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Associational Resistance and Associational Susceptibility: Having Right or Wrong Neighbors

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Abstract

Specific plant associations may decrease (associational resistance, AR) or increase (associational susceptibility, AS) the likelihood of detection by, and/or vulnerability to, herbivores. We discuss presumed mechanisms leading to AR and AS, suggest others, and conduct meta-analyses on plant and herbivore traits affecting AR and AS, and the effects of habitat.

Specific plant associations determine the likelihood of detection and/or vulnerability of focal plants to herbivores. AS is more likely with insects and AR more likely with mammals. Unpalatable neighbors increase the likelihood of AR. An herbivore's feeding guild, diet breadth, and habitat type do not influence the likelihood of AR or AS. The effectiveness of AR in reducing herbivore abundance is independent of whether neighboring plants are within a plot of focal crops or along the edge of a plot. AR and AS may be applicable to associations among herbivores, and may be appropriately studied from a landscape perspective.

INTRODUCTION: THE HISTORY OF THE CONCEPTS OF ASSOCIATIONAL RESISTANCE AND ASSOCIATIONAL SUSCEPTIBILITY

In this review, we focus on direct and indirect interactions between plants in close proximity, in which the influence of one plant on another (hereafter referred to as the focal plant) increases (associational susceptibility, henceforth AS) or decreases (associational resistance, AR) the likelihood of detection by, and/or vulnerability of a focal plant to, herbivores (above and beyond its innate ability to avoid detection or damage owing to herbivory). The outcomes of these plant-plant interactions are viewed from a phyto-centric perspective and, thus, typically measured as changes in the degree of herbivory and/or abundance of herbivores.

Root and colleagues (Root 1973, Tahvanainen & Root 1972) were among the earliest to affirm the importance of specific plant-plant associations in the likelihood that a plant will be detected and/or vulnerable to herbivory. Atsatt & O'Dowd (1976) discussed AR, stressing the importance of the right kind of diversity, that is, suggesting that not all plant species diversity results in changes in detection by, and/or vulnerability to, herbivores. They also suggested [and Evans 1983, Wada et al. 2000, and Karban & Maron (2002) later demonstrated] that adjacent plants conferring AR could be conspecifics that differ in some fashion, as well as individuals of different species.

To date, AR and AS have been demonstrated in terrestrial plants affected by vertebrate (Hjältén et al. 1993, McNaughton 1978) and invertebrate herbivores (Finch et al. 2003), in marine algae-mesograzers interactions (Hay 1986, Pfister & Hay 1988) and in mussel-plant epiphyte interactions (Laudien & Wahl 1999), and speculated for sponges (Wulff 1997) and phytoplankton (Steiner 2001). Thus, AR and AS are widespread ecological interactions, although AS has been reported less frequently (but see Parker & Root 1981, Rand 1999, Thomas 1986, White & Whitham 2000).

Contrasting Associational Resistance, Associational Susceptibility, and Other Basic Ecological Interactions

Fundamental ecological associations include consumer-resource interactions, competition, mutualism, amensalism, commensalism, facilitation, epibiosis, and, we would add, AR and AS. All of these interactions are commonly contrasted based on whether the interaction is favorable, detrimental, or neutral for the interacting species (that is, $+/-$, $+/+$, $-/-$, $+/0$, $-/0$). Thus, consumer-resource interactions are $+/-$, competitive interactions $-/-$, amensalisms $-/0$, and commensalism $+/0$. AR, AS, and the two closely related interactions, facilitation and epibiosis can be similarly described. In AR, the outcome of the interaction is $+$ for a focal plant, with regard to avoidance of detection and reduction of herbivore damage, and $-$ in AS. The impact on neighboring plants can be 0 , $+$, or $-$. Epibiosis is a relationship in which one (epiphytic) organism lives attached to another and may be benefited or harmed as a result of the intimate relationship, depending on the influence of the substrate species (Wahl & Hay 1995). Facilitation involves associations between species that benefit at least one species and cause no harm to the associated species (Stachowicz 2001). Thus, some facilitation interactions can be described as AR if the benefit accrued is protection from herbivory (Callaway 1995) and some epibiosis can result in AR or AS if attachment increases or decreases herbivory of the plant epiphyte (Hay 1986, Wahl & Hay 1995). (For further details see **Supplemental Text 1**. Follow the **Supplemental Material link** in the online version of this article or at <http://www.annualreviews.org/>.)

Although AR and AS (like other interactions such as consumer-resource interactions, competition, mutualism, and so on) involve interactions between two organisms (that is, plants), the outcome of the interactions affect, and is affected by, a third (herbivorous) species. We previously

represented AR and AS as two-species interactions. However, AR and AS can be viewed as indirect interactions that depend on differential responses of herbivores (perhaps via apparent competition), differential responses of natural enemies to plant traits (see discussion below), or plant-plant interactions involving a plant other than the focal or neighboring plant.

ASSOCIATIONAL RESISTANCE AND ASSOCIATIONAL SUSCEPTIBILITY: A REVIEW OF MECHANISMS

Understanding the mechanisms that underlie AR and AS helps to characterize and comprehend these phenomena. However, data on mechanisms that drive AR and AS interactions are primarily anecdotal. Although some experimental investigations of mechanisms are reviewed, these are insufficient to undertake a meta-analysis. Thus, we review and discuss mechanisms traditionally considered to be important in AR and AS, and propose novel mechanisms yet to be evaluated. In general, AR and AS may occur as a result of the differential response of focal and neighbor plants to key resources (that is, abiotic factors) or as a result of differential responses of focal plants or associated animals to neighboring plants (biotic factors).

Abiotic Mechanisms: Effects on Plants and Animals

Clearly, there are many abiotic factors that may alter the likelihood of detection by, and/or vulnerability of a focal plant to, herbivores. We offer two examples. The availability of soil macronutrients to focal plants may be influenced by neighboring plants. They may alter the quantity or quality of soil nutrients needed for defense and growth of focal plants, both of which may determine abundance of, and vulnerability to, herbivores. For example, defoliation of *Trifolium repens* can increase the transfer of N from this legume to a neighboring perennial ryegrass (*Lolium perenne*) (Ayres et al. 2007). In addition, if a long-lived focal plant grows adjacent to a N-fixing neighbor, in theory, it could ultimately have a larger pool of nitrogen via decomposition of dead neighbor plants or tissues (van Ruijven & Berendse 2005). A similar increase in soil richness may occur as a consequence of herbivory of neighboring plants. Frass deposition by herbivores can enrich the soil and enhance growth of adjacent focal plants (Frost & Hunter 2007) or alter their defensive capacity.

Changes in microclimate, caused by neighboring plants, can influence the behavior of herbivores and their natural enemies. Few studies have investigated whether this mechanism might lead to AR or AS. Nevertheless, such changes in microclimate (e.g., light intensity, temperature, and humidity) could influence herbivore colonization and herbivory of focal plants (Osisanya 1970), via changes in oviposition and survival. Herbivore abundance and damage also may be affected by microclimate indirectly, if it influences natural enemy host finding, foraging, and mating. One, or all, of these changes may determine the likelihood of AR or AS.

Biotic Mechanisms

Biotic mechanisms may include (a) traits of neighboring plants that directly alter the behavior or survival of focal plant herbivores or their natural enemies, (b) plant-plant competition that alters focal plant traits affecting herbivore colonization and damage, and (c) differences in the relative abundance of focal and neighboring plants that directly or indirectly affect herbivore colonization and damage.

Finding and accepting host plants: constitutive plant traits and signals. The ability of neighboring plants to camouflage (Perrin & Phillips 1978), confuse, or in some way interfere with



the ability of herbivores to orient toward and find focal plants (Finch et al. 2003, Hay 1986, McNaughton 1978, Pfister & Hay 1988) may play a key role in AR. Avoiding detection by herbivores may be a relatively simple but nevertheless effective mechanism leading to AR. This may be achieved via precontact cues [such as volatile signals and water borne cues (Toth 2007) or visually perceived traits], as well as via postcontact deterrents or antifeedants of neighboring plants, which cause herbivore dispersal away from focal plants. Of course, the concept of escape through concealment or evasion is dependent on the sensory modality used by herbivores to find, evaluate, and accept host plants, or reject nonhosts.

Visual cues from neighboring plants may disrupt colonization by invertebrate herbivores. For example, leaf color of neighboring plants can disrupt host finding by the cabbage root fly (Finch et al. 2003). Similarly, neighboring plant architecture may play a role in the ability of neighboring plants to mask, repel, or confuse focal plant herbivores (Marquis et al. 2002). Ultimately, the occurrence of AR or AS depends on whether herbivore repulsion results in long- or short-distance dispersion, that is, whether herbivores move to distant plants or adjacent focal plants (Potting et al. 2005). Long distance repulsion has been demonstrated in managed habitats and is the basis of the disruptive crop strategy, which relies on the emigration-inducing effect of the neighboring vegetation on pests (Vandermeer 1989). Precontact responses to neighboring plant volatiles may be associated with the presence of toxic compounds and may be a mechanism by which contact with adjacent focal plants is avoided. Herbivores may respond to toxic plant allelochemicals as they respond to some synthetic toxins (Nauen 1995) by being repelled even at low concentrations. Such a rejection of neighboring plants may potentially alter focal plant vulnerability.

Neighboring plants may impede access simply by visually blocking the focal plant and reducing the likelihood of detection (Rausher 1981) or by interfering with herbivore movement, as demonstrated or speculated by Risch (1981), Coll & Bottrell (1994), and Holmes & Barrett (1997). Repeated physical encounters with neighboring plants, even if random, may induce herbivore movement out of a patch. *Diabrotica balteata* beetles tend to emigrate more from polycultures that include a nonhost plant than from host monocultures (Risch 1981). Monocultures also are more likely to induce area restricted movement, making herbivores less likely to leave a patch (Bach 1980b, Holmes & Barrett 1997, Risch 1981).

Alternatively, neighboring plants may act as attractant (or decoy) plants (Tahvanainen & Root 1972) and retain herbivores (Holmes & Barrett 1997), thus reducing colonization and feeding on nearby focal plants, or permitting focal species, age classes, or morphs to escape a relatively vulnerable stage (Atsatt & O'Dowd 1976). In managed habitats, this concept is the basis of the trap-crop strategy that relies on "attractive plants" as sinks for pests and results in reduced colonization of crop plants. Examples include borders of sorghum trap-crops that intercept green stinkbug colonization of cotton fields (Tillman 2006) and rows of beans in the middle of a field that effectively attract beet armyworms away from tomatoes (Rosset et al. 1985).

Neighboring plants that act as sinks also may lead to AS of focal plants via a spill-over effect, where herbivores move from sink plants onto focal plants (Wada et al. 2000, White & Whitham 2000). For instance, the occurrence of *Opuntia corallicola* anywhere in the immediate vicinity of the cactus *Opuntia stricta* results in severe infestation by the herbivore *Cactoblastis cactorum*, and in death of *O. corallicola* (Stiling et al. 2004).

Induced defenses and communication between plants. Since the early to mid-1980s, evidence has accumulated that herbivore damage can result in the production of volatiles that trigger defensive responses in nearby conspecifics or unrelated plants. Although the concept has been the subject of debate (Dicke et al. 2003, Shonle & Bergelson 1995), there is sufficient evidence from past and recent research to support the concept of interplant communication (that is, eavesdropping).

Eavesdropping provides an effective mechanism by which plant associations might lead to AR, via its effects on the behavior and survival of herbivores (Karban & Maron 2002) and their natural enemies (Dicke 1994), although experimental data from field studies is lacking.

Thus, the impact of neighbors on focal plants may be mediated by chemical and visual cues. Herbivory of neighboring plants may produce volatiles that influence the likelihood of detection and/or vulnerability of neighboring or focal plants. For example, undamaged wheat seedlings attract aphids, whereas odors released from aphid-infested wheat seedlings repel aphids (Quiroz et al. 1997). These types of changes have the potential to temporally alter the vulnerability of any nearby aphid-susceptible focal plants. In general, if focal and neighboring plants share herbivores, the impact of the presence of herbivores on neighboring plants may lead to repulsion of focal plant herbivores, or spill-over onto focal plants.

Neighboring plant volatiles may either directly induce the production of defensive volatiles in a focal plant or prime its defense physiology (Engelberth et al. 2004). In a priming interaction, signaling compounds from a damaged neighboring plant may be insufficient to elicit a change in the defensive chemistry of a focal plant but may prepare its defensive physiology to quickly produce defense compounds, if damaged. The quantities of the signaling compound methyl jasmonate, released by sagebrush (*Artemisia tridentata*), are insufficient to elicit the production of defensive compounds in a nearby plant. However, exposure to volatile organic compounds (VOC) (such as methyl jasmonate) from damaged neighboring plants change focal plants so that they are ready (primed) to induce defenses if damaged, and therefore, respond more rapidly (or to a greater degree) than unprimed plants. Both conspecifics (Farmer 2001, Heil & Kost 2006) and unrelated focal plants (Kessler et al. 2006) may be primed by damaged neighbors, but priming may be a species-dependent phenomenon. For example, proteinase inhibitor activity in native *Nicotiana attenuata* can be primed by a VOC bouquet emanating from damaged sagebrush (Kessler et al. 2006). However, VOC from *Manduca sexta*-infested *N. attenuata* fails to prime nearby conspecifics (Paschold et al. 2006).

Although the induction of defensive compounds, or priming, of focal plants by neighbors, may be effective mechanisms leading to AR, these mechanisms are likely to be spatially limited. Induced volatiles may only trigger changes over short distances. Dolch & Tscharrntke (2000) found that defoliation of alder *Alnus glutinosa* by leaf beetles led to a local change in susceptibility to herbivory of nearby plants, but the response was greatly reduced within a few meters of the damaged tree. Sagebrush plants experienced less damage by herbivores only within 60 cm of experimentally clipped conspecifics (Karban et al. 2006). Eavesdropping by unrelated species appears to occur over even shorter distances (Karban 2001; Karban et al. 2004, 2006). Eavesdropping by tobacco responding to cues released by sagebrush occurred over distances of up to 10–20 cm (Karban et al. 2003), and mule's ears (*Wyethia mollis*) plants gained protection within 10–15 cm of a sagebrush canopy (Karban 2007). Thus, volatile-mediated AR may be a fine-grained phenomenon.

Volatiles from damaged plants also may induce indirect defenses in focal plants. For example, an artificial blend of VOC that resembled the blend from herbivore-infested lima bean plants enhanced the secretions of extrafloral nectar, a resource for natural enemies (Kost & Heil 2006). Similarly, VOC-exposed maize plants produced enhanced levels of aromatic and terpenoid volatiles between 180 and 300 min after defense elicitation, which coincided with the time period in which improved attraction of the parasitoid *Cotesia marginiventris* was observed (Ton et al. 2007).

Not only may airborne communication be important in AR and AS, but belowground communication or connections between focal and neighboring plants also may mediate AR and AS. Species in the plant parasitic genus *Castilleja* (indian paintbrush) do not produce alkaloids but take up alkaloids (like lupanine) when parasitizing hosts in the genus *Lupinus*. Indian paintbrush individuals parasitizing bitter lupines (which contain alkaloids) were subject to less damage from

herbivores than those parasitizing sweet lupines, which only contain a trace amount of alkaloids (Adler 2000). Different paintbrushes facing herbivory by specialists and generalists may achieve AR or AS depending on the lupine with which they are associated (Marvier 1998). Lupine alkaloids vary quantitatively and qualitatively and, thus, vary in toxicity to herbivores (Wink et al. 1995). Thus, the likelihood of detection and/or vulnerability of *Castilleja* species to herbivores (and thus AR or AS) may be determined by the chemistry of neighboring host plants (but see Schädler et al. 2005). Other examples provide supportive evidence. The uptake of defensive mycotoxins from endophyte-infected host grass enhances the resistance of the hemiparasitic plant *Rhinanthus serotinus* to a generalist aphid herbivore (Lehtonen et al. 2005).

Root exudates from neighboring plants also may protect focal plants or increase the likelihood of detection by, and/or vulnerability to, herbivores. For example, the roots of a large number of legumes produce defensive isoflavonoids that are deterrent or insecticidal compounds. These compounds are effective against soil-borne insect larvae (Dakora 2003). Root exudates may be induced and have an indirect effect on herbivores. For example, the entomopathogenic nematode *Heterorhabditis megidis* is attracted to the sesquiterpene (E)- β -caryophyllene, which is released by maize roots damaged by larvae of the beetle *Diabrotica virgifera virgifera* (Rasmann et al. 2005). Although, more research is needed, AR or AS interactions may be mediated by these and other mechanisms, acting belowground.

The importance of physical defenses. Focal plants may gain protection from herbivory owing to their proximity to neighboring plants defended by antiherbivore physical traits (Baraza et al. 2006, González-Teuber & Gianoli 2008, Rousset & Lepart 2000). For example, survival and growth of transplanted *Quercus robur* trees is severely suppressed in grasslands and woodlands, in the presence of cattle and rabbits. Only when they were near young, thorny *Prunus spinosa* shrubs did transplanted *Q. robur* seedlings survive and grow equally well within and outside exclosures, showing the importance of this form of AR (Bakker et al. 2004). The protection of focal plants by neighboring plants with spines is a clear example of a mechanism by which access to focal plants is limited (Bakker et al. 2004, Baraza et al. 2006). However, spines don't protect plants against invertebrate herbivores and may not protect against small vertebrate herbivores such as rabbits and voles that can go underneath and in between thorns and spines (Manson et al. 2001). Spineless plants also can physically impede or prevent access to focal plants by vertebrates (Gómez et al. 2001) or invertebrates (Rauscher 1981).

Physical mechanisms limiting access to focal plants also can be observed in marine habitats. The sweeping motion of the brown algae *Desmarestia viridis* repels the green sea urchin, *Strongylocentrotus droebachiensis*. *Agarum cribrosum* juveniles escape grazing by sea urchins by inhabiting areas under the canopy of *D. viridis*, where urchin densities are markedly reduced, compared to the surrounding area (Gagnon et al. 2003). Additional field tests of all of the potential mechanisms discussed above, within the context of AR and AS, are needed.

Accumulation of natural enemies. Natural enemies may accumulate upon neighboring plants for a variety of reasons but this aggregation, potentially, may have an impact on the vulnerability of nearby focal plants to herbivory. For example, one might predict AR when neighbors provide food (that is, nectar or pollen) and or shelter (domatia or abandoned leaf tiers) for herbivore natural enemies. For example, a pollen-producing plant can indirectly decrease herbivore densities on a nearby plant by attracting omnivorous predators (Harmon et al. 2000). If the resources attract or retain herbivores, then AS would be likely. That is, one might predict AS when neighbors provide herbivores nutrients such as nectar, and non-nutritional resources such as habitat, enemy-reduced space, and so on.

Natural enemies, be they parasitoids or predators, also respond to chemical traits such as constitutive and damaged-induced volatiles (Dicke 1994, Kessler & Baldwin 2001). Although most available data suggest that induced volatiles attract natural enemies to an infested plant, it is possible that other induced volatiles may repel natural enemies and thus either AR or AS may result. Nevertheless, attraction of natural enemies to a neighboring plant could potentially reduce the movement of natural enemies from neighboring plants to focal plants, resulting in AS due to a reduced impact of natural enemies on focal plant herbivores. However, it is perhaps more likely that attraction of natural enemies to neighboring plants may result in movement onto nearby focal plants, a spill-over effect providing AR.

The additional consequence of the spill-over may be reduced herbivory. In general, parasitized herbivores consume less than unparasitized individuals (Hopper & King 1984, Powell 1989); the only exception is hosts parasitized by gregarious or polyembryonic parasitoids (Jones et al. 1982). Thus, AR (if based on damage imposed) may result even without an immediate reduction of herbivore numbers. Unfortunately, little research has been conducted on the consequences to AR or AS of the attraction of natural enemies to volatiles of damaged or undamaged neighboring plants.

Relative abundance of focal and neighboring plants. Conclusions on AR and AS invariably have been confounded by the potential importance of the relative abundance of focal and neighboring plants. In some circumstances, the occurrence of AR and AS may have less to do with specific traits of neighboring plants and more to do with the relative abundance of neighboring plants, that is, the relative concentration or intensity of traits that affect herbivores. For instance, the strongest predictor of egg load of the Eurasian flower head weevil, *Rhinocyllus conicus*, on wavyleaf thistle (*Cirsium undulatum*) was the availability of flower heads of the native congener Platte thistle (*Cirsium canescens*). More important, egg load on wavyleaf thistle decreased as the number of Platte thistle flower heads increased (Russell & Louda 2005). However, data on the relationship between plant density and herbivore abundance are equivocal. There are numerous examples of a positive correlation between plant density and herbivore abundance. On the other hand, herbivore density in sparse plantings or isolated plants of species such as *Brassica*, sugar beets, beans, and oaks may be many times greater than that on plants in dense stands (Cromartie 1975, Futuyma & Wasserman 1980, Thompson 1978).

In part, the reason may be because differences in plant density can be confounded or compensated for by plant species biomass. That is, individuals of a plant species vary widely in their size. The number of insect herbivores associated with a plant may be correlated with the plant biomass. The density of two plant species may be the same but their biomass may differ. Plants that offer a larger resource may have greater herbivore species richness and abundance (Bach 1980a, Evans 1983, Marques et al. 2000). Thus, AR or AS may depend not just on the number of individuals of a neighboring plant but on their biomass. For example, the palatable epiphytic algae *Hypnea musciformis* occurs only among dense patches of the unpalatable brown seaweed *Sargassum filipendula*. *H. musciformis* is protected by *S. filipendula* but only if the mass of *H. musciformis* is less than 10–15% of that of *S. filipendula*'s mass (Hay 1986).

Competition. In immobile organisms like plants, competition for resources (among adjacent plants) is a key determinant of survival, growth, development, and size, among other things. Thus, competition between neighboring and focal plants may influence herbivory and the likelihood of AR or AS (Agrawal 2004, Agrawal et al. 2006, Hambäck & Beckerman 2003). Competition-related changes in focal plants may include the quantity and/or quality of nutrients and antiherbivore defenses, or plant secondary metabolites used by specialists to find, accept, and initiate feeding

(Bach 1980a; Gold et al. 1990; Letourneau 1990, 1995; den Belder et al. 2000), all of which may influence AR and AS. For example, focal milkweed (*Asclepias syriaca*) plants received up to 2.6 times the photosynthetically active radiation and 1.6 times the red to far-red ratio of light when neighboring grasses were clipped (to simulate herbivory) thereby reducing light competition (Agrawal & Van Zandt 2003). Increased exposure to light also may improve milkweed defense because cardenolide content increases in light environments (Kosinski 1996). If focal milkweed plants occur next to grass species that are attractive to and defoliated by herbivores, they may experience AR owing to enhanced defenses as well as release from competition.

However, competition and herbivory on focal and neighboring plants act in a complex and nonadditive fashion (Agrawal 2004, Barton & Bowers 2006). Milkweeds growing next to grass are subject to AS and suffer 10% greater herbivory by adults of specialist *Tetraopes* beetles than milkweeds growing alone. Neighboring grass species enjoy competitive release because beetle herbivory on milkweed roots completely alleviates the competitive effect of milkweed on grass (typically, a 23% reduction in grass biomass). However, in some other plant associations there may be no significant interaction between competition and defoliation (Augner et al. 1997).

Clearly, more experimental evidence is needed to address the circumstances under which plant competition leads to AR and AS, if indeed it does. Herbivory and competition may be inseparable and interacting forces. Thus, determining cause and effect relationships may be a daunting task (Augner et al. 1997, Hambäck & Beckerman 2003, Mulder & Ruess 1998). Predicting whether an association between competing plants will result in AR and AS is, at best, a complex and circumstance-specific phenomenon, depending on the focal and neighboring plant species, the herbivore, and extant biotic and abiotic conditions.

INSIGHTS FROM A META-ANALYSIS

Although experimental data on AR and AS mechanisms are lacking, there is sufficient data to conduct meta-analyses on the importance of plant and herbivores traits in AR and AS. In addition, we conducted a meta-analysis to determine if the likelihood of observing AR and AS differs in managed and unmanaged habitats and whether traits unique to managed habitats influence the likelihood of AR and AS.

We scored a total of 164 unique plant-herbivore-plant interactions obtained from 68 published studies investigating 118 plant species and 78 herbivore species. In the meta-analyses, a positive effect size (Hedges' d) indicates that a greater level of herbivore abundance/damage was observed in the presence of a neighboring plant (AS), whereas a negative effect size denotes a lower level of herbivore abundance/damage in the presence of a neighbor (AR). An effect size near zero suggests that neighboring plants had little-to-no impact on focal plant herbivores. For details on meta-analysis methodology and a list of studies used with associated effect sizes, see **Supplemental Text 2** and **Supplemental Table 1**, respectively.

Having Right or Wrong Neighbors

Results of our meta-analysis supported our main prediction that the presence of neighboring plants does make a difference in the likelihood that herbivores will detect and/or damage focal plants. The cumulative effect size for both response variables was negative (herbivore abundance, $d_+ = -0.6765$; plant damage, $d_+ = -0.0509$), indicating that, in the presence of a neighbor, AR is observed. However, the effect was significant only when herbivore abundance was the predictor variable (**Figure 1a**) but not when plant damage was the predictor variable (**Figure 1b**). This dichotomy may be an artifact because the most compelling demonstrations of AR are in managed



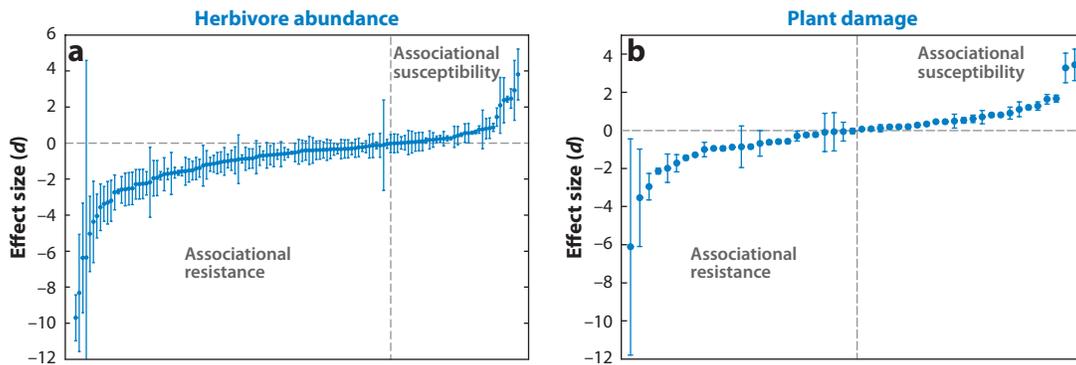


Figure 1

The distribution of effect sizes across all studies measuring either (a) herbivore abundance or (b) plant damage as a means for quantifying associational resistance (AR) and associational susceptibility (AS) (error bars = variance). Each data point is a unique observation in our dataset and arranged in rank order. Positive effect sizes are indicative of AS, whereas negative effect sizes denote AR.

habitats, and studies of AR in managed habitats almost always report differences in herbivore abundance rather than plant damage. Alternatively, neighboring plants may have a more significant impact on herbivore abundance because neighboring plant precontact cues may reduce herbivore attraction to focal plants. If these cues fail to prevent colonization, avoidance of damage may be difficult, that is, neighboring plants may be less likely to reduce focal plant damage once herbivores colonize.

Nevertheless, these results indicate that neighboring plants, as a whole, can reduce herbivore abundance on focal plants. Furthermore, an effect size of 0.7–0.8 is considered to be a large effect (Tonhasca & Byrne 1994), suggesting a strong impact of AR, when herbivore abundance is the response variable. These are robust results given the large number of nonsignificant observations that would need to be added to our database to change the outcome of this analysis; the fail-safe value for herbivore abundance was 1822.

We detected significant heterogeneity in effect sizes for both herbivore abundance [$n = 126$, $Q_T = 171.52$ (where Q_T describes total heterogeneity in effect sizes, $P = 0.0037$)] and plant damage ($n = 49$, $Q_T = 69.97$, $P = 0.0210$). This indicates that the variation among effect sizes is greater than expected based on sampling error and suggests that additional factors should be investigated as potential explanatory variables. We therefore proceeded to evaluate the importance of various plant and herbivore traits on AR and AS.

Importance of Herbivore Traits in Associational Resistance and Associational Susceptibility: Predictions and Results

Herbivore taxonomy. Most AR and AS studies can be broadly divided into those investigating herbivorous insects and those focusing on (mostly mammalian) vertebrates. This distinction is likely to be important because of the gross differences in how these two types of herbivores detect and forage for food. There are other differences, not the least of which is that, in general, terrestrial phytophagous mammals may be more likely to use visual cues to find plants and to browse multiple plants during feeding bouts. Insects often primarily exploit chemical and visual signals to locate plants. The feeding stage of herbivorous insects may live most of its life in association with a single host plant individual, once the female finds it and oviposits. These and other differences suggest

that the key mechanisms leading to AR or AS may be distinct for mammals and insects. Thus, we predicted that AR and AS involving insects and mammals should differ.

Our meta-analysis supported the prediction that AR and AS interactions involving insects and mammals should differ. Although AR and AS were observed in plant associations involving both mammals and insects, AS was more likely in interactions involving herbivorous insects and AR more likely in those involving mammals (**Figure 2a**; $Q_B = 4.04$, $P < 0.05$). This may reflect

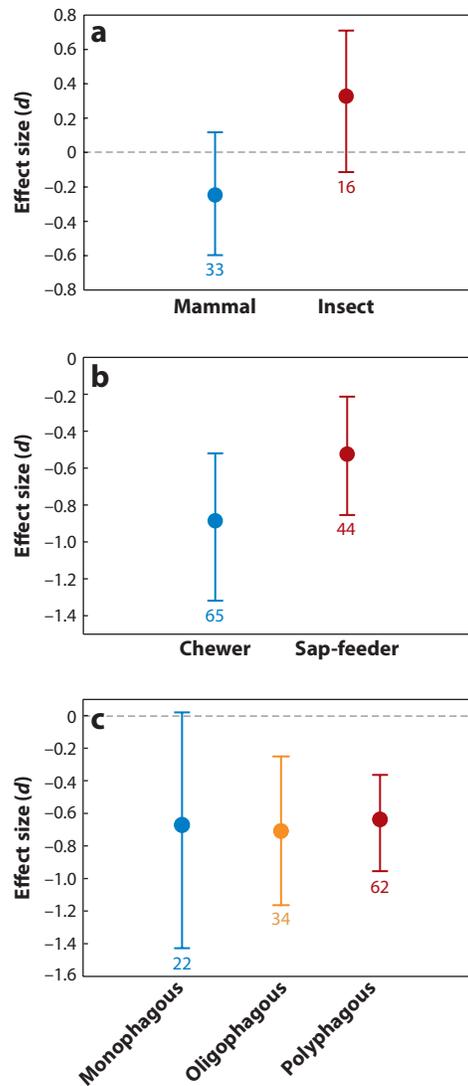


Figure 2

The effects of herbivore taxonomy (a), insect feeding guild (b), and herbivore diet breadth (c) on associational resistance and susceptibility (response variables = plant damage, herbivore abundance, and herbivore abundance, respectively). Error bars = 95% bootstrap confidence intervals. Numbers below error bars represent the number of observations used to calculate effect sizes in each category. Because the significance of effect sizes can be assessed based on whether or not their confidence interval overlaps zero, a dotted line is included at zero to visually interpret the significance of each effect size.

the predominance of studies on vertebrate herbivores that focused on the importance of spines of neighboring plants in providing AR to focal plants, against vertebrate herbivores, and the relative ease with which the impact of spines can be demonstrated.

Feeding guild. Some of the more likely mechanisms for AR rely on the attractant, repellent, or masking effects of volatiles produced by neighboring plants. Visual cues like color, leaf shape, and so on, also are important and may work in concert with olfactory cues (Patt & Sétamou 2007). However, there is relatively little data suggesting that species in different feeding guilds respond in significantly different ways to plant chemicals or most morphological traits. Thus, we predicted no differences in the occurrence of AR or AS based on feeding guild. A significant negative overall effect size indicates that the impact of both leaf-chewers and piercing-sucking insects is reduced as a result of specific plant associations (**Figure 2b**). However, there was no significant difference in the effect of plant associations on the two feeding guilds ($df = 1$, $Q_B = 1.78$, $P > 0.1827$), supporting our prediction that herbivores in different feeding guilds do not respond differently to specific plant associations. Our results suggest that the plant traits used by both chewing and piercing-sucking insects or their responses to those traits are not sufficiently different to influence the impact of plant associations with regard to AR and AS.

Diet breadth. The diet breadth of herbivores also may determine whether a specific plant association will result in AR or AS. For example, one might assume that AR and AS are more likely if herbivores are polyphagous because they may respond to both focal and neighboring plants and do so differentially.

In contrast, monophagous herbivores appear to discriminate host plant quality more effectively than polyphagous species and exhibit greater behavioral efficiency in host finding. Further, monophages may respond more acutely to plant signals (Bernays 1998, Janz & Nylin 1997). However, monophagous herbivores may be just as readily influenced by neighboring nonhost plants even though, typically, they are attracted to only a single or a few plant species. That is, attraction of a monophagous herbivore to a host plant may involve the simultaneous influences of host traits that attract and neighboring nonhost traits that repel (Hambäck et al. 2000). Thus, the presence of neighboring plants may lead a greater abundance on monophagous herbivores on the focal plant (AS), not because it attracts them to the immediate area but because when herbivores are in the area it repels them and they are more likely to move toward and aggregate on their focal plant host. Thus, we predicted that diet breadth should not influence the likelihood of AR and AS, although the mechanisms and the nature of the interactions involving monophagous and polyphagous herbivores may differ.

Our meta-analysis supported the prediction that diet breadth of an herbivore should not influence the likelihood of AR or AS (**Figure 2c**; $Q_B = 0.06$, $P = 0.9697$). These results are in contrast with quantitative reviews by Andow (1991) and Jactel et al. (2005) in which they concluded that specialist (monophagous and oligophagous) herbivores were more negatively affected by habitat diversification than polyphagous herbivores. However, unlike these studies, our focus was on the effects of having a particular plant adjacent to a focal plant, not the effects of habitat-wide plant diversity. We conclude that it may not be possible to predict the impact of specific plant associations on herbivore colonization or damage simply by knowing the diet breadth of an herbivore involved.

Importance of Plant Traits in Associational Resistance and Associational Susceptibility: Predictions and Results

Palatability of neighboring plants. Palatability of plants, whether based on nutritional quality or the type and quantity of antiherbivore defenses, may be critical determinants of AR and AS (Bergvall et al. 2006). Relatively unprotected and palatable focal plants are likely to enhance their fitness by associating with less palatable neighboring plants (Baraza et al. 2006, Callaway et al. 2005). Thus, one could assume that AR or AS should be likely when the neighboring plant is unpalatable to focal plant herbivores and either repels them from the area or results in a spill-over onto focal plants. Alternatively, the neighboring plant may be significantly more palatable (and attractive) to herbivores than the focal plant and act as a sink, reducing their impact on focal plants (that is, AR). Of course, implicit in these scenarios is that focal and neighboring plants share herbivores (Thomas 1986, White & Whitham 2000). Similarly, traits other than palatability also may be important in the likelihood of AR or AS. Thus, we predicted that palatability of the neighboring plant should influence the likelihood of AR or AS.

Our meta-analysis generally supported the prediction that the palatability of neighboring plants should influence the likelihood of AR and AS. In general, our analysis indicated that AR is most likely when the neighboring plant is unpalatable relative to the focal plant and that AS is most likely when the neighboring plant is palatable. Neighboring plant palatability significantly affected insect herbivore abundance (**Figure 3a**; $Q_B = 5.07, P < 0.05$) and plant damage by mammalian herbivores (**Figure 3b**; $Q_B = 10.58, P = 0.0011$), but not plant damage by insect herbivores (**Figure 3c**; $Q_B = 0.15, P = 0.70$). Herbivore abundance on focal plants declined when unpalatable neighbors were present (AR) but did not differ in the presence of palatable neighbors (e.g., **Figure 3a**). When plant damage was measured, unpalatable neighbors provided AR, and having palatable neighbors resulted in AS (e.g., **Figure 3b**). However, when we separately analyzed the effect of plant palatability on the abundance of polyphagous insects, we found no significant effect. This suggests that species with narrower host ranges are driving this effect (the effect of neighboring plant palatability on polyphagous insect abundance: $Q_B = 1.17, P = 0.2779$).

Taxonomic similarity. The degree to which a focal plant and its neighbor are taxonomically related also may play an important role in determining the likelihood of AR and AS (Moore et al. 1991). Focal and neighboring plants that are closely related may be more likely to share herbivores. Therefore, one might logically assume that taxonomically related plants may be more likely to be involved in AS interactions, whereas taxonomically dissimilar plants may be more likely to interact in ways that lead to AR. In managed habitats there may be fewer arthropod pests when plants are associated with other taxonomically or genetically different plants (Andow 1991, Tonhasca & Byrne 1994). Thus, we predicted that the relatedness of neighboring and focal plants should influence the likelihood of AR and AS.

Results on the influence of plant taxonomic relatedness were equivocal. Plant taxonomic relatedness affected herbivore abundance (**Figure 3d**; $Q_B = 12.77, P < 0.05$) but not plant damage (**Figure 3e**; $Q_B = 4.17, P > 0.5251$). When herbivore abundance was used as the response variable, we found AR among plants that were most distantly related (kingdom and class) and no impact of neighboring plants of the same family, genus, or species, a pattern that is somewhat consistent with our prediction in that we predicted that AR would be more likely between distantly related plants. For purposes of brevity we report the effects of taxonomic similarity using

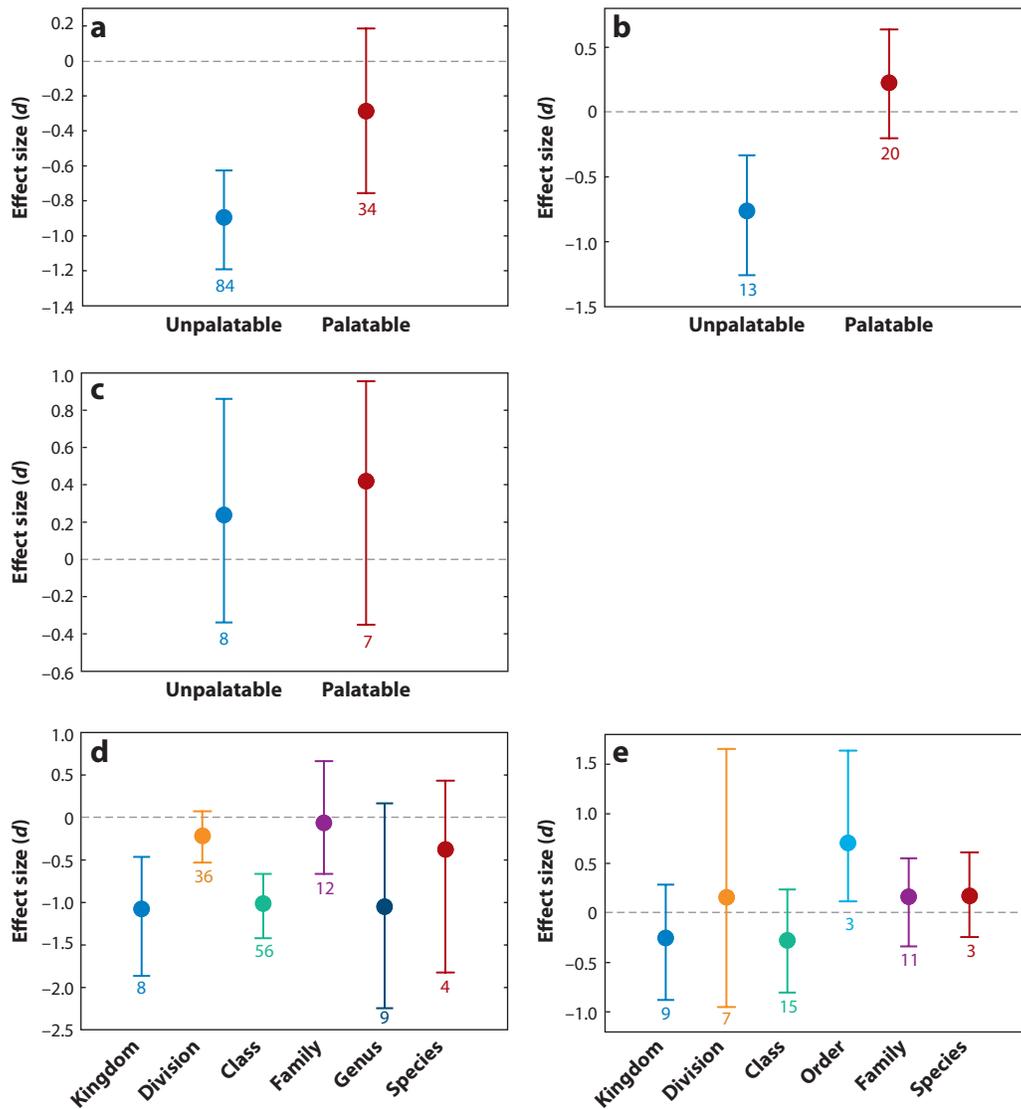


Figure 3

Impact of the palatability of neighboring plants (*a-c*) and plant taxonomic relatedness (*d-e*) on associational resistance and susceptibility (response variables = insect herbivore abundance, mammalian herbivore damage, insect herbivore damage, overall abundance, and overall damage, respectively). Error bars = 95% bootstrap confidence intervals. Numbers below error bars represent the number of observations used to calculate effect sizes in each category. Because the significance of effect sizes can be assessed based on whether or not their confidence interval overlaps zero, a dotted line is included at zero to visually interpret the significance of each effect size.

the entire dataset. However, if the dataset is subdivided according to herbivore taxonomy (that is, insect or mammal) or neighboring plant palatability, the results are qualitatively the same.

For an analysis of the effects of habitat management (e.g., agricultural systems) on the strength of AR and AS, see **Supplemental Text 3**.

ASSOCIATIONAL RESISTANCE AND SUSCEPTIBILITY: EXPANDING THE CONCEPT

Associational Resistance and Associational Susceptibility among Herbivores

How broadly should AR and AS interactions be applied? In general, associational interactions have been observed and reported with regard to changes in detection and vulnerability of plants to herbivores. However, significantly less attention has been given to the idea that associations among herbivores may influence the likelihood of detection by, and/or vulnerability to, predators, pathogens, parasites, or parasitoids and, thus, may result in AR or AS (but see Redman & Scriber 2000). The potential for AR or AS due to the co-occurrence of particular herbivores is distinct from the idea that differential responses of natural enemies can mediate (or act as a mechanism that results in) AR or AS between plants (Stiling et al. 2003). In contrast, an example of AS among herbivores is provided by Stenberg et al. (2007) who found that associations of the perennial herb *Filipendula ulmaria* and purple loostripe *Lytbrum salicaria* affect levels of herbivory because the hymenopteran parasitoid *Asecodes mento* attacks two conspecific chrysomelid beetles (*Galerucella tenella* on *F. ulmaria* and *G. californiensis* on *L. salicaria*). Parasitism of *G. tenella* was negatively correlated with percentage leaf area consumed of *F. ulmaria*. Mixed populations of *F. ulmaria* and *L. salicaria* supported higher densities of their shared parasitoid *A. mento*, and air from flower-bearing *F. ulmaria* stems attracted more than twice as many gravid *A. mento* females as air from flower bearing *L. salicaria*.

Barbosa & Caldas (2007) provided indirect evidence suggesting that AS occurs among a large number of co-occurring herbivores. Lepidopteran larvae shared traits that enhanced their parasitism by a suite of parasitoids, suggesting the potential for AS. Other mechanisms leading to AR or AS are highlighted by Shiojiri et al. (2001) and Heimpel et al. (2003), although their research did not specifically focus on AR or AS. These are potential mechanisms based on differential allocation and survival of parasitoid eggs in different hosts and differences in volatiles (affecting parasitoid host-finding) emitted from plants with one or two herbivore hosts.

Interestingly, analogous phenomena have been known for many years. In Batesian mimicry, the association of model and mimic herbivores protects against predators. Sharing of morphological traits by vulnerable and defended species reduces predation of the vulnerable species (that is, results in AR).

Associational Resistance and Associational Susceptibility from a Landscape Perspective

In managed habitats, the concepts of AR and AS have been expanded in that AR and AS are assumed to be achievable either by the use of adjacent plants in the plots or by the use of patches of noncrop plants adjacent to the focal crop plot. We suggest that AR or AS also may occur at even larger spatial scales, that is, at a landscape level. Even after three decades of research we still do not know the effective distance at which neighboring plants influence focal plants (but see Evans 1983). This may be, in part, because we were asking the wrong question. Rather than asking, at what distance are AR and AS effective, it may be more useful to ask, do the types of mechanisms that bring about AR and AS at different spatial scales differ? For example, AR that is dependent on induced volatiles and priming would likely only be effective for focal and neighboring plants in close proximity. Other mechanisms such as the relative abundance of focal and neighboring plants may be applicable to landscape level AR or AS.



Similarly, relatively immobile herbivores may respond to differences in plant composition at small scales, whereas perception by large or highly mobile herbivores may occur on a larger scale. The scale of animal movement may determine the likelihood of landscape-level AR or AS (Grez & Gonzalez 1995). Banks (1998) found that of three herbivores, the most dispersive (mobile) species showed no response to the small-scale fragmentation treatment. In general, there may be a similar optimal scale at which one should expect particular herbivores to be affected by the association of plants.

Identifying the role of the landscape may be important in predicting the strength and direction of associational responses of herbivores (Thies et al. 2003). Landscape-level AS might be likely if critical resources needed by herbivores are available in the surrounding habitats (such as the habitats that border some crop fields), or if overwintering survival is enhanced in surrounding habitats. Nearby habitats that do not enhance resource availability for herbivores may lead to landscape level AR. For example, grape cluster infestation by grape berry moth is lower in vineyards that are next to grass fields compared to ones bordering woodland habitats. The latter harbor an alternate plant host of the pest (Botero-Garcés & Isaacs 2004). Nearby habitats also may act as dispersal barriers between crop fields (Bhar & Fahrig 1998) and provide landscape-level AR for focal crop plants.

An adjacent habitat also may facilitate AR by providing critical resources for natural enemies of the herbivores in a focal habitat. Predators or parasitoids may have alternate hosts/prey or use some other resources found in surrounding habitats, which help maintain an abundant population. Alternatively, natural enemy populations may build up in adjacent habitats and spill-over into an adjacent focal habitat, via at least three basic mechanisms: (a) simple diffusion or spread from areas of high predator density into an adjacent habitat, (b) movement of natural enemies in response to temporal shifts in prey availability in an adjacent habitats, or (c) the complementary use by natural enemies of resources found in both habitats (Rand et al. 2006).

An example of the latter mechanism involves the parasitoid *Anagrus epos* that is only effective as a biological control agent of a grape pest in vineyards located near to native habitats, even if they occur some distance from the vineyard (Doutt & Nakata 1973). The presence of an alternative host in native riparian habitats maintains high parasitoid densities. The likelihood of natural enemy buildup and spill-over leading to AR depends on whether herbivores in both habitats share natural enemies and on the relative abundance of herbivore and natural enemy populations in each habitat. Ultimately, landscape differences in the occurrence of AR or AS will depend on whether adjacent patches or habitats provide complementary resources for herbivores or natural enemies and how herbivore and natural enemy behavior and movement reflects a response to differential resource distributions across the landscape. Movement of herbivores (or their natural enemies) to and from adjacent habitats and the spatial and temporal availability of resources in adjacent habitats are among the other factors that are likely to determine landscape-level impacts of AR and AS.

EPILOGUE

In conclusion, the large number of direct and indirect interactions affecting the fitness of adjacent interacting species makes it difficult to predict the relative importance of any particular interaction like AR or AS. The long-term benefit or detriment to the focal plant experiencing AR or AS (whether reflected in overall change in fitness or in yield) will depend on the outcome of other concurrent or subsequent direct or indirect interactions between the plants. The strength, consistency, and relative impact of AR or AS on plant fitness also are likely to vary temporally and spatially as environmental conditions and herbivore and plant abundance change. Furthermore, the impact of herbivory is dependent on the relative fitness value of lost tissues and/or the ability



of plants to cope with damage via mechanisms such as plant tolerance, plant compensation, and plant defense. Indeed, there are few studies on long-term population and community-level effects of AR and AS, and this is perhaps where our efforts should be directed.

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