

THE QUARTERLY REVIEW *of* BIOLOGY



A CONCEPTUAL FRAMEWORK FOR ASSOCIATIONAL EFFECTS: WHEN DO NEIGHBORS MATTER AND HOW WOULD WE KNOW?

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KEYWORDS

associational resistance, frequency dependence, plant-herbivore interactions, plant-pollinator interactions, neighborhood effects, ecological consequences of diversity

ABSTRACT

Interactions between individual consumer and resource organisms can be modified by neighbors, e.g., when herbivory depends on the identity or diversity of neighboring plants. Effects of neighbors on consumer-resource interactions ("associational effects") occur in many systems, including plant-herbivore interactions, predator-prey interactions (mimicry), and plant-pollinator interactions. Unfortunately, we know little about how ecologically or evolutionarily important these effects are because we lack appropriate models and data to determine how neighbor effects on individuals contribute to net interactions at population and community levels. Here we supply a general definition of

The Quarterly Review of Biology, March 2014, Vol. 89, No. 1

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0033-5770/2014/8901-0001\$15.00

associational effects, review relevant theory, and suggest strategies for future theoretical and empirical work. We find that mathematical models from a variety of fields suggest that individual-level associational effects will influence population and community dynamics when associational effects create local frequency dependence. However, there is little data on how local frequency dependence in associational effects is generated, or on the form or spatial scale of that frequency dependence. Similarly, existing theory lacks consideration of nonlinear and spatially explicit frequency dependence. We outline an experimental approach for producing data that can be related to models to advance our understanding of how associational effects contribute to population and community processes.

INTRODUCTION

IN MANY interactions between organisms, an individual's vulnerability to predation or parasitism can be influenced by the identity of nearby organisms. For example, herbivore attack on individuals of one plant species can be influenced by neighboring plant species, and predation risk for one butterfly species can be influenced by other butterfly species in the area. "Associational effects" is one term that is often used for these neighbor effects on the vulnerability of individuals to predation/parasitism. Because attack by predators and parasites can affect the fitness of both consumers (e.g., herbivores or predators) and resources (e.g., plants or butterflies), it is expected that associational effects should influence population-level processes (e.g., Atsatt and O'Dowd 1976; Thomas 1986; Pfister and Hay 1988; Russell and Louda 2005). For example, effects of neighboring plants on herbivore attack might alter the outcome of plant competition, and local frequencies of butterfly species might alter the outcome of natural selection on butterfly appearance. Associational effects have the potential to contribute to ecological and evolutionary patterns in the broad range of consumer-resource interactions that are spatially structured, especially given that associational effects can occur at the level of neighboring genotypes (Hambäck et al. 2009) as well as species. If associational effects influence population processes, they would constitute *individual-level* mechanisms generating indirect effects, which are generally measured at the *population* level. Unfortunately, our understanding of how associational effects contribute to net ecological and evolutionary outcomes is incomplete. A recent review of the extensive empirical literature on associational effects in plant-herbivore interactions (Barbosa et al. 2009), for example, concluded that

while we know these individual-level effects exist, we have little direct evidence of when or how they contribute to long-term or larger scale outcomes.

How would we determine how associational effects on individual vulnerability to predation or parasitism contribute to net ecological and evolutionary processes? Although direct empirical investigations following whole populations with and without neighbors over time might seem ideal, in most cases this is not practical, and might not lend much insight into the underlying processes producing different outcomes. Because the strength of associational effects should depend on both the frequencies and densities of resource organisms in a particular area, and our interest is in how neighbor effects *change* those frequencies and densities over time or space, it is clearly critical to understand the joint roles of frequency and density dependence in these systems. Mathematical models that include such frequency and density dependence could be used to predict the circumstances under which associational effects will change ecological or evolutionary outcomes, and could be fit to data to characterize how associational effects combine with other processes (e.g., direct competition between plants or natural selection from sources other than the consumer) to determine net outcomes (e.g., relative plant abundance or frequencies of butterfly traits). Although many empirical and theoretical studies have addressed neighborhood effects, empirical studies documenting mechanisms at the individual level generally have not provided the necessary data on local frequency dependence, and theory describing population- and community-level patterns mostly fails to address mechanisms at the

individual level that generate different forms and scales of frequency dependence. This lack of connection between theory and data means that we actually know little about how ecologically or evolutionarily important associational effects might be in many systems.

In this paper we address the question of how neighbor effects on consumer attack contribute to population-level processes. We do not review the extensive empirical literature documenting individual-level associational effects; such reviews already exist for particular types of systems (e.g., Ruxton et al. 2004, mimicry; Barbosa et al. 2009, plants and herbivores; Mitchell et al. 2009, pollination) and for apparent competition more generally (Chañeton and Bonsall 2000; van Veen et al. 2006). Instead, we first provide a synthesis of what is known about the contribution of associational effects to net population-level outcomes. To do this we develop a precise and general definition of associational effects that can be used across biological systems (e.g., predator-prey, plant-herbivore) and then use that definition to review relevant results from ecological and evolutionary theory. Second, we identify important gaps in previous modeling and empirical studies and suggest directions for future theoretical and experimental work. Our goal is to encourage the development of appropriate data and theory so that we can move beyond the clear message from previous work that associational effects exist at the level of interactions among individuals to understanding whether and how they contribute to long-term ecological and evolutionary outcomes.

WHAT ARE ASSOCIATIONAL EFFECTS? A DEFINITION

There are four distinct ways that other resource organisms around some focal individual might influence consumer attack on that individual: attack might be influenced by the diversity of resource organisms in the area, by the density or frequency of a particular type of resource organism, or by the density of the focal resource. The term “associational resistance” was originally coined

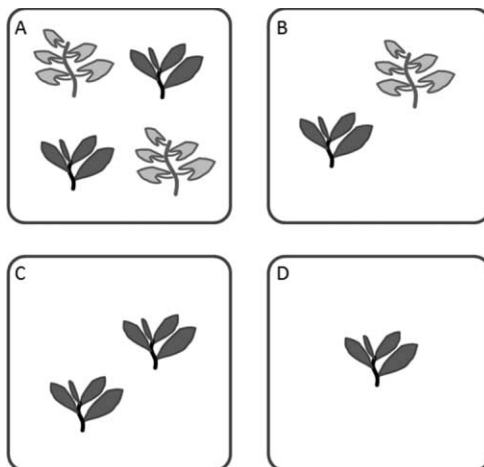


FIGURE 1. EXPERIMENTAL TREATMENTS OFTEN USED IN EMPIRICAL STUDIES OF ASSOCIATIONAL EFFECTS

Common experimental manipulations lead to changes in total density (A, C), the density of focal resource types (dark plants; B, C), the frequency of neighboring alternative resource types (light plants; B, D), or combinations thereof. Distinguishing effects of resource density from effects of neighbor frequency and type (associational effects) will require experimental designs such as response surfaces that manipulate both the density and frequency of resource types. One may also need to manipulate resource patch sizes.

to refer to differences in herbivore damage to individuals of a focal plant species between a diverse natural plant community (e.g., the polycultures in Figure 1 A or B; Tahvanainen and Root 1972) and a monoculture of the focal plant species (e.g., Figure 1 C or D). Unfortunately, this definition makes a mechanistic understanding of associational effects difficult because it encompasses all four ways in which neighborhood composition might influence attack. An observed effect of the diversity of neighbors around a focal individual might be due to diversity per se or to associated changes in focal organism density in that neighborhood and/or the identity or relative frequency of particular neighboring organisms (Bernays 2001; Lavandero et al. 2005; Hughes et al. 2008; Schröder and Hilker 2008). Since the term associational effects was coined, terminology for this

TABLE 1
Terms that have been used to refer to associational effects

Term	Meaning	Representative reference
Associational resistance	Neighbor diversity reduces damage to focal plant.	Tahvanainen and Root 1972
	Focal plant damage reduced by immediate neighbor through masking or repellency.	Agrawal et al. 2006
	A change in the spatial pattern of attack within a plant with more related neighbors.	Orians and Björkman 2009
Pollinator facilitation	Pollination of a focal plant is increased by neighboring plants of another species.	Feldman et al. 2004
Plant defense guilds	Plants are “functionally . . . interdependent with respect to their herbivores”; encompasses many mechanisms, including attraction of enemies, repellent plants, and attractant-decoy plants.	Atsatt and O’Dowd 1976:24
Magnet species	A rewarding plant species increases pollination of a neighboring species by attracting pollinators to the area.	Thompson 1978
Associational damage (versus associational protection)	“[I]ncreased damage to a plant growing amid a mixture of other species as the result of populations of some of its herbivores being supported or attracted by other plants in that plant community.”	Thomas 1986:115
Associational defense	Interchangeable with associational resistance.	Hay 1986
Associational refuge	A “plant that is susceptible to herbivory gains protection from herbivory when it is associated with another plant.”	Pfister and Hay 1988:118
Associational susceptibility	Increase in damage due to neighbors.	Letourneau 1995
Shared doom	Increase in damage caused by association with a more attractive species.	Wahl and Hay 1995
Neighbor contrast defense (or susceptibility)	Damage influenced by frequency of neighbors with different resistance levels in a patch when herbivores choose within patches rather than among patches.	Bergvall et al. 2006

For associational resistance we include three different uses to emphasize that this particular term has been used in many different ways. Except for the alternative uses of associational resistance, we attempt to cite the first use of each term.

phenomenon has proliferated (Table 1) and has been used to describe interactions between consumer and resource species at higher trophic levels (Barbosa and Caldas 2007; Hughes et al. 2010), for interactions between plants and pollinators (Thomson 1978; Johnson et al. 2003), and for interactions among plant genotypes with different levels of resistance (Tuomi et al. 1994). However, none of the terms in Table 1 clearly distinguishes the four types of neighborhood effects.

To develop a more precise definition for associational effects, we suggest excluding effects of the density of the focal organism type (e.g., species or genotype) in a neighborhood from associational effects. The term “associational” implies an effect of neighbors, by which we mean organisms of a different species or genotype than the

focal individual’s type, and many studies on neighborhood effects on consumer attack focus on effects of neighbors rather than focal organism density. An effect of the density of individuals of the same type as the focal individual could occur without neighbors, in monocultures of varying densities (i.e., resource dilution or concentration effects; Root 1973; Otway et al. 2005; Stephens and Myers 2012; see Figure 1 C versus D). Density dependence and effects of neighbor frequency could influence consumers differently at both individual and population levels, and both density and frequency dependence will need to be considered to understand how neighborhood effects influence populations. Although these processes must be separated to determine the contribution of associational (i.e., neighbor) effects to population-level re-

sponses, the vast majority of empirical studies of associational effects have used designs that preclude separating effects of the frequency or density of neighbors from effects of the local density of the focal organism (but see Rand and Louda 2004; Russell et al. 2007 for observational approximations). We suggest the following definition:

Associational effects occur when consumer effects on individuals of one resource organism type, at a given density of that type, are a function of the neighborhood composition of other resource types at particular spatial scales.

Associational resistance (or susceptibility) would be defined as reduced (or increased) consumer effects in a neighborhood with nonfocal neighbors relative to a monoculture of the focal organism. Resource organism types are groups of organisms that differ from other groups in traits that influence consumer behavior or performance, as associational effects might occur among organisms differing in relevant phenotypic traits at any level of taxonomic resolution, including species or genotypes (Agrawal et al. 2006) or even among genetically identical organisms with different phenotypes (e.g., induced defense level or ontogenetic stage). This definition avoids a common source of confusion in studies of ecological effects of diversity in general. Effects of diversity are often expressed or measured as effects of *number* of types (e.g., plant species; Andow 1991), but this is only relevant if types differ in traits affecting the response variable of interest (Hughes et al. 2008). For example, if plant species are identical in traits that influence herbivore attack (either directly or indirectly), then there can be no differences in attack between neighborhoods with different compositions and thus no associational effects. Consumers may also respond to total resource density, which is affected by all plant types. Although we exclude such total density effects from our definition of associational effects, it will be important for future researchers to separate the contributions of focal density, frequency, and total density.

Our definition specifies neighborhood *composition* to encompass both effects of a particular neighbor type, and effects of the diversity of neighbor types. Most models relevant to associational effects consider the dependence of consumer attack on the frequencies of two resource types (effectively modeling associational effects of a particular neighbor type). However, empirical studies, including the study coining “associational resistance,” often focus on neighbor diversity rather than frequency. For both effects of neighbor type and diversity, we expect that associational effects will be best described as a continuous multivariate function of the *frequencies* of neighbors, rather than as simply whether neighbors are present or absent. The shape of this function and how it changes with total density will dictate how associational effects influence population or community dynamics.

Finally, our definition specifies that associational effects are inherently spatially structured because most hypothesized mechanisms depend on spatial proximity or on a patchy spatial structure. Neighborhood size could vary from immediate neighbors to entire populations depending on the mechanism, and might even occur at landscape scales, but particular types of associational effects should have characteristic spatial scales. Mechanisms for associational effects in systems with mobile predators and prey (e.g., mimicry, where mobile prey species influence each other’s risk of predation) are likely to operate at larger scales than mechanisms in herbivore-plant systems, where plants experience direct and indirect interactions most strongly with immediate neighbors (Harper 1977). In this paper we focus on mechanisms for associational effects that depend on relatively fine-scale spatial structure, but mention related mechanisms with less spatial structure where appropriate.

POPULATION- AND COMMUNITY-LEVEL CONSEQUENCES OF ASSOCIATIONAL EFFECTS—WHAT DO WE KNOW?

The large empirical literature on associational effects demonstrates that associational effects exist, but few studies separate

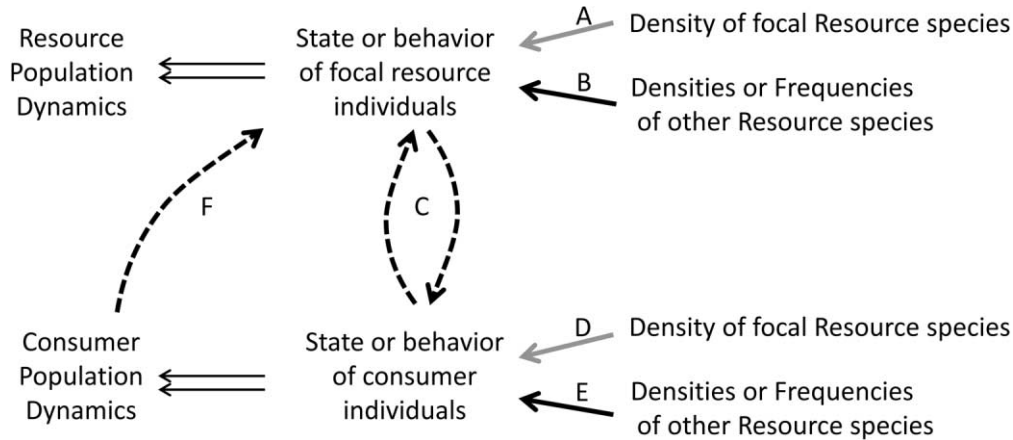


FIGURE 2: TYPES OF ASSOCIATIONAL EFFECTS

Associational effects can arise from a wide variety of mechanisms in many types of biological interactions, and can be positive (Holmes and Jepson-Innis 1989; Letourneau 1995) or negative (Tahvanainen and Root 1972; Holmes and Jepson-Innis 1989) for the focal resource. Here we sketch broad pathways through which associational effects can be generated. Because changes in neighbor frequency often entail changes in focal resource density, we also indicate focal density effects (gray arrows, A and D). At the broadest level, associational effects might be generated by effects of neighborhood composition on either resource (arrow B) or consumer (arrow E) traits. For example, neighboring plants might alter the quality of a focal plant for an herbivore by influencing the production of defensive traits (Cipollini and Bergelson 2001) or they might alter herbivore behavior by changing cues perceived by herbivores (Rausher 1981). There could also be feedback between the states of consumers and resources (arrow C), for example, if a change in plant quality changes herbivore movement (i.e., herbivores leave low-quality plants; van Dam et al. 2000) and herbivore attack changes plant quality through induced resistance (Karban and Baldwin 1997). Neighborhood composition can influence consumers at two levels. First, neighbors might affect individual consumer states/behavior (arrow E, trait-mediated effects). For example, Bernays (1999) found that whiteflies move among plants more frequently when they encounter host plants of varying quality, spending less time on high-quality hosts than they would otherwise. Second, effects of neighbors on consumer state/behavior might alter consumer population dynamics (arrow F, density-mediated effects), as in Underwood (2009) or Utsumi et al. (2011), where aphid population size was influenced by variance in quality among host plant genotypes. Finally, effects of neighbors on resources or consumers might be mediated by other classes of organisms (not shown in figure); for example, the enemies hypothesis suggests that neighboring plants may decrease damage to a focal plant by providing resources (e.g., nectar) or hosting alternative prey that attract herbivore predators or parasitoids (Elton 1958). Similarly, effects of neighboring plants on focal plant resistance to herbivores might be mediated by mycorrhizal fungi or other soil organisms (Pedersen and Sylvia 1996).

effects of focal density from neighbor density or frequency or diversity effects, and none provide these data as a function of spatial scale. These studies thus do not produce the data necessary to determine how associational effects influence net population or evolutionary dynamics (but see Underwood 2009; Dangremond et al. 2010). Moreover, few mathematical models use the terminology of “associational effects” (Table 1; but see Goulson 1994), so it might seem that little theory exists to address how

associational effects should influence populations. However, associational effects can arise in many different ways (Figure 2), and at various temporal and spatial scales (Figure 3), and relevant theory has been developed in several disparate fields. Many models include frequency-dependent, consumer-resource interactions (e.g., models of apparent competition and frequency-dependent selection), thus including associational effects phenomenologically. Below we review relevant theory in ecological and evolutionary

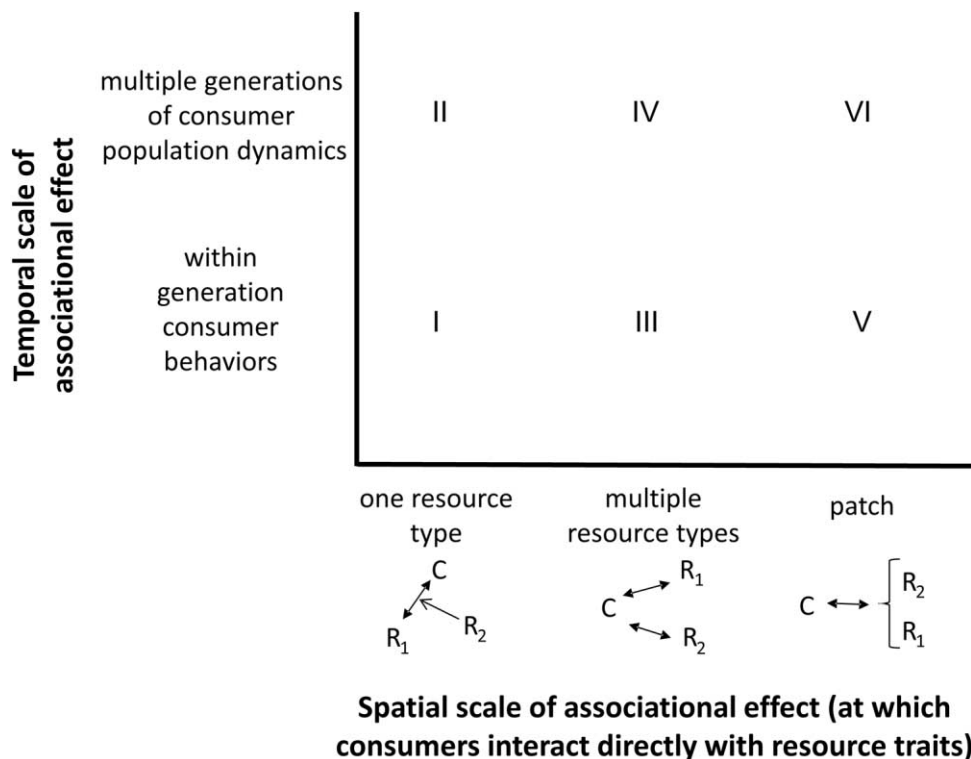


FIGURE 3. TEMPORAL AND SPATIAL SCALES OF ASSOCIATIONAL EFFECTS

Associational effects can arise at a variety of spatial and temporal scales; processes at multiple spatial scales may interact to produce net associational effects. There are two basic temporal scales of associational effects (top versus bottom of the y-axis): effects mediated by changes in consumer behavior occur within a single consumer generation, while effects mediated by population growth manifest across consumer and/or resource generations. This distinction is like that between short- (Holt and Kotler 1987) and long-term (Holt 1977) apparent competition, where for associational effects the response variable is the state of resource individuals, and for apparent competition the response is the size of resource populations. We distinguish three spatial scales of associational effects (x-axis). At the most local scale, neighbors modify consumer response to the focal resource without direct interaction between the consumer and neighbor (x-axis, “one resource type”). For example, neighboring plants might alter host plant quality by changing the availability of resources for production of defensive chemicals (Cipollini and Bergelson 2001). This scale of associational effect should occur only for consumers specializing on particular resource types (specialists). At a slightly larger scale, specialist or generalist consumers could interact with multiple resources within a patch (x-axis, “multiple resource types”). At this scale, consumer responses to different resource types could be either independent (additive), or nonadditive (not predictable from interactions with individual resource types in isolation). An example of a nonadditive effect would be if an herbivore’s propensity to accept a host were positively related to the resistance of recently encountered hosts (the herbivore might get hungrier if it rejects previous plants and thus is more likely to accept a suboptimal host; Finch and Collier 2000). Associational effects will also arise at a larger scale if consumers respond to patches of resources (x-axis, “patch”). This effect occurs when consumers are attracted to a patch from a distance or select among patches and then among plants within patches (Hjältén et al. 1993; Bergvall et al. 2006). For instance, if two plant types differ in volatile chemical emissions that herbivores use as cues for locating patches, and plants are distributed randomly within a patch, herbivores can be attracted to a combination of signals from all plants (the patch as a whole) rather than individual plants (Hambäck et al. 2014). Arrows in the x-axis legend indicate interactions resulting in the associational effect; additional interactions (e.g., competition between R_1 and R_2) are possible. Roman numerals refer to empirical examples and theoretical studies relevant to each scale of mechanism listed in Table 2.

models, and summarize what these models can and cannot tell us about associational effects.

ECOLOGICAL THEORY

Most ecological models that address long-term consequences of associational effects focus on apparent competition, which is the idea that a shared consumer (e.g., herbivore) mediates interactions between resource species (e.g., plants). Although the basic structure of apparent competition (two resource species and one consumer) matches that for associational effects, the initial model (Holt 1977) did not include frequency-dependent effects or differences in resource organism traits and thus did not model associational effects. This type of apparent competition could nevertheless cause a short-term empirical pattern that is indistinguishable from an associational effect, while transient dynamics influence attack rates.

Later models show that adding frequency dependent predation, within and among patches, on resources that differ in resistance or attractiveness to consumers can affect their coexistence (Holt and Kotler 1987; Kuang and Chesson 2010). Most other models also consider associational effects arising from consumers responding to patch-level properties (Table 2; regions V and VI in Figure 3). Other mechanisms are less well represented in models. Only two models address associational effects at the within-patch scale, making the individual risk of herbivory depend on individual resource neighbors (Underwood 2004; Orrock et al. 2010a; regions III and IV in Figure 3), and only Ishii and Crawley (2011) consider associational effects arising from consumer choice among patches. Models of frequency-dependent predation and plant competition often consider both behavioral and numerical consumer responses, although numerical responses are not required for the associational effect to influence resource coexistence (Holt and Kotler 1987; Orrock et al. 2010b).

Two additional model types have structures similar to apparent competition, but are different in focus. First, Underwood

(2004) focused on consumer population dynamics rather than resource organism frequency or coexistence, and showed that when host plants vary in quality (i.e., support different herbivore population growth parameters), herbivore population size on each plant type is influenced by trait variance among plants within a patch. This is an associational effect that operates across consumer generations. A second set of models focuses on ecological and evolutionary consequences of associational effects mediated by pollinators, which are both consumers and mutualists. When plants share pollinators, neighbors can influence the pollination success of a focal plant (e.g., Thomson 1978, 1983; Johnson et al. 2003; Mitchell et al. 2009) either by changing the number of visits received through attracting more pollinators to the area or diluting a limited pool of pollinators or by causing ineffective visits when pollinators move interspecifically and carry heterospecific pollen. Most models with shared pollinators include associational effects by making either visits or the effectiveness of visits depend on plant frequencies (e.g., Levin and Anderson 1970; Straw 1972; Goulson 1994). However, not all shared pollinator models include associational effects, for example, when visits depend only on the total density of flowers (e.g., Feldman et al. 2004) or when visits are frequency dependent due to dilution (e.g., Ishii and Higashi 2001); in neither case do results arise from differences in traits that influence pollinators between focal plants and neighbors. Most models of pollen competition contain no consumer population dynamics (but see Rodríguez-Gironés and Santamaría 2007; Benadi et al. 2012), and assume pollinators interact with multiple plant types within a patch (Table 2; Figure 3, region III). In contrast, Levin and Anderson (1970) considered pollinator attraction to a patch as a whole, and Tachiki et al. (2010) allowed for pollinator choice among patches (Table 2; Figure 3, region V).

EVOLUTIONARY THEORY

Theory has also explored how associational effects alter natural selection (e.g.,

TABLE 2
Empirical examples of mechanisms for associational effects and mathematical models addressing consequences of associational effects operating at different temporal and spatial scales

Location on Figure 3	Temporal scale	Minimum spatial scale	Empirical examples from plant-herbivore interactions	Mathematical models
I	Within consumer generation	One resource individual	Repellant plants (higher resistance neighbors cause herbivores to avoid focal plant; Hay 1986; Hambäck et al. 2000); insectary plants/enemies hypothesis (neighbors attract natural enemies that spill over to kill or frighten away herbivores on the focal plant; Stiling et al. 2003)	None
II	Multiple consumer generations	One resource individual	None	None
III	Within consumer generation	Two or more resource individuals	Herbivore oviposits on neighbor; neighbors thus increase damage on focal plant (Agrawal 2004)	Tuomi and Augner 1993; Tuomi et al. 1994; Orrock et al. 2010a
IV	Multiple consumer generations	Two or more resource individuals	Aphid populations on each plant genotype are a function of variance in aphid population growth parameters (r , K) across plant genotypes (Underwood 2009)	Underwood 2004
V	Within consumer generation	Patch	Voles and hares choose plants at both the patch level and the within patch level (Hjältén et al. 1993)	Holt and Kotler 1987; Turchin 1991; Tuomi et al. 1994; Leimar and Tuomi 1998; Orrock et al. 2010b
VI	Multiple consumer generations	Patch	None	Hambäck 1998; Yamauchi and Yamamura 2005; Křivan and Eisner 2006; Kuang and Chesson 2010; Ishii and Crawley 2011

References are examples, not exhaustive lists of all relevant studies.

the evolution of herbivore resistance in plants or the evolution of mimicry in butterflies). A series of models from the 1990s considers ways in which the local frequency of resistant and susceptible genotypes influences relative fitnesses in the presence of an herbivore feeding on two plant types. Some of these models consider associational effects at the scale of a patch (e.g.,

Tuomi et al. 1994; Leimar and Tuomi 1998; Table 2; Figure 3, region V), and others consider associational effects arising from interactions of consumers with multiple plant types within a patch (Tuomi and Augner 1993; Tuomi et al. 1994; Table 2; Figure 3, region III). These evolutionary models include associational effects mediated by consumer behavior, but not effects

mediated by population dynamics. Two models (Tuomi and Augner 1993; Leimar and Tuomi 1998) are phrased in terms of whether synergistic selection (i.e., fitness increasing with proximity to similar genotypes) affects the evolution of resistance. There are also models showing that associational effects mediated by pollinators can influence plant evolution (e.g., Sargent and Otto 2006; Muchhala et al. 2010). Like ecological models of pollen competition, these are based on pollinator behavior rather than population dynamics, and consider effects arising from interactions of consumers with multiple plant types within a patch (Figure 3, region III).

A large body of theory addresses the evolution of mimicry, where selection on resource species traits is affected by a shared consumer (Ruxton et al. 2004). Although for some species the spatial scale of prey mixing and time scale of predator behaviors may be large enough to preclude associational effects (as defined above), many mathematical models for the evolution of mimicry include associational effects mediated by consumer behavior, at the scale of a single patch (Table 2; Figure 3, regions I, III, and V). These models include variation among local prey neighborhoods and assume that consumers respond to collective properties of a group of resource individuals (e.g., Sherratt 2002; Speed and Ruxton 2010). Several types of models of mimicry do not include associational effects, where consumer behavior depends only on total resource density or density of a single resource species (e.g., Sherratt 2003), genetic models of mimicry with implicitly infinite and well-mixed populations (e.g., Balogh et al. 2010), and the many models that focus on highly mobile species in a single, well-mixed patch or population without spatial dynamics.

WHAT EXISTING MATHEMATICAL MODELS TELL US

Existing theory indicates that associational effects can influence the outcome of competition between resource organisms for a wide variety of systems and processes. A common observation in these studies is that spatially structured frequency depen-

dence (one phenomenological representation of associational effects) alters the conditions for coexistence of two resource types or the equilibrium abundances of resource types. Different fields of study have, however, focused on different mechanisms and scales, so cross-field comparisons may provide novel ideas for researchers studying a particular system. For example, plant-herbivore studies suggest that neighbor species can affect local consumer densities (e.g., Hambäck et al. 2000; Agrawal 2004). Similar associational effects are likely to occur in mimicry systems when the presence of toxic species affects habitat preferences by generalist consumers, but such dynamics are not generally considered in models of mimicry. Conversely, some models of the evolution of mimicry focus on mechanisms of consumer behavior and how they generate neighbor effects (Ruxton et al. 2004); studies in plant-herbivore systems could benefit from a more mechanistic understanding of herbivore behavior.

FUTURE DIRECTIONS

Despite data showing that the effects of consumers can be influenced by neighboring resource types, and models demonstrating the potential consequences of associational effects, there are clear gaps in both our theoretical understanding of associational effects and empirical work testing for these effects. We discuss areas that future theory should address, noting relevant empirical work as appropriate, and then examine strategies for new empirical work.

MODELING FREQUENCY DEPENDENCE

The most fundamental gap in our knowledge of how associational effects influence populations or communities is an incomplete understanding of several aspects of frequency dependence. First, few models address how specific traits of individuals (e.g., consumer sensory abilities and resource mobility) influence the form of associational effects (but see Goulson 1994; Hambäck et al. 2014). Specific traits may determine the form of frequency dependence (linear to nonlinear, monotonic to

humped) and thereby indirectly how associational effects influence population or community outcomes. The mimicry literature includes detailed models of predator sensory systems, but the mechanisms are included in such a way that the responses of individual consumers do not scale easily to population-level phenomena. Second, current models of frequency dependence lack a theoretical synthesis of how large-scale outcomes might *vary* with alternative forms of neighborhood frequency dependence. Hump-shaped local frequency dependence (Kim et al. 2012) could lead to alternative equilibria or cyclic dynamics, whereas linear or simple monotonic functions are more likely to have a single stable outcome. Previous models have typically examined a single type of frequency dependence (generally linear) and have used different response variables, so results are difficult to compare.

A third problem is that models of frequency dependence are generally restricted to two resource types, thus precluding the effects of resource type *diversity* that are commonly discussed in the empirical literature (Hughes et al. 2008). One could model resource diversity effects by describing a distribution of relevant resource traits, once such traits are identified (e.g., production of a plant volatile) or measured as an herbivore response (e.g., distance moved after contact with a plant). Moments of this distribution (mean, variance, and skew) can then predict population-level consequences of additive associational effects (Underwood 2004), with individual neighbor effects being a special case of a general diversity effect. However, this approach will only work if associational effects of different neighbors are additive, with their joint effects predictable from their independent effects, yet whether associational effects are additive in any real system is unknown. If associational effects are nonadditive, then they may arise from resource diversity *per se* (e.g., herbivore response to variance in plant traits) and will require a different modeling approach.

MODELING SPATIALLY EXPLICIT RESOURCE DISTRIBUTIONS

Another major impediment to our understanding of how associational effects will scale up is a lack of theory that takes into account spatially explicit distributions of resource patches and consumers. Most current models ignore spatial structure and consider interactions of consumers with well-mixed resource organisms within one closed population (Table 2; Figure 3, regions III and IV). Such models ignore the fact that the spatial scale and strength of aggregation will determine the amount of variance in local neighborhoods, which could in turn affect the strength of associational effects. To include such spatial dependence, one solution may be spatially explicit mathematical models with biologically realistic treatment of neighborhoods (as in plant competition models, e.g., Pacala 1986; Bolker et al. 2003), including the full spectrum of distributions from well-mixed to highly aggregated. Unfortunately, few relevant models are spatially explicit (but see Orrock et al. 2010b). Some models include a minimal spatial structure, with a single patch of resources and an open population of consumers that come and go from an unspecified pool (e.g., Holt and Kotler 1987; Figure 3, regions V and VI). In contrast to these models that emphasize the absolute value of patch properties, models that keep track of consumers moving among patches would instead emphasize the importance of relative patch properties. This distinction is important because a patch may be unattractive to consumers, yet still contain a high density of consumers if other resource patches are even less attractive. Mimicry theory is beginning to consider spatial processes (Endler and Rojas 2009), and empirical studies have begun to measure associational effects at multiple spatial scales (Hambäck et al. 2009), but more work is needed to know what the characteristic spatial scales of different associational effects might be.

Spatially explicit theory could also help us understand how associational effects

generate spatial patterns in consumer distributions or consumer influence on resources, both within and among patches. Understanding how spatial distributions of pests, their damage, or resulting crop yield are generated could improve the agricultural use of associational effects; for example, to improve yield in forest and row crops through methods such as inter- and trap cropping (Vandermeer 1989; Hokkanen 1991; Cook et al. 2007). Even in a genetic monoculture of plants such as a typical agricultural field, associational effects could arise if plasticity in trait expression generates spatial variation in plant traits. For example, if plants have inducible resistance, differences in damage among plants could generate differences in resistance (Underwood et al. 2005) that allow for associational effects between resistance phenotypes. Despite strong interest in agricultural applications, associational effects on spatial distributions of damage, yield, or other plant phenotypes have rarely been modeled (but see Vandermeer 1989).

ADDITIONAL THEORETICAL ASPECTS

At least three additional aspects of associational effects deserve further theoretical attention. First, most models (but see Orrock et al. 2010a,b) address generalist consumers (consumers that feed on more than one resource type), although associational effects are often described for specialist consumers (e.g., Root 1973; Barbosa et al. 2009). Second, to our knowledge all but two existing models of associational effects consider resource traits to be categorical (e.g., defended/not) rather than continuous (but see Leimar and Tuomi 1998; Underwood 2004), yet many relevant resource and consumer traits are continuous. Even models of mimicry often treat traits as categorical, but mimics may vary continuously in similarity to the model, and willingness to eat mimics might depend on continuous traits such as a predator's hunger (e.g., Sherratt 2003). Treating traits as continuous will be important particularly when variance in traits mediates an associational effect (e.g., Underwood 2004), allowing for more sensitive feedback between resource-type frequen-

cies and consumer population sizes. Third, although most models relevant to associational effects focus on coexistence of resource species or genotypes, altered consumer population dynamics may be a consequence of, as well as a mechanism for, associational effects (Figure 2, arrow F). Although the mechanisms that mediate associational effects (e.g., effectiveness of consumer foraging) are likely to influence consumer population growth, to our knowledge only one model (Underwood 2004) and empirical study (Underwood 2009) have addressed associational effects on consumer population growth.

MEASURING ASSOCIATIONAL EFFECTS IN THE FIELD

Empirical studies of associational effects are needed both to support constructing appropriate theory and to determine how associational effects contribute to net ecological and evolutionary interactions in particular systems. To develop new theory we need to know, for a variety of systems, the spatial scale of effects, the form of frequency and density dependence in consumer attack, and whether associational effects from different neighbors are additive. To measure the contribution of associational effects to net interactions, we should also investigate the fitness consequences of attack, and the density and frequency dependence of resource interactions in the absence of consumers. Data on the mechanisms generating net associational effects would help in understanding how these characteristics of associational effects might change with changes in the biotic or abiotic environment.

Choosing Relevant Systems and Scales

If a goal is to predict the role of an associational in a natural system, a logical starting point would be determining if the interaction of interest is common and if the consumer has a substantial effect on resource fitness; if neither is true, then the interaction is unlikely to be important. The relationship to fitness will determine whether and how strongly associational effects on traits like damage affect population and community processes. Surprisingly, empirical studies of associational effects rarely

document how often the distributions of interacting species overlap in nature or the magnitude of fitness effects. One recent approach to including species distributions in studies of associational effects is to predict where associational effects may occur by modeling distributions of resource species (Recart et al. 2013). In any study of an associational effect, one should choose a relevant spatial and temporal scale at which to study the interaction (Figure 4), based on existing distributions of the resource species in the field (i.e., the scale at which resources intermix), or on the basis of knowledge about scales at which consumers move or perceive resources (e.g., Hambäck and Beckerman 2003; Figure 3, x-axis). A study might also test explicitly how associational effects vary with spatial scale, using an experimental design that produces variation in distances between and local frequencies of neighbors (e.g., a Nelder fan design; Goelz 2001). The choice of temporal scale will depend on whether one is quantifying associational effects mediated by consumer population dynamics (Figure 2, arrow F). Regardless of study system, future studies should focus on neighbors that differ in traits relevant to consumers, rather than on species or genotype identity.

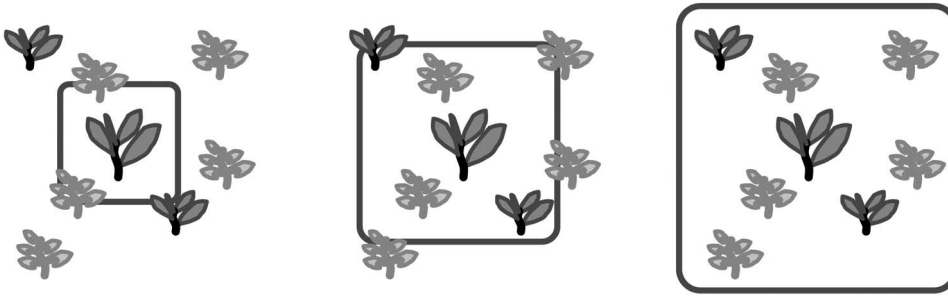
Separating Frequency and Density Dependence

Once an appropriate spatial scale has been identified, experiments can be used to measure the effects of neighborhood composition on focal resource individuals as a function of both the frequency of neighbor types (Figure 2, arrows B and D; Figure 4, steps 2 and 3) and the densities of both neighbor and focal resource individuals (Figure 2, arrows A and C; Figure 4, steps 2 and 3). This would allow both a full characterization of neighborhood effects on consumer attack, and isolation of associational effects from effects of focal resource density. Although it is widely appreciated that frequency-dependent consumer attack can influence ecological competition and natural selection (competition among genotypes; e.g., Heino et al. 1998; Rudolf and Antonovics 2005), there are almost no data on the

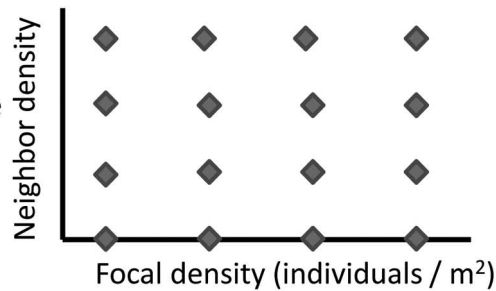
form or spatial scale of local frequency dependence. The two designs that have been used in most empirical studies of associational effects provide little information about density and frequency dependence. One common experimental design compares focal individuals with neighbors of a different resource type to focal individuals with no neighbors (e.g., Agrawal 2004), thus changing total resource density. Experiments with this design confound associational effects of neighbors with changes in total patch size. The other common design compares focal individuals with neighbors of their own type to focal individuals with immediate neighbors of a different resource type, while holding total density constant (a replacement series design; e.g., Hjärtén et al. 1993; White and Whitham 2000). This design confounds focal resource density and neighbor identity. In both designs, the focal resource type usually has a frequency of either 1 (a focal individual has a conspecific neighbor or no neighbors) or 0.5 (a different neighbor). Other studies test for effects of presence or absence of a second resource type without controlling densities of either the focal resource or neighbors (e.g., Stenberg et al. 2007, where populations with neighbors present or absent were observed but densities of the focal and neighbor species were not recorded).

Although a design with only two neighbor frequencies (Grosholz 1992; Rand 2003) precludes comparing forms of frequency dependence and cannot separate associational and density effects, even characterizing this limited frequency dependence can be useful for determining how associational effects play out over time (e.g., Tuomi and Augner 1993). To separate fully the effects of neighbor frequency and focal density each factor must be varied independently in a response surface design (Inouye 2001; Figure 4, step 2). Although these designs can require many experimental units, the payoff in improved understanding of associational effects could be great. Data on effects of neighbor frequency and focal organism density could inform models with more biologically reasonable assumptions or test detailed predic-

Step 1: Decide upon relevant spatial scale of neighborhood.



Step 2: Create variation in neighborhood composition. Separating frequency dependence from effects of resource density will require a response surface experimental design.



Step 3: Measure associational effects as a function of resource density and composition. Associational effects may depend on (A) total density, (B) only focal density, or (C) a combination of frequency and density. The axis labels for B and C are same as shown for A.

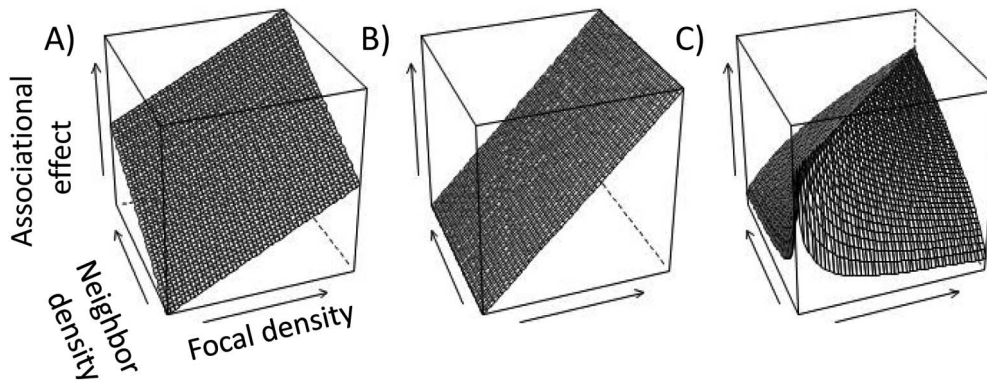


FIGURE 4. POTENTIAL STEPS IN THE DESIGN OF AN EXPERIMENT TO CHARACTERIZE EFFECTS OF RESOURCE NEIGHBORHOOD ON ATTACK BY CONSUMERS, INCLUDING BOTH EFFECTS OF FOCAL RESOURCE DENSITY AND ASSOCIATIONAL EFFECTS

tions for the expected form of frequency dependence built upon mechanistic work.

Data on the form of frequency and density dependence of associational effects can also be used to determine the contribution of associational effects to net interactions between resource types. Doing this will require comparing the fit to data of models of the dynamics of these interactions with and without associational effects. This is both because population and community dynamics can be too slow to observe in short-term experiments, and because empirically manipulating the existence of an associational effect is likely to be difficult, although not impossible. For example, associational effects mediated by consumer perception of volatile compounds might be manipulated by artificially augmenting local volatiles, or creating resource genotypes for which pathways of volatile production have been “knocked out.” Data needed to fit these models could come from response surface experiments crossing the presence and absence of consumers with simultaneous manipulation of the density and frequency of the resource types.

Identifying Mechanisms

Finally, once an associational effect (as function of neighborhood composition) has been characterized, one would want to identify the mechanism(s) that generate(s) that effect, first by describing the spatial and temporal scale of the effect and then by exploring how individual consumer and resource traits generate the effect. A few models of effects of focal plant density and patch size on mobile insect herbivore distributions provide useful null hypotheses for studies of associational effects (e.g., Hambäck and Englund 2005; Hambäck et al. 2014), however, mechanistic explorations of most potential mechanisms are lacking. Determining whether an associational effect is the result of interactions with only focal resources, with multiple resources in a patch, or at the patch level will require good natural history knowledge and use of the substantial existing literature on the sensory abilities of different consumers (e.g., Hambäck et al. 2003).

Addressing Diversity

The techniques described to this point address associational effects from a single neighbor resource type on a focal resource type. To address how associational effects function in diverse communities, an important first step would be to determine if associational effects from multiple neighbors are additive. This would require experiments that characterize associational effects on the focal resource produced by each neighbor type alone and then in combination. Data from experiments of this kind would also suggest reasonable approaches for modeling associational effects in diverse communities.

CONCLUSIONS

Whereas the terminology of associational effects (resistance and susceptibility) has mostly been limited to studies of interactions between plants and herbivores, associational effects clearly operate in many different areas of ecology and evolutionary biology. In addition to the plant-herbivore, plant-pollinator, and mimicry systems discussed most in this paper, phenomena as diverse as mixed flocks in birds and associations of cleaner fish with larger fish might fit the definition of an associational effect, and associational effects could result from both negative interactions (e.g., plant competition) and positive interactions (e.g., facilitation) as long as the resource organisms are spatially structured. These associational effects on individual risk of attack might then scale up to contribute to population-level indirect effects, which are recognized as widely important in ecological and evolutionary interactions (Strauss 1991). Besides being of interest to basic science, associational effects are an active area of research and application in agricultural science (Cook et al. 2007). Empirical studies have demonstrated that there are many pathways through which these effects can occur, and theory tells us that when these effects are frequency dependent they should influence the outcome of interactions among resources. Yet despite broad interest in the phenomenon, we do not know how much

any particular associational effect contributes to net the ecological or evolutionary dynamics of interactions between resources and consumers. To determine this contribution in any particular system or more generally in theory, it will be critical to characterize associational effects as a function of frequencies of neighbors while separating out effects of focal resource density and to explicitly consider the spatial scale of the associational effect. In addition, the substantial existing knowledge of consumer perception and behavior can be used to generate theoretical expectations for the form of frequency and density dependence for particular types of associational effects. Associational resis-

tance is an old and intuitively appealing idea. We hope that this paper facilitates linking ideas about associational effects across systems to understand how they contribute to ecological and evolutionary dynamics.

ACKNOWLEDGMENTS

We thank Stockholm University and Florida State University for facilitating the discussions that led to this paper. Suggestions from T. E. X. Miller, T. Kim, W. Morris, and J. Travis greatly improved this manuscript. Funding that supported this work was provided by the Fulbright Foundation (B. Inouye), grant #621-2009-4943 from Vetenskapsrådet (P. Hambäck), and NSF DEB grant #0717221 (N. Underwood and B. Inouye).

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Handling Editor: James D. Thomson