfactory searchers, and should affect immigration rates to these patch types. If plant colors and sizes are similar, a visual searcher may not distinguish between mixed and monoculture patches, and patch type will have a small effect on immigration rates. In contrast, the strength of odor signals depends directly on the number of plants of each type in a patch. If plant types' odors are detectable at different distances, then patch detection distances will differ between mixtures and monocultures. We consider two cases for how olfactory searchers use plant information; real-world cases will vary between these end points. First, olfactory searchers may use the same volatiles for detecting the two plant types (or the same olfactory receptor detects multiple volatiles). In this quantitative case, plant types are *substitutable* sources of information, although they may have quantitatively different emittance rates. The maximum distance for detecting a mixed-plant patch will be a function of the combined odor plume from the two plant types (Table 1, Fig. 2; P_{f}). Second, searchers may detect qualitatively different odor molecules from the two plant types, using different receptors, making the two types *unique* sources of information on patch quality (Fig. 2; p_x). Because the two cases make similar predictions about herbivore load, equations for the qualitative case are given in Appendix A only.

When arriving in a patch, herbivores may land on either plant type (m or n). This process is not fundamentally different for contact, visual, and olfactory searchers because olfactory searchers typically use visual and contact cues to distinguish plants at short range due the poor directional information in olfactory cues (Finch and Collier 2000). We assume that relative landing rates on plant types in a patch depend on a combination of detection and selection. This process can be described with a selection coefficient similar to a functional response. When the selection coefficient $a = 1$, herbivores arrive on the two plant types in proportion to plant frequency. When $a > 1$, landing is biased toward plant type n and vice versa when $a < 1$. The final part of the immigration function translates the number of herbivores arriving at a certain plant type to herbivore load (herbivores per plant), by dividing by the number of plants within a patch (Table 2).

Within-patch movements and emigration

When herbivores leave a plant, they may leave the patch entirely or move to a neighboring plant. The probability of these events depends on the herbivore decision process.

For example, pierid butterflies leaving a plant fly for some time before landing again (Bukovinszky et al. 2005); movements among plants in a patch are thus less likely than movements out of a patch. Other herbivores, such as chrysomelid beetles, move more randomly within a patch until randomly leaving it (Kareiva 1985). Finally, some herbivores, such as root flies and aphids, move randomly until finding a suitable host plant; emigration may be induced by repetitive encounters with less suitable plants (Kennedy and Stroyan 1959, Finch and Collier 2000). In our model, we distinguish three rates determining movement within and out of patches: leaving from each plant type, movements onto a plant neighbor of either type, and movements out of the patch (Table 2; within-patch movements and emigration). Movements onto a plant neighbor are guided by the same rule as when the patch is found originally. We describe the redistribution of individuals as: −[the leaving rate from plant *m*] + [the proportion landing on plant *m*] × [the total number leaving all plants]. Patch-leaving rates can depend on patch area as well as plant number (Englund and Hambäck 2004), but we assume that plant density varies within a patch of a common size and ignore area dependence.

Because the rate of change in herbivore load on each plant type is linear with respect to the herbivore load on that type, the differential equation system can be integrated to derive functions describing the temporal dynamics of herbivore loads. The resulting equations are quite complex, so we only show the expression for equilibrium herbivore load (Table 2).

MODEL ANALYSES

We use our model to identify the strength and sign of neighborhood effects under different conditions for how herbivores move, and for both replacement and additive experimental designs, as both designs are commonly used and reflect real-world properties of plant patches. The most common replacement design uses a fixed total number of plants per patch, varying only the plant type frequency (Fig. 1). In our model, this design corresponds to holding total plant number T constant and varying frequency v in the model (Fig. 3, Table 2), where the patch is a monoculture when $v = 0$ or $v = 1$. In an additive design, the density of one plant type is held constant while the density of the other type is varied. To implement this design in our model, mixed patches are modeled as before, but monocultures correspond to setting the number for one plant type to zero, leaving holes in the patch for the removed plants (Fig. 1, Table 2).

To make our results comparable to field experiments, we show outcomes for two measures of herbivore attack: the distribution of herbivore loads between plant and patch types and the expected sign and magnitude of neighborhood effects (Fig. 3). We express neighborhood effects as the log ratio of herbivore loads in mixed vs. monoculture patches (LRR_x or LRA_x for replacement or additive designs, respectively; Fig. 3, Table 2). Positive log ratios indicate greater herbivore loads in mixed patches (indicating associational susceptibility, AS), whereas negative log ratios indicate greater loads in monoculture (indicating associational resistance, AR). Log ratios may differ from zero because of effects of either neighbor frequency or plant density, depending on which experimental design is used (Fig. 4). Because dilution effects should only contribute to AR, positive log ratios can safely be interpreted as AS, but AR could be a combination of frequency and density effects.

RESULTS AND PREDICTIONS

For most parameter combinations, the herbivore load per plant in mixed patches differs dramatically from the load in monoculture patches. These neighborhood effects almost always depend nonlinearly on the relative frequencies of plant types in a patch, indicating associational effects. Most commonly, insect loads are lower on plants in mixed than monoculture patches, indicating AR. However, the magnitude and direction of the effects depend on the relative detection distances for and emigration rates from plant types, the within-patch responses to plant types, and the experimental design (additive vs. replacement).

We will summarize when we observe associational resistance, associational susceptibility, or a mix of both responses (where mixed responses can mean different responses for the two plant types, or different responses for the same type depending on relative plant frequency). In some cases, outcomes depend on the relative proportion of plants in a patch. Here we describe the general findings, but detailed discussion of outcomes for a wider range of parameter combinations can be found in Appendix B. In the analysis, we focused on four parameters and their combinations (Table 1), representing herbivore and plant trait effects on host selection at different stages: the relative detection distance of the two plants (d), representing long-distance search; the within-patch selection (a); and the plant-dependent patch-leaving rates (ε_m or ε_n). The model contains additional parameters (Table 1), but effects on herbivore load always come from changes in patch arrival and leaving rates (which influence the number of herbivores per patch) and within-patch selection. Our focal parameters cover all of these events. Different combinations of parameter values match different typical insect behaviors. For example, assume that long-distance patch detection and emigration from the patch depend on plant identity (i.e., $d \neq 1$, $\varepsilon_m \neq \varepsilon_n$), whereas within-patch selection is random ($a = 1$). These assumptions would mimic host-finding by insects such as cabbage root flies, where patches are found using host plant odors, selection within patches is random (females land on every green object including non-host plants), and leaving rates depend on plant identity (Prokopy et al. 1983, Finch and Collier 2000). Alternatively, assume that herbivores are unable to differentiate among patches from a distance ($d = 1$), but select strongly among plant types within patches ($a \neq 1$). These

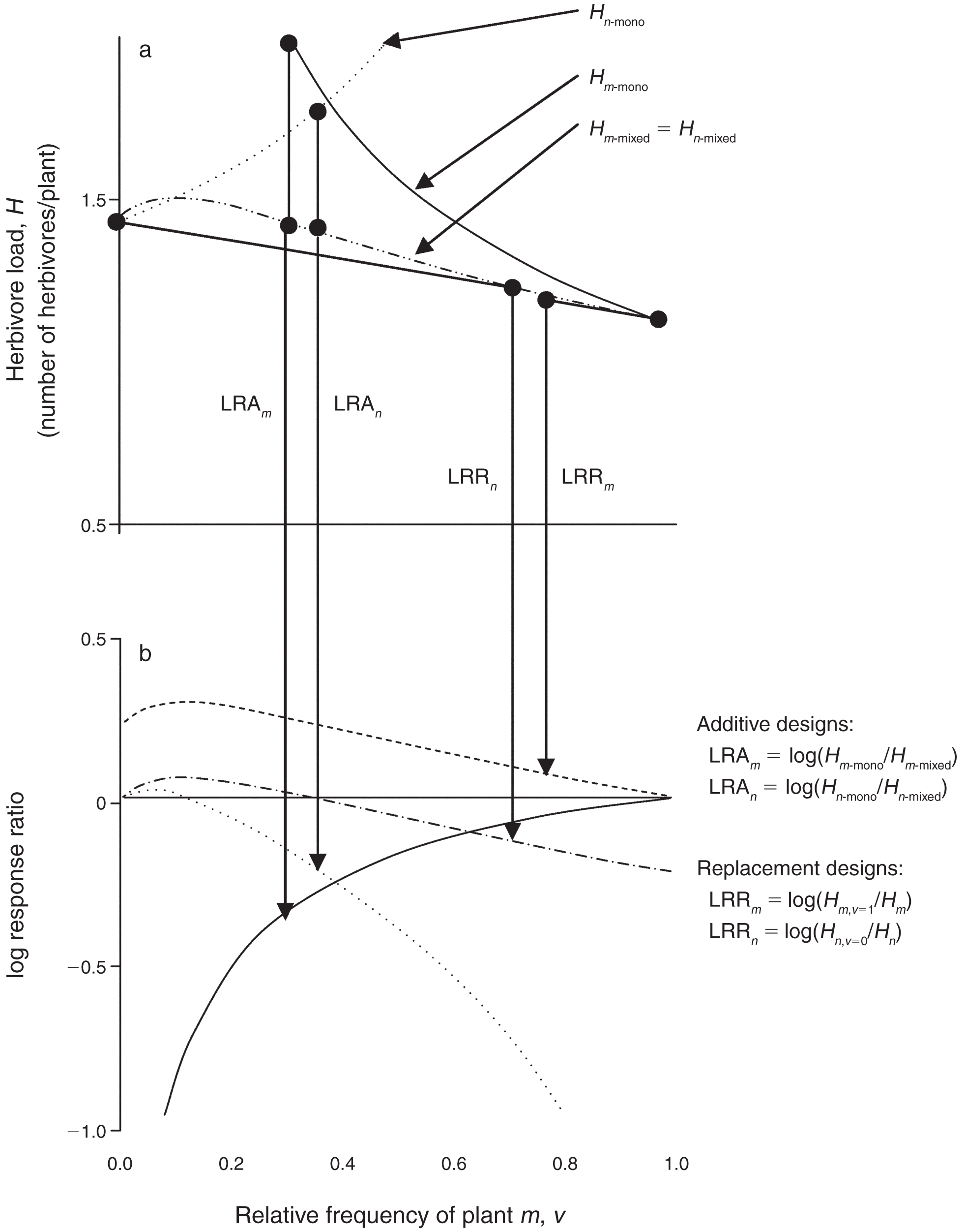

FIG. 3. (a) Herbivore load (H) and (b) log response ratios (LRA for additive designs; LRR for replacement designs) for the two plant types (m and n). In panel (a) the line types indicate per plant loads for the type m monoculture (solid line), type n monoculture (dotted line), and mixed patches (dot-dashed line). Note that because there is no within-patch selection for the results presented here ($a = 1$), the herbivore loads in the mixed patches are identical for the two plant types. The log response ratios in panel (b) are based on the ratios of herbivore loads in mixed patches and monocultures (solid line, LRA$_m$; dotted line, LRA$_n$; dashed line, LRR$_m$; dot-dashed line, LRR$_n$). Parameter values (defined in Table 1) are: $i = 1$, $a = 1$, $d = 0.1$, $T = 20$, $f_m = f_n = 0.2$, $\varepsilon_m = 0.2$, $\varepsilon_n = 0.05$.

assumptions mimic host-finding by butterflies such as pierids, which seem to select host plants based on close-distance comparison (Hambäck et al. 2009).

Identical plant types

To grasp the general idea of the model, first consider a patch with two identical plant types ($a = 1$, $d = 1$, $\varepsilon_m = \varepsilon_n$). In this case, mixed and monoculture patches in *replacement* designs contain identical resources from the herbivore perspective. Changing the relative frequency in a replacement series of the two plants does not affect either herbivore load (Fig. 5a; dashed-dot line) or log response ratios (LRR$_m$ = LRR$_n$ = 0, Fig. 6a); thus there are no neighborhood or associational effects. In

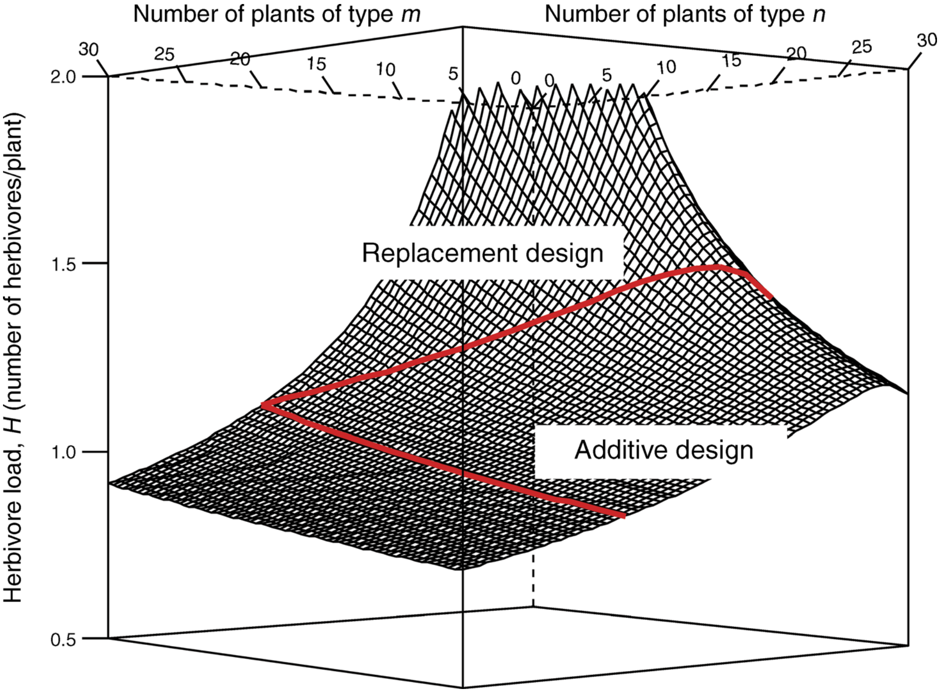

FIG. 4. Response surface showing the herbivore load for combinations of plant m and n densities. Thick lines indicate the points that would be observed using replacement and additive designs, illustrating why different experimental designs can lead to different conclusions about the sign or magnitude of an associational effect. The line for the additive design (parallel to the plant m axis) holds focal plant density constant, thus isolating the effect of increasing neighbor density from focal plant density. The line for a replacement design holds total plant density constant, thus showing the combined influence of neighbor frequency effects and density-dependent effects. Parameter values are as in Fig. 3.

contrast, mixed and monoculture patches in *additive* designs differ because the mixed patches have more plants. The square-root relationship between plant density and odor plume detection (Table 2) means that resource dilution effects occur, because an increase in the number of plants in a patch outstrips the increase in arriving herbivores. Thus, herbivore loads on the focal plant are lower in mixed than in monoculture patches (LRA_m and LRA_n are negative; Fig. 6a, solid and dotted lines) because herbivores perceive plants identically and are subject to resource dilution (Fig. 5a, solid and dotted lines). This pattern might be interpreted as AR even though it has nothing to do with the frequency of plant types, because different plant traits do not vary.

Mixed responses: AR for one plant type and AS for the other plant type

We start with this prediction because previous work (both theoretical and empirical) has commonly found such mixed responses. Our analyses suggest that mixed responses should indeed be the most commonly observed pattern, with some notable exceptions, but mainly in replacement designs. This pattern arises in two main cases: (1) when parameters are such that herbivore loads differ between plant m and n monocultures, or (2) when herbivore loads are the same in mixed and monoculture patches, but herbivores select between plants within mixed patches. In the first case, loads differ between plant monocultures because plant types are detected from different distances ($d \neq 1$; Fig. 5c) or when one plant type induces a higher emigration rate from the patch ($\varepsilon_m \neq \varepsilon_n$; Fig. 5b, f). If within-patch selection is random ($a = 1$), then loads on the two plant types are similar in plant mixtures and vary monotonically between the loads for the plant types in monoculture. Consequently, the plant with a lower herbivore load in monoculture will have a higher load in mixtures, and vice versa (Fig. 5b, c, f), leading to AR for one plant and AS for the other (Fig. 6b, c, f). In the second case, a pattern with mixed responses arises even though loads are similar in the two plant monocultures ($d = 1$, $\varepsilon_m = \varepsilon_n$), because herbivores select among plant types within patches ($a \neq 1$), causing densities to be higher on one plant type than the other in mixed patches. In additive designs, mixed responses are possible for essentially the same reason, but over a smaller range of parameter values where the effect of plant density is quantitatively more important than the effect of plant relative frequency for herbivore load.

In a third case, and only for replacement designs, the model prediction depends on plant relative frequency. When loads in monocultures differ due to a difference in emigration rate and within-patch selection is nonrandom ($a > 1$ and $\varepsilon_m > \varepsilon_n$), the magnitude of AS for plant

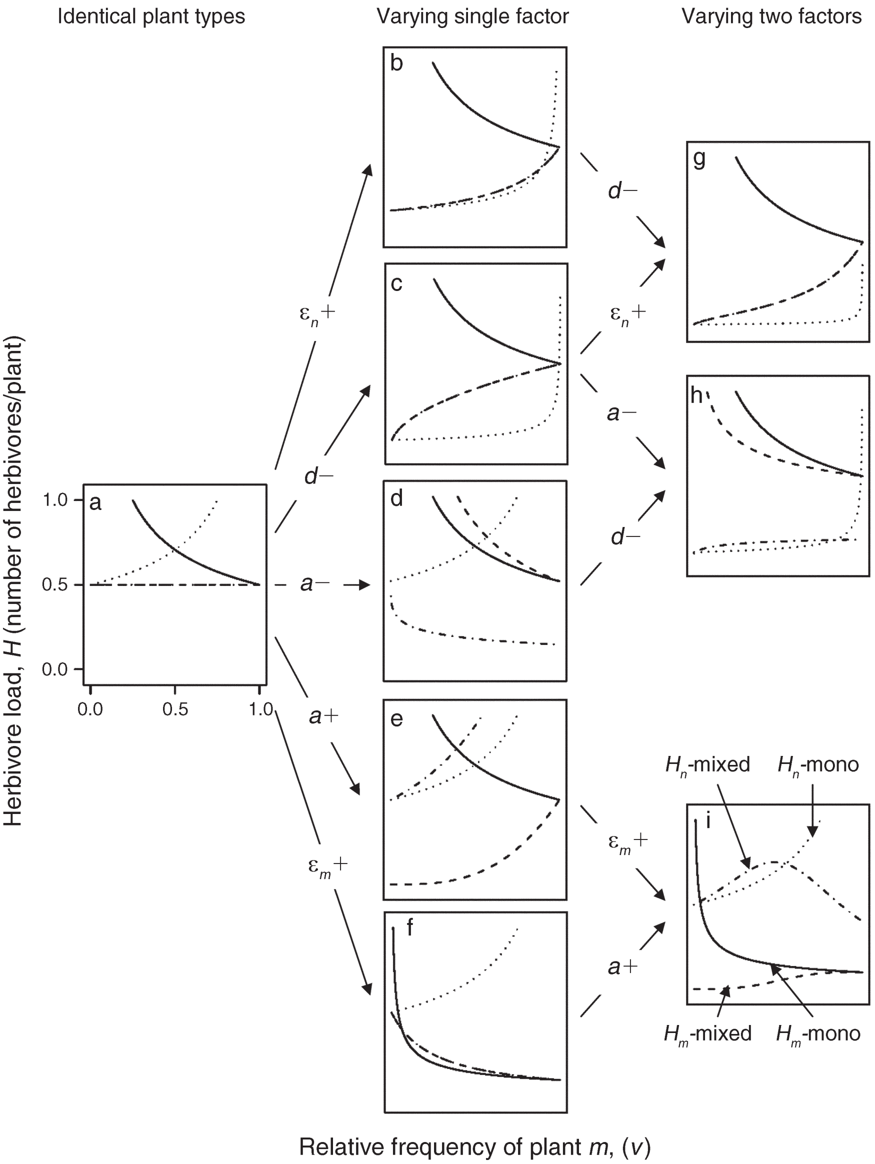

FIG. 5. The effect of varying model parameters on herbivore load in monoculture (type *m*, solid line; type *n*, dotted line) and mixed patches (type *m*, dashed line; type *n*, dot-dashed line). All *x*-axes show relative frequency of plant type *m*; all *y*-axes show herbivore load, *H*. Note that these lines completely overlap for many parameter values, as in panels (a–c) and (g). Panel (d) is the baseline model when parameters are identical for the two plant types. Parameter values for the baseline model are: $a = 1$, $d = 1$, $\varepsilon_m = \varepsilon_n = 0.2$. Modified parameter values in panels (b–i) are: $\varepsilon_n+ = 0.8$, $d- = 0.01$, $a- = 0.25$, $a+ = 4$, $\varepsilon_m+ = 1$. Other parameter values are as in Fig. 3.

n changes nonlinearly (Fig. 6i), is strongest at intermediate plant frequencies, and can switch to AR at a low relative frequency of plant *n* (high *v*). To understand this pattern, recall that $a > 1$ implies biased landing on plant *n*, while a higher ε for either species increases the overall leaving rate from the patch. As $\varepsilon_m > \varepsilon_n$, the leaving rate increases and thus the total herbivore density decreases with plant *m* frequency. This reduced total herbivore density in the patch lowers the load on both plants in mixtures compared to their respective monocultures, resulting in AR. However, at high plant *n* frequency (low *v*), compared to the plant *n* monoculture, the biased landing on plant *n* increases the load on plant *n* more than the increased total leaving rate decreases it, resulting in AS for plant *n*.

Associational resistance (AR) for both plant types

Our analysis suggests that AR for both plants is a common pattern for additive designs, whereas this pattern should almost never be observed for replacement designs (Fig. 6). Because additive designs vary relative frequency and total plant density simultaneously,

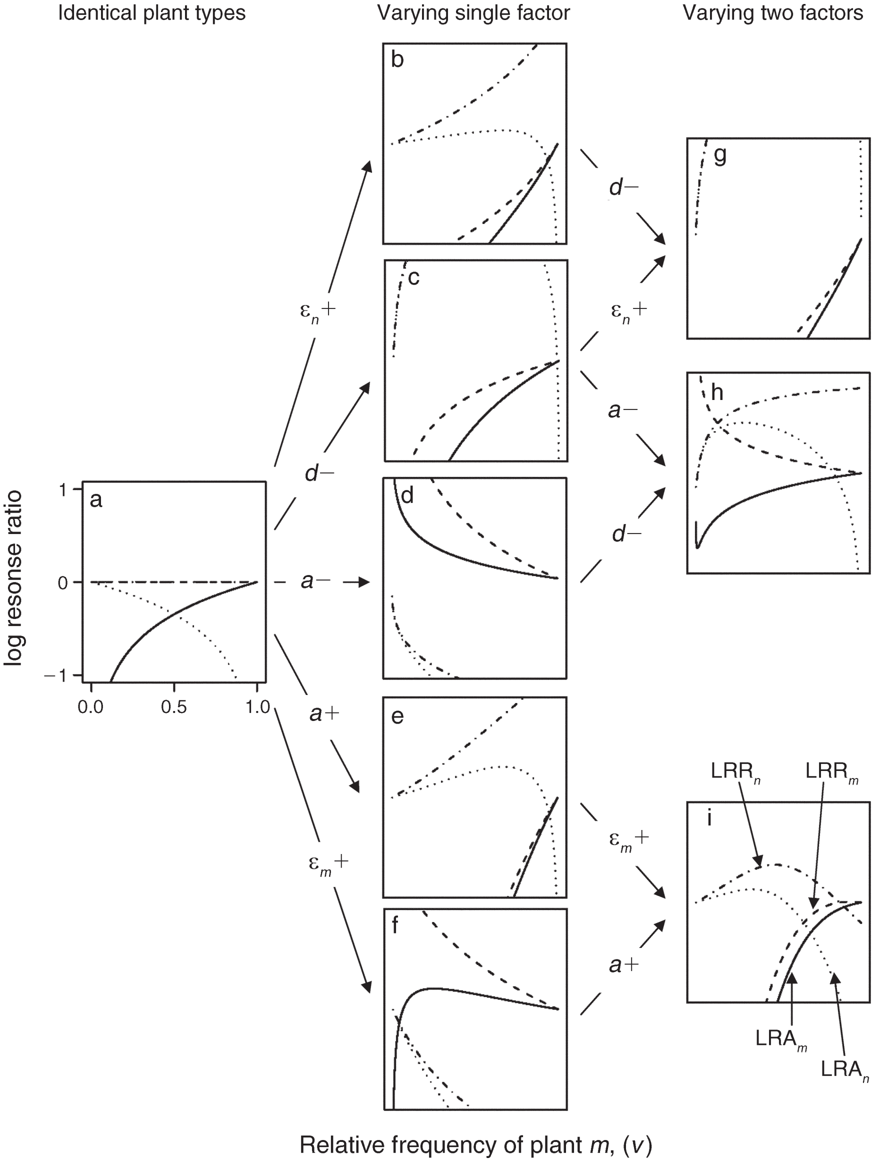

FIG. 6. The effect of varying model parameters on log response ratios for additive (solid line, LRA_m; dotted line, LRA_n) and replacement (dashed line, LRR_m; dot-dashed line, LRR_n) designs. All x-axes show relative frequency of plant type m; all y-axes show the log response ratio. Parameter values are as in Fig. 5.

changes in herbivore load in additive designs are due to a combination of effects of relative plant frequency and plant density (dilution effects). Dilution effects occur when herbivore immigration rates do not increase proportionally to the number of plants in a patch, which in this model is due to the square-root relationship between plant density and odor plume detection. In a resource-dense patch, herbivores have more plants over which to be distributed and the load on each plant is lower than in a resource-sparse patch. Total plant densities in additive designs are invariably higher in plant mixtures than in the focal plant's reference monoculture (Fig. 4), so dilution effects almost always cause lower herbivore loads for both plant types in mixtures.

For AS to occur in additive designs, trait differences causing frequency-dependent associational effects have to override dilution effects. In the model analysis, AS was observed for some parameter combinations, but the sign and magnitude of neighborhood effects depended on plant frequency. For instance, when $\varepsilon_n > \varepsilon_m$ (Figs. 5b and 6b), or vice versa when $\varepsilon_n < \varepsilon_m$ (Figs. 5f and 6f), AS was predicted for plant n at a high to intermediate plant n frequency, and AR was observed at a low plant n frequency. To interpret this pattern, note that relative to the plant n monoculture ($v = 0$), when $\varepsilon_n > \varepsilon_m$, adding a few m plants (small v) reduces the overall leaving rate from the patch, increasing herbivore loads on individual plants more than the dilution effect (due to increasing total plant density) lowers the herbivore load. On the other hand, at high v, dilution effects are quantitatively more important.

Associational susceptibility (AS) for both plant types

In our analysis, AS for both plants was only observed in replacement designs, and only when the detection distance (d) and within-patch selection (a) both strongly differed from 1. Specifically, AS was observed for both plant types when the plant type that is detected from a longer distance is also more attractive within the patch ($a < 1$ and $d < 1$, or when $a > 1$ and $d > 1$; Fig. 6h, $\mathrm{LRR}_n > 0$ and $\mathrm{LRR}_m > 0$). Although both plant types experience AS in mixed patches for this set of parameter combinations, the effect on the two plants occurred for different reasons. For plant n, loads in monocultures are low because plant n is not detected from a distance and patches therefore receive few immigrants. Adding even a few plant m individuals radically increases patch detection rates and at least some herbivore individuals land on plant n, increasing plant n loads in mixtures relative to monocultures (AS). Plant m loads in mixtures are higher than loads on plant m in monoculture for a different reason. Although individuals of plant n do reduce immigration of herbivores to the mixed patch (which would tend to decrease loads on plant m), they also reduce the number of plant m individuals in the mixture. Because herbivores mainly land on plant m, lowering the number of plant m individuals increases loads on plant m, a dilution-type effect. Increasing plant n frequency decreases immigration to the patch more slowly than it decreases plant m frequency, resulting in AS for plant m. As differences in detection distance become weaker ($d \rightarrow 1$), the pattern reverts to AS for one plant type and AR for the other type.

Discussion

Effects of plant neighborhood on herbivore responses to plants have been observed in many systems (Root 1973, Andow 1991, Feldman 2008), but are highly variable among studies in their presence, magnitude, and sign. This variation is probably due to the fact that herbivore search is a multi-scale process, and is affected by both herbivore and plant traits that affect detection and movement choices. Previous theory for neighborhood effects largely lacks mechanistic foundations. The models we develop here provide a framework for predicting effects of relative frequency and density of plant types on herbivore attack rates on plants in mixed patches, accounting for the hierarchical decision process of herbivores searching for and selecting resources both within and among patches. We found that associational and density-dependent effects can arise through processes acting at each hierarchical level, due to differences among plant types in detection distance, consumer selectivity within a patch, and patch-leaving rates. The predicted net changes in herbivore loads are usually nonlinear functions of plant relative frequency. Our results show that systems in which movement processes occur at multiple spatial scales can show a variety of associational effects, and that the effects that can be observed are constrained by the choice of experimental designs.

The pattern most often observed in empirical studies of plant–herbivore systems is that the presence of a less preferred food type lowers attack on a more preferred type, and vice versa (Pfister and Hay 1988, Hjältén et al. 1993, Hambäck and Beckerman 2003). Our analysis reproduces this pattern for many parameter combinations, for instance where herbivore loads on a less apparent plant, i.e., one less detectable from a distance, are higher when growing with more apparent plants than in a monoculture, and vice versa. However, we also find that more complex patterns are possible, which may explain the highly variable outcomes among field experiments (Andow 1991). For instance, higher landing rates on one plant type and higher leaving rates from the other type, common behavioral decision rules in plant–insect systems, can result in a hump-shaped relationship between plant frequency and herbivore load (Fig. 5i).

We find that the choice of experimental design strongly influences the type and magnitude of associational effects that will be observed. This result should hold across systems. Our analyses show that associational susceptibility (AS), at least for one of the plant types, should be commonly observed in experiments that use replacement designs, whereas associational resistance (AR) will be the dominant pattern for experiments using additive designs. This difference arises because additive designs manipulate total plant density and plant relative frequency simultaneously, whereas replacement designs only manipulate plant frequency (Figs. 1 and 4). Monoculture patches in additive designs always have a lower total plant density than mixed patches, and higher plant density invariably leads to a dilution effect. Whether the dilution effect is quantitatively stronger than the effect caused by varying plant frequency depends on parameter values, but dilution is strongest when herbivores either detect plants from very different distances (d is far from 1) or when landing on plant types within patches is strongly biased (a is far from 1). In replacement designs, dilution effects are generally weak, so that net changes in herbivore loads are largely due to shifts in the frequencies of plants with different traits. Only a few studies have combined additive and replacement designs, providing partial tests of these predictions. As predicted by our models, Hambäck et al. (2010), working with a mixture of cabbage herbivores, found that AR was strong with an additive design and absent in a replacement design; two studies working with cassava hornworms (Gold et al. 1990) and cucumber beetles (Bach 1980) found stronger AR in the additive than in the replacement design. In a fourth study, on Mexican bean beetles (Coll and Bottrell 1994), there was no effect of varying plant density per se, suggesting that in this system the dilution effect was weak.

Our model suggests that ecologists using additive vs. replacement experimental designs are likely to derive different inferences about mechanisms for neighborhood effects on herbivore attack and opposite conclusions about whether these effects are positive or negative, even within the same system (Fig. 4). In addition, when associational effects are humped rather than linear, experiments that compare only two frequencies of plant types could detect positive, negative, or no effect of increasing the relative frequency of a focal plant type, depending on which two frequencies are compared. To help make results of different studies comparable, future studies should report the frequencies and absolute densities of the two (or more) resources used in experiments. For studies focusing on natural systems, it is also important to document how density and frequency of plant types in mixed patches (co)vary in nature.

Our results show, not surprisingly, that the effects of plant neighborhoods on herbivores depend on how herbivore and plant traits combine to determine herbivore behavior. When resource selection depends only on long-distance detection and on patch-leaving, our prediction is AR for the more apparent (and AS for the less apparent) plant types in mixed patches. This pattern will be most likely for species where landing on plants within patches is random (e.g., root flies; Finch and Collier 2012). On the other hand, when herbivores have biased landing rates on plants within patches, our analysis predicts that both plant types will experience AS (in the likely case where the more apparent plant is also more attractive within patches). When decisions are made through a combination of local (within-patch) attraction and patch-leaving behavior, the most likely scenario is that the plant that is more likely to cause herbivores to leave a patch will also be less attractive at short distances. In this case, our analysis finds a combination of AR and AS, but the strength of AS varies strongly with plant relative frequency and can even shift to AR. The fact that herbivore and plant traits influence associational effects so strongly suggests that it is unlikely that a single model of associational effects will apply to all systems. Herbivores that respond to plants at the patch scale vs. a within-patch scale should show different patterns of associational effects. To derive predictions for a wider range of herbivores, detailed information is needed on variation in the host-finding decision process among systems.

Ideal tests of the predictions from our model require manipulations of both plant relative frequency and density and quantifying components of the herbivore decision process. Our analyses suggest three behavioral traits to be quantified. First, the relative detection distances (d) for two resource types can be estimated with electrophysiological methods, such as electroantennograms, or with live animals by observing biased movements in wind tunnels or mark–release–recapture studies (Östrand and Anderbrant 2003, Andersson et al. 2013). The other two traits, movements within patches and leaving rates from plants, can be estimated by following individual insects (e.g., Bukovinszky et al. 2007, 2012). Quantifying these traits would make it possible to directly compare data to our model; deviations from predicted outcomes might suggest that features not included in our model, such as synergistic or inhibitory effects of multiple odor cues, strongly influence associational effects.

Associational effects may, of course, be influenced by factors not considered in our analyses. First, odor plumes are affected by the physical structure of the habitat (Voskamp et al. 1998, Murlis et al. 2000). Predictions for associational effects could therefore differ for forests vs. open areas, where strong winds can cause fast dilution of odor signals and sources are detected at shorter distances (Voskamp et al. 1998). Second, changing plant relative frequency often changes plant size, which indirectly affects attractiveness to herbivores. For instance, plant size should decrease with an increasing plant frequency when interspecific competition is weaker than intraspecific competition. Such variation could be phenomenologically included in our model by assuming that the strength of an odor signal is proportional to plant biomass rather than plant number. Third, selection among plant types within patches can depend on distances among individual plants (Alm-Bergvall et al. 2006, Hambäck et al. 2009). Finally, these processes should be integrated with population models that also account for competition between plants, such as a study by Stephens and Myers (2012) that examines the interactions between plant competition, herbivory, and patch size. A similar model of plant mixtures could use the predictions from our model to explore consequences for plant growth and population density.

Although our model focuses specifically on insect herbivore responses to plant neighborhoods, aspects of this model are applicable to other insect consumers, especially pollinators and natural enemies of herbivores. Pollinators and insect predators move at similar scales as herbivores, and are known to respond to plant traits including odor plumes and size, although pollinators may be more reliant on visual cues. Natural enemies such as many parasitoids respond to cues from prey and their host plants, making their distributions functions of both prey associational effects and predator associational effects. There may also be reasons to expect pollinators and natural enemies to respond differently to resource complexity; these effects may be traced to differences in the type of cues used and in the cognitive capacities of foraging insects. For instance, social hymenoptera are central-place foragers that may recruit additional foragers to flower patches, which may modify the distribution of foragers in the landscape (Baude et al. 2008). Similarly, both herbivores and natural enemies are known to respond to volatiles induced by plants upon attack. The effect of such positive feedbacks on consumer distributions in patch size gradients have been previously explored both theoretically and empirically (Turchin 1989, Bukovinszky et al. 2010, Hambäck et al. 2012).

In conclusion, the complexity of behavioral responses by insects and other consumers to resource heterogeneity necessitates a more quantitative approach than has normally been used in field experiments addressing associational effects. Most experiments use designs that do not separate effects of plant relative frequency and density, but assume that any observed effects are due to plant relative frequency. The nonlinearities predicted in this study suggest that future studies should use a wider range of density and frequency manipulations. Herbivores searching for a plant may respond to both the density of specific plants and the relative frequency of different plant types. Ultimately, we would like to be able to use small and short-term experiments to predict larger scale or longer term effects of associational effects, such as designing uses of mixed plantings to control agricultural pests, or inferring how associational effects might influence plant communities. To extrapolate beyond a particular study, qualitative manipulations (i.e., comparing presence and absence of one plant type) are insufficient. We advocate an approach in which behavioral responses are specifically measured over a range of variation in both plant density and frequency, such that models for herbivore responses can be parameterized.

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SUPPLEMENTAL MATERIAL

Appendix A

Model analysis of qualitative case, when herbivores use qualitatively different olfactory information to find different plant types (*Ecological Archives* E095-118-A1).

Appendix B

Detailed results on the effects from varying model parameters for the quantitative case (*Ecological Archives* E095-118-A2).