TITLE: Anthropogenic fragmentation of landscapes: mechanisms for eroding the specificity of plant-herbivore interactions

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Abstract

Reduced ecological specialization is an emerging, general pattern of ecological networks in fragmented landscapes. In plant-herbivore interactions, reductions in dietary specialization of herbivore communities are consistently associated with fragmented landscapes, but the causes remain poorly understood. We propose several hypothetical bottom-up and top-down mechanisms that may reduce the specificity of plant-herbivore interactions. These include empirically plausible applications and extensions of theory based on reduced habitat patch size and isolation (considered jointly), and habitat edge effects. Bottom-up effects in small, isolated habitat patches may limit availability of suitable hostplants, a constraint that increases with dietary specialization. Poor hostplant quality due to inbreeding in such fragments may especially disadvantage dietary specialist herbivores even when their hostplants are present. Size and isolation of habitat patches may change patterns of predation of herbivores, but whether such putative changes are associated with herbivore dietary specialization should depend on the mobility, size, and diet breadth of predators. Bottom-up edge effects may favor dietary generalist herbivores, yet top-down edge effects may favor dietary specialists owing to reduced predation. An increasingly supported edge effect is trophic ricochets generated by large grazers/browsers, which remove key hostplant species of specialist herbivores. We present empirical evidence that greater deer browsing in small forest fragments disproportionately reduces specialist abundances in lepidopteran assemblages in northeastern USA. Despite indirect evidence for these mechanisms, they have received scant direct testing with experimental approaches at a landscape scale. Identifying their relative contributions to reduced specificity of plant-herbivore interactions in fragmented landscapes is an important research goal.

Keywords: biotic homogenization, diet-breadth, edge effects, trophic interactions, trophic ricochet.

Introduction

There is increasing evidence that communities in anthropogenically fragmented landscapes lose ecological specialization, meaning that habitat specialist species and specific interactions between species disappear with increasing fragmentation (Clavel et al. 2011; Burkle et al. 2013; Martinson and Fagan 2014; Rossetti et al. 2017). This loss of ecological specificity has been repeatedly demonstrated in plant-insect-herbivore interactions, with insect herbivore assemblages in fragmented landscapes shifting towards species with broad diet breadths (Tscharntke et al. 2002; Cagnolo et al. 2009; Öckinger et al. 2010; Hagen et al. 2012; Rossetti et al. 2017). While the diminution of specific interactions in fragmented landscapes is expected to have important implications (e.g. functional homogenization; Clavel et al. 2011), predicting those consequences and identifying management tools to mitigate them are hampered by a limited understanding of the mechanisms that erode ecological specialization. The goal of this article is to explore how anthropogenic fragmentation of landscapes (hereafter "landscape fragmentation") might erode the specificity of plant-herbivore interactions by reducing dietary specialization of insect herbivore communities.

Top-down and bottom-up forces need to be investigated as potential mechanisms because communities of insect herbivores are shaped by both the availability and distribution of resources and interactions with their natural enemies (Mooney et al. 2012; Moreira et al. 2016; Vidal and Murphy 2018), both of which are modified in small, isolated habitat patches and at habitat edges (Ryall and Fahrig 2005; Gravel et al. 2011; Wimp et al. 2011; Cirtwill and Stouffer 2016; reviewed in Murphy et al. 2016). Furthermore, the diet breadth of insect herbivores influences the extent to which their populations are controlled by bottom-up and top-down forces (Mooney et al. 2012; Vidal and Murphy 2018). Combining these patterns suggests that altered interactions of herbivores with both their host plants and their predators could explain the reduced dietary specialization of insect herbivores observed in fragmented landscapes (some possible pathways are illustrated in Figure 1).

With respect to bottom-up effects, landscape fragmentation alters plant species composition and diversity (Harper et al. 2005; Haddad et al. 2015; Collins et al. 2017), as well as trait distributions, induced physiological responses and genetic diversity (Kolb and Diekmann 2005; Leimu et al. 2010; Guerin et al. 2014). These changes to their hostplants have the potential to modify herbivore communities and plant-herbivore interactions (Faeth et al. 2005; Wirth et al. 2008; Hunter 2016). Because dietary specialist herbivores rely on particular plant species and are adapted to overcome specific plant defenses (Ali and Agrawal 2012), we expect specialist herbivores to be more sensitive to the bottom-up effects of such changes to their hostplants. With respect to top-down effects, predator communities are likely to change dramatically in fragmented landscapes because sensitivity to fragmentation increases with trophic rank (Kruess and Tscharntke 1994; Holt et al. 1999; Hunter 2002). These changes will potentially alter dietary specialization of insect herbivore communities because distinct groups of natural enemies are known to exert top-down control of dietary specialist versus generalist herbivores (Gentry and Dyer 2002; Stireman and Singer 2003; Singer et al. 2014; Zvereva and Kozlov 2016). Ultimately, the influence of fragmentation on plant-herbivore interactions will depend on the extent to which bottom-up control of herbivores is strengthened or countered by the responses of natural enemies (top-down controls) to landscape modification (Hunter 2016).

The powerful and widespread anthropogenic changes being wrought on ecosystems at a landscape scale provides a strong impetus for developing a predictive framework for the implications for species interactions (Hunter 2002; Tscharntke and Brandl 2004; Tscharntke et al. 2012). By drawing on the literature on landscape fragmentation, wildlife ecology, and plant-insect interactions, we propose several mechanisms by which landscape fragmentation is expected to reduce dietary specialization in insect herbivore communities (Figure 1). Because very little work has addressed this issue directly, this article is a synthesis of hypotheses arising from different subdisciplines in ecology rather than a strict review of existing empirical work. We focus on forest ecosystems, but draw inferences and examples from other ecosystems as well.

To illustrate some of our points in the context of this literature, we also present original, preliminary data from an ongoing study of the mechanisms impacting dietary specialization of larval Lepidoptera in fragmented forests in Connecticut, USA.

Area and isolation effects

Reduced patch area and increased isolation are two of the predominant drivers of negative effects on biodiversity and ecosystem functioning in fragmented landscapes (Haddad et al. 2015). Their effects are often synergistic and overlapping (Didham et al. 2012), so we consider them collectively. The loss of specialist consumers has been robustly associated with reductions in patch size (Öckinger et al. 2010; Martinson and Fagan 2014; Rossetti et al. 2017) and, to a lesser extent, isolation (Martinson and Fagan 2014; but see Steffan-Dewenter & Tscharntke, 2000), but the causes have received limited study and both bottom-up and top-down mechanisms may play a role.

Bottom-up effects

Several mechanisms alter plant communities in small and isolated habitat fragments, and the absence of certain species and altered trait distributions will likely affect herbivore communities through bottom-up pathways. The presence or absence of any particular species in an area of habitat results partly from a neutral sampling process: larger patches represent larger samples, and are therefore more likely to include a given plant species (Connor and McCoy 1979). Additionally, as outlined by the Theory of Island Biogeography (MacArthur and Wilson 1967), larger patches support larger populations that are less prone to extinction (Lande 1988; Hanski 1999). Persistence of populations in small fragments and other marginal habitats can be increased by immigration from better performing populations (Brown and Kodric-Brown 1977; Hanski 1999). Therefore, isolated habitat patches that receive fewer immigrants will suffer higher extinction of existing species and lower colonization rates by new species. Both neutral sampling and island biogeography cause the probability of any particular plant species occurring in a habitat patch to decline with reduced patch area and greater isolation.

That the absence of a plant species will perforce exclude its specialist herbivores is a well-established theory termed “sequential dependency” (Holt 1996, 2010). Sequential dependency filters out dietary specialist herbivores from small, isolated patches as their hostplants are progressively lost (Holt 1996, 2010; Gravel et al. 2011; Figure 1). Sequential dependency shrinks the area of habitat available to herbivores to the area occupied by their host species, which decreases geometrically with the dietary specificity of herbivores. Therefore, sequential dependency could mediate the steeper species-area relationships observed for specialist versus generalist herbivores (Steffan-Dewenter and Tscharntke 2000; Öckinger et al. 2010; Franzén et al. 2012), and disproportionate loss of dietary specialists in fragmented landscapes.

Empirical tests of sequential dependency are rare, however. Analysis of 1111 populations of butterflies in the UK, spanning 27 species and 54 sites, showed that the abundance of dietary specialist species depended on hostplant availability, whereas hostplant availability did not predict the abundance of dietary generalists (Curtis et al. 2015). Reanalysis of data from a classic study on arthropod recolonization of six mangrove islands in the Florida Keys, USA, after experimental defaunation with insecticide (Simberloff and Wilson 1969) indicated that more specialized species tended to colonize later (Piechnik et al. 2008). Further reanalysis found that arthropod species were less likely to go extinct if they could exploit basal resources or when their prey were present on islands (Cirtwill and Stouffer 2016), consistent with sequential dependency.

Host availability in a patch of habitat is dynamic, not constant, and the success of an herbivore in a patchy landscape requires it to track its hosts through space and time, especially when herbivores have a limited diet breadth. Theoretically, the population dynamics of prey and their specialist predators can be stabilized in patchy landscapes (Huffaker 1958; Swihart et al. 2001; Johst and Schöps 2003; Ryall and Fahrig 2005) as prey find refuge in previously unoccupied patches and reproduce before predators arrive. A consequence of the prey's ability to escape is that specialist predators, especially poor dispersers, decline with increasing fragmentation (Bascompte and Solé 1998; Swihart et al. 2001; Kondoh 2003). In contrast, generalist predators are less sensitive to isolation in small habitat patches (Swihart et al. 2001; Kluger et al. 2011), largely because they are not dependent on tracking a particular host. In the context of plant-herbivore interactions with plants as prey and herbivores as predators, these results suggest that the ability to establish and maintain populations in isolated, small habitat fragments will increase with herbivore diet breadth and mobility.

Insect movement and host-tracking behavior within patches may also affect specialist and generalist herbivores differently. Because insect movement generally follows a correlated random walk (Kareiva and Shigesada 1983), herbivore persistence requires that randomly moving individuals stay in a patch long enough to reproduce (i.e., find and oviposit on an appropriate host). The probability of finding an appropriate host will decrease with patch size (Crone and Schultz 2003; Brown and Crone 2016), especially for specialists dependent on encountering a particular host. Additionally, the permeability of habitat edges will influence insect search behavior. Hard edges, which deter individuals from crossing them, may be less detrimental for specialists than more permeable edges if they increase the probability of remaining in the patch and thus of finding a specific host (Stamps et al. 1987; Ries and Debinski 2001; Schtickzelle and Baguette 2003). Alternatively, deterrence from crossing edges will inhibit emigration and finding a new patch with suitable hosts. Understanding the consequences of these combined responses for dietary specialization in fragmented landscapes will likely require species-specific knowledge about how movement and host-tracking behaviors vary among species and with traits like diet breadth (Haddad and Baum 1999; Hambäck and Englund 2005).

Even when dietary specialist herbivores locate their hosts in small fragments, fragmentation may alter the food quality of those hosts for insects in ways that advantage generalists more than specialists (Figure 1). In particular, plant populations in small and isolated habitat patches are more likely to be inbred (Honnay et al. 2005; Leimu et al. 2010), which may alter the nutritional quality (Ridley et al. 2011; Kittelson et al. 2015) and defense metabolism of hostplants (Carr and Eubanks 2002; Hull-Sanders and Eubanks 2005; Ouborg et al. 2006; Campbell et al. 2013). Although less resistant plants should benefit herbivores in general (Hayes et al. 2004; Campbell et al. 2013), the benefits are likely to be larger for dietary generalists than for specialists that are specifically adapted to overcome their hosts' defenses (Cornell and Hawkins 2003; Hull-Sanders and Eubanks 2005; Ali and Agrawal 2012; Mooney et al. 2012). For example, the pupal mass of two specialist chrysomelid beetles feeding on outbred *Ipomoea hederacea* var. *integriuscula* plants was higher than that attained on inbred plants (Hull-Sanders and Eubanks 2005). Generalist herbivores differed in their response to host inbreeding, with pupae of a polyphagous Lepidoptera species (*Spodoptera exigua*) having greater mass on outbred plants while inbred plants supported larger populations of polyphagous cotton aphids (Hull-Sanders and Eubanks 2005). This example suggests that inbreeding in plants might reduce population growth of specialists more than generalists, but there are several counterexamples in which specialist herbivores have preferred or performed better on inbred hosts (Delphia et al. 2009; Campbell et al. 2013). Therefore, although the prediction that landscape fragmentation might cause plant inbreeding that advantages polyphagous herbivores over dietary specialists is plausible, the current evidence is mixed and indirect.

The reduction of dietary specialization by herbivores in fragmented landscapes could result from additional responses to limited hostplant availability or quality in small habitat patches. Host choice is context dependent and, denied access to their preferred hostplants, some herbivores will use alternative plant species (Fox and Morrow 1981). It is possible, then, that oligophagous herbivores might use alternative, related hosts when their preferred hosts are unavailable in small habitat patches. Use of alternative hosts can occasionally be fatal when female Lepidoptera oviposit on hosts completely unsuitable for their offspring (so-called "lethal oviposition mistakes", Bowers and Schmitt 2013) and, in general, the use of less preferred hosts is likely to reduce herbivore performance, especially when herbivores have restricted diet breadth (Gripenberg et al. 2010). There are exceptions, however, and herbivores may actually have higher population growth rates on alternative hosts with the appropriate chemistry (Brown et al. 2017) or be able to rapidly adapt to alternative or novel hosts in fragmented landscapes (e.g. Singer et al. 1993). Consequently, some dietary specialist populations might expand their hostplant range in the absence of preferred hosts, while others might decline due to fitness deficits imposed by the use of alternative hosts. Either response erodes the specificity of plant-herbivore interactions as patch size diminishes.

Top-down effects

The effects of patch size and isolation on top-down control of herbivores are complex and depend on the landscape context and the specialization and dispersal of the predators and herbivores (Kondoh 2003; Ewers and Didham 2006; Ryall and Fahrig 2006; Liao et al. 2017). In general, the reduction in abundance in small, isolated habitat patches increases with trophic rank (Holt et al. 1999), releasing prey species from top-down control (Kruess and Tscharntke 1994; Anton et al. 2007; Schüepp et al. 2014; Liao et al. 2017; Figure 1). Effects of patch size and isolation on top-down control of insect herbivores have been found to depend on traits of the natural enemies involved, such as dispersal ability, and competition among parasitoids (e.g. Roland and Taylor 1997; Nieminen and Nouhuys 2017). The dietary specificity of predators and parasitoids is a trait of special importance, as several studies show that specialist predators are more sensitive to fragmentation than are generalists (Swihart et al. 2001; Ryall and Fahrig 2005; Cagnolo et al. 2009), so top-down control of herbivores from specialist natural enemies should decline in small, isolated patches, whereas attack by generalist natural enemies should be undiminished. To the extent that dietary generalist enemies target dietary generalist herbivores (e.g. Dyer 1995; Singer et al. 2014; Zvereva and Kozlov 2016) and specialist enemies target specialist herbivores (e.g. Gentry and Dyer 2002; Stireman and Singer 2003; Zvereva and

Kozlov 2016), small, isolated fragments will provide an enemy-free space advantage to specialist herbivores.

Relatively large predators, such as insectivorous birds, also impose strong top-down effects on insect herbivores (Van Bael et al. 2008; Mooney et al. 2010; Mäntylä et al. 2011). Despite being generalist insectivores or omnivores, many bird species show “area-sensitive” responses to habitat patch size, which often translate into reduced avian species richness in smaller fragments (e.g., Robbins et al. 1989; Askins 1993; Bregman et al. 2014). This general pattern of loss from small habitat fragments extends to many species of insectivorous forest birds (Robbins et al. 1989; Bayard and Elphick 2010; Bregman et al. 2014) and manipulative experiments that exclude birds (Mols and Visser 2002; Van Bael et al. 2008; Singer et al. 2014) or increase their population sizes (Jedlicka et al. 2011) have shown that insectivorous birds can reduce both herbivorous arthropod populations and herbivory. Evidence that dietary specialist insect herbivores experience lower bird predation risk than generalists (Singer et al. 2014) raises the possibility that decreased avian predation in small habitat fragments primarily benefits dietary generalist herbivores (Figure 1).

A loss of area-sensitive predator species owing to reductions in patch size, however, does not necessarily imply a change in the strength of top-down effects of the predator community. It is possible that alternative predator species might compensate through species turnover, or that those species that remain will increase in their abundance or foraging activity (Yachi and Loreau 1999). Community-level compensation for lost predators is unlikely for specialist predators, such as parasitoids, but it is plausible for large generalist predators like birds. Bayard and Elphick (2010) found that the abundance of a given bird species decreased with patch size in only 25% of almost 1500 tests, and increased in about 13% of tests, suggesting less clear effects of patch area on abundance than species richness. Furthermore, Morante-Filho *et al*. (2016) report that forest specialist bird species lost from fragmented landscapes were substituted with habitat generalist species, suggesting some degree of compensation. Clearly, to assess the top-down effects of avian predators, we need to know how the effects of patch size on species occurrence and richness translate into the total number of avian predators, and hence consumption. These results demonstrate that top-down effects can be important, but without clearer knowledge of density-dependent predation, prey partitioning and area/isolation sensitivity of different predator groups, it is not clear how top-down habitat area and isolation effects relate to the loss of dietary specialization in herbivore communities.

Edge effects

Edge effects are likely to dominate when a landscape becomes fragmented with relatively little total loss of habitat area (Fahrig 2017). Species able to use a wide range of resources, i.e. resource generalists, typically respond positively to edges (Ries et al. 2004; Wirth et al. 2008; Hagen et al. 2012). Herbivore abundance typically increases at habitat edges (Wirth et al. 2008) and a meta-analysis of edge effects on insect herbivore abundance and herbivory showed positive responses overall, especially for Lepidoptera and Orthoptera, but did not consider the potential role of dietary specialization (De Carvalho Guimarães et al. 2014). Although we know of no formal quantitative analysis that specifically considers the potential for edge effects to differ with insect herbivore diet breadth, a review by Wirth et al. (2008) reported several examples of specialist insect herbivores responding negatively to habitat edges and generalist herbivores invariably benefiting. It therefore appears likely that the decrease of dietary specialization by insect herbivores in fragmented landscapes is partly driven by edge effects.

A growing literature has sought to organize the various processes that modify natural communities at habitat edges, especially those due to anthropogenic fragmentation of landscapes (Fahrig 2003; Ries et al. 2004; Murphy et al. 2016; Fahrig 2017; Ries et al. 2017). The edge resource model of Ries and Sisk (2004) considers the edge a boundary zone between habitat types potentially differing in resource availability. The response of a particular species to a habitat edge depends on the distribution of limiting resources on either side of the edge; the extent that resources spill across the edge and the degree to which the resources provided by the adjoining habitats are supplementary or complementary (Ries et al. 2004; Ries and Sisk 2004). Ries et al. (2004) expanded the edge resource model to incorporate interactions between focal species and competitors, predators and mutualists that themselves respond to edge-induced resource gradients. The edge resource model was formulated to predict edge responses of individual species, but it has also successfully predicted responses of groups of species that share resource requirements (Wimp et al. 2011; Murphy et al. 2016; Ries et al. 2017). It therefore provides a useful framework for understanding how diet breadth might modulate the response of insect herbivores to habitat edges. Predictions of the specificity of plant-herbivore interactions based on the edge resource model depend on whether edge responses of herbivores or predators dominate multi-trophic dynamics.

Bottom-up effects

Habitat edges typically experience distinct microclimatic conditions relative to interior parts of a habitat type. For example, typical forest:matrix edges are characterized by increased light, temperature, and wind, and decreased humidity (Ries et al. 2004; Ewers and Banks-Leite 2013). Such altered microclimates are less suitable for many plant species specialized to forest interiors, driving a switch in plant species composition and hence the resources available to herbivores (Wirth et al. 2008). The sensitivity of herbivores to turnover in plant composition decreases with their diet breadth because generalists are less likely to lose all their host plants and are more likely to consume alternative plant hosts (Ries et al. 2004). In addition, dietary generalist herbivores are more likely to benefit from exploiting complementary resources provided by adjoining habitats than are specialists.

Edge effects may also work against dietary specialist herbivores by increasing the representation of exotic and invasive plant species in local communities (Harper et al. 2005; Figure 1; Allen et al. 2013). Increased exotic abundance is expected to limit hostplant availability for native dietary specialist herbivores to a greater degree than for dietary generalist herbivores that may potentially use the exotic plants (Burghardt et al. 2010). Indeed, arthropod communities found on exotic trees and shrubs in the northeastern USA are much impoverished in terms of diversity and abundance relative to those on native plants (Tallamy and Shropshire 2009; Burghardt et al. 2010; Burghardt and Tallamy 2013). In a common garden study with dozens of exotic and native woody plant species, Burghardt et al. (2010) found that dietary specialist caterpillar assemblages were less abundant and species-rich on exotic plants relative to natives, even in comparisons of congeneric plants. By contrast, dietary generalist herbivores, especially large grazers and browsers, can opportunistically forage on many exotic plant species (e.g., Morrison and Brown 2004).

Top-down effects

Top-down effects of predators on herbivores and plants can also be modified at habitat edges (Murphy et al. 2016). In support of the resource edge model (Ries and Sisk 2004), several studies show that generalist predators tend to respond positively to edges (Rand et al. 2006; Frost et al. 2015) whereas specialist predators respond negatively (e.g. Valladares et al. 2006; Valladares et al. 2012; Figure 1). While Valladares et al. (2006) found reduced parasitoid abundance at woodland edges, they also found increased parasitism rates of leafminers along edges. Further study revealed a disproportionate loss of interaction specificity in food webs in smaller habitat patches (Valladares et al. 2012), suggesting that host-specialist parasitoid species were being replaced by generalist parasitoids, which were driving the increased parasitism near edges. In another case, Frost et al. (2015) found that generalist vespid wasps “spilled over” from exotic plantation forest to native forest as they opportunistically tracked the abundance of caterpillar prey. Experimental reduction of caterpillar prey in the plantation forest decreased the generalist predator spillover, whereas the spillover of relatively host-specific parasitoids was unaffected by the caterpillar manipulation. If the edge resource model’s predictions hold, the shift in the predator community toward generalists along edges is likely to differentially affect dietary specialist and generalist herbivores. Based on evidence discussed above that specialist herbivores have relatively specialized enemies compared to generalist herbivores, we expect increased predation on dietary generalist herbivores relative to dietary specialists, resulting in increased specificity in herbivore-plant interactions near edges.

Trophic ricochets

An extension of the resource edge model considers not only direct effects on herbivores, but also indirect effects on other herbivores and predators. Deer appear to benefit greatly from the proliferation of forest edges, and increased deer browsing has been identified as a type of edge effect (Alverson et al. 1988). In temperate forests globally, deer respond positively to forest edges with increased density or reproduction (e.g., Japanese sika deer, *Cervus nippon,* Miyashita et al. 2008; North American white-tailed deer *Odocoileus virginianus*, Massé and Côté 2012; European roe deer, *Capreolus capreolus* Brazaitis et al. 2014). According to the "trophic ricochet" hypothesis (Nuttle et al. 2011), large grazers and browsers, such as white-tailed deer in the USA, can drastically alter vegetation abundance composition, and structure, with a ricochet effect that propagates up to insect herbivores and their predators (Nuttle et al. 2011; Bressette et al. 2012; Wheatall et al. 2013). In support of the trophic ricochet hypothesis, several studies provide evidence that deer-excluded areas contained more caterpillars and forest birds than deer-accessible areas in the northeastern USA (Nuttle et al. 2011; Bressette et al. 2012; Wheatall et al. 2013). While the effect of large herbivores on the community-level specificity of plant-herbivore interactions has not been explored, we hypothesize two potential mechanisms of opposing effect.

One possible mechanism for reduced specificity of plant-insect interactions is due to altered plant community structure in heavily browsed, fragmented forests. Deer herbivory tends to reduce woody vegetation (e.g., Horsley et al. 2003; Nuttle et al. 2011; Habeck and Schultz 2015) on which many forest insect herbivores, such as caterpillars, also feed (Wagner et al. 2002; Wagner 2005; Wagner 2011). Evidence suggests that above-ground insect diversity is indeed higher in the absence of deer (Chips et al. 2015). Dietary specialist herbivores may be especially vulnerable to this ricochet effect in smaller habitat patches, where the probability of finding their preferred hostplant species has already been reduced (Figure 1). The negative ricochet impact of deer herbivory is further exacerbated by the overlap in plant preference by deer and dietary specialist herbivores. Although deer preference for particular plants can vary depending on landscape context, analysis of a global dataset found that large mammal herbivory reduced arthropod diversity, with a trend towards reduced abundance as well (Daskin and Pringle 2016). The strength of the effects found by Daskin and Pringle (2016) increased in areas of low primary productivity, indicating that the strength of the mechanism proposed here is likely to vary across ecosystems in a similar manner.

A mechanism of opposing effect is that browsing by large herbivores could sometimes indirectly benefit dietary specialist herbivores. Deer browsing, in particular, can alter the morphology and chemistry of plants in ways that may benefit dietary specialist herbivores in the same community. Although Lind et al. (2012) found that overall herbivory by both dietary generalist and specialist insect herbivores was highest on unbrowsed spicebush (*Lindera benzoin*), consistent with the mechanism above, caterpillars of the toxin-sequestering dietary specialist spicebush swallowtail (*Papilio troilus*) both preferred and had higher growth rates on browsed leaves, perhaps because they benefited from increased levels of induced chemical defenses. Based on existing theory predicting how varying levels of induced plant toxins affect insect herbivore performance (Ali and Agrawal 2012), we expect browsing effects on induced plant phenotypes to mainly benefit dietary specialist herbivores that sequester induced toxins from their host plants, a trait frequently associated with the use plant secondary metabolites as host recognition cues (Bernays and Chapman 1994). Herbivory by dietary generalists and specialists may also exert opposing selective pressures on defensive chemistry of particular plants: in the absence of dietary specialists, plant populations may evolve increased chemical defenses, but in the absence of dietary generalists, plant phenotypes with decreased defenses may be favored because they deter toxin-sequestering dietary specialists (Lankau 2007; Ali and

Agrawal 2012). If deer herbivory exerts selection to increase plant defenses, this may increase the detectability of the plants by their specialist insect herbivores (Lankau 2007), which would be beneficial regardless of patch size, and could help to mediate competition with generalist herbivores and counter declines in smaller patches.

Lepidopteran diet breadth in forest fragments in Connecticut

Ongoing work in a fragmented forest landscape in Connecticut, northeastern USA, provides some support for some of the pathways described in this review. In May – July 2015 we sampled lepidopteran larvae in four 100 m^2 plots in each of 10 fragments of temperate deciduous forest (size range: 3 – 400 ha). The proportion of dietary specialist species increased with fragment area (Figure 2), a trend that we tested statistically using a Binomial Generalized Linear Mixed Model (GLMM) including a random intercept for fragment identity ($z = 2.21$, $P = 0.027$). We surveyed the vegetation from the same plots and classified woody plant species into deer sensitive or insensitive categories. This classification was based on a literature survey that collated the effects of deer-exclusion experiments on woody plant species in northeastern USA (see Appendix for sources). The abundance of specialist caterpillars increased more steeply with the abundance of woody plants sensitive to deer browsing (Figure 3a; negative binomial GLMM: z=2.93, P=0.003) than abundance of generalists did (z=0.73, P=0.47). The densities of deer-preferred plant species declined in smaller forest patches (Figure 3b; negative binomial GLMM: z=2.48, P=0.013), perhaps contributing to the decrease in specialist herbivores we observed (Figure 2). These data suggest that the overabundance of deer observed in many temperate forest regions, especially at forest edges (Alverson et al. 1988), could disproportionately disadvantage dietary specialist insect herbivores.

Conclusions and future directions

We hope that this review stimulates further research into the mechanisms that control the specificity of plant-herbivore interactions in fragmented landscapes. In summary, the observed loss of dietary specialist herbivores in anthropogenically fragmented landscapes can arise from reduced area and increased isolation of habitat patches, as well as from direct and indirect effects of habitat edge proliferation. The landscape structure and the dispersal and habitat-preference traits of species in local communities will determine which of these landscape components dominates this multi-dimensional phenomenon. Our examination of theory and evidence suggests that bottom-up and top-down mechanisms have the potential to play important roles in the erosion of plant-herbivore specificity in fragmented landscapes. Pathways of feedback between bottom-up and top-down mechanisms represent an important future direction of study (Hunter 2016). Both the trophic theory of island biogeography and the edge resource model offer useful insight into the phenomenon. Their general predictions find much support in plant-herbivore communities, but significant gaps in our understanding remain regarding the relative strength of multiple predicted effects.

Reading the literature at face value suggests that bottom-up effects are likely to predominate in landscape fragmentation’s reduction of plant-herbivore specificity. However, this impression might be due to the more limited study of top-down compared to bottom-up mechanisms and theory. Here we identify several key research questions to guide future study of this issue. To give adequate consideration to hypothetical top-down mechanisms, we need to know how area-sensitivity compares between large, generalist predators versus small, specialist predators. Additionally, how much do predator communities compensate for the loss of the most area-sensitive species, and what are the functional consequences of these altered predator communities for dietary specialist and generalist herbivores? The strong functional roles of particular species, such as large grazer/browser species, highlight the importance of species identity effects in altering the plant-herbivore communities in fragmented landscapes. Here again, significant questions remain: how much does the reduced abundance and species richness of dietary specialist herbivores in fragmented forests owe to neutral, sampling effects versus deterministic, species identity effects driving variation in plant communities? In the realm of bottom-up effects, components of landscape fragmentation may modify plant variation and plant-herbivore interactions by acting at the plant phenotypic level. Does intraspecific phenotypic variation in anti-herbivore resistance traits in plants, including induced resistance, respond directly or indirectly to area or edge effects? To what extent might these landscape-level processes organize community-level variation in plant and herbivore phenotypes?

To address these and related questions, further research is needed that combines landscape level observations with experimental manipulations to provide rigorous tests of alternative mechanisms. Field experiments will be especially valuable for gaining inferences in the context of real communities, while lab and mesocosm experiments will be valuable for elucidating mechanisms that act at relatively small spatial and temporal scales. Indeed, it is not clear to what extent the overall pattern of loss of plant-herbivore specificity depends on the spatial and temporal scales of landscape fragmentation, let alone how the underlying mechanisms might depend on scale. Given this uncertainty, studies at multiple spatial and temporal scales are needed to identify possible mechanisms.

Future studies will also maximize their utility by using measures of ecological specialization that can be quantified and compared among species and communities. Descriptors such as “specialists” and “generalists” without any clear reference to the resource in question are problematic alone because the concept of specialization is inherently relative and context-dependent (Forister et al. 2012). In other words, one study’s specialist may be another study’s generalist. If research on the loss of ecological specialization in fragmented landscapes were to use recently proposed metrics for quantifying ecological specialization of particular resources (e.g. Devictor et al. 2010; Poulin et al. 2011; Jorge et al. 2017), empirical studies could reveal new quantitative patterns. Likewise, this move would enable more powerful re-analyses and meta-analyses on this topic.

We presently know that landscape fragmentation is eroding the specificity of plant-herbivore interactions, but in order to understand the dimensions of the problem and its causes, new approaches are needed. To conclude, studies of plant-herbivore interactions would do well to consider landscape context in which they occur, as conclusions about dietary specialization (population/community studies) and interaction specificity (e.g., network analyses) will be affected by landscape fragmentation.

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Figure Legends

Figure 1: A model system illustrating a subset of the bottom-up and top-down pathways by which landscape fragmentation is hypothesized to reduce the abundance of dietary specialist herbivores more than dietary generalists, including area and isolation effects, edge effects, trophic ricochet, and mechanism-independent effects (indicated by different colored arrows). Arrows can indicate positive or negative relationships and their signs are multiplicative through pathways (pathways containing even or odd numbers of negative effects would be, respectively, positive or negative overall). This model system reflects features of fragmented forests we study in Connecticut: area and edge effects are likely to dominate, with minimal influence of isolation effects and negligible dispersal limitations of woody plants, Lepidoptera (small specialist and

generalist herbivores), white-tailed deer (large generalist herbivores), parasitoids (small specialist and generalist predators), and insectivorous birds (large generalist predators).

Figure 2: Effects of patch area (log scale) on the proportion of larval Lepidoptera that are dietary specialists in temperate deciduous forest fragments in Connecticut. Points (and error bars) indicate the mean observed proportion (± s.e.m) of caterpillars that were specialists from four 100-m^2 plots in each of 10 forest patches surveyed in 2015. Lines and shaded areas are the expectations and 95% confidence intervals from a binomial GLMM fitted to the data.

Figure 3: (a) The abundance of dietary specialist caterpillars increased more steeply with the abundance of deer-sensitive plant species than did the density of generalists in 10 temperate deciduous forest patches of varying size in Connecticut. Deer-sensitive plant species were found to be preferentially browsed by deer in deer-exclusion experiments conducted in the northeastern USA (see Appendix for sources). Points indicate the numbers of caterpillars collected in four 100-m^2 plots in each forest patch, and the expectations and 95% confidence intervals of a negative binomial GLMM fitted to the data are indicated by the lines and shaded envelopes respectively. (b) The number of individuals between 1 – 2 m in height of deer-sensitive woody plant species increased with patch area. Points indicate the mean total abundance of saplings across all species (± s.e.m) occurring in four 100-m^2 plots in each of 10 forest patches. The line and shaded envelope are, respectively, the predicted relationship and confidence envelope from a negative binomial model fitted to the data.

Figure 1

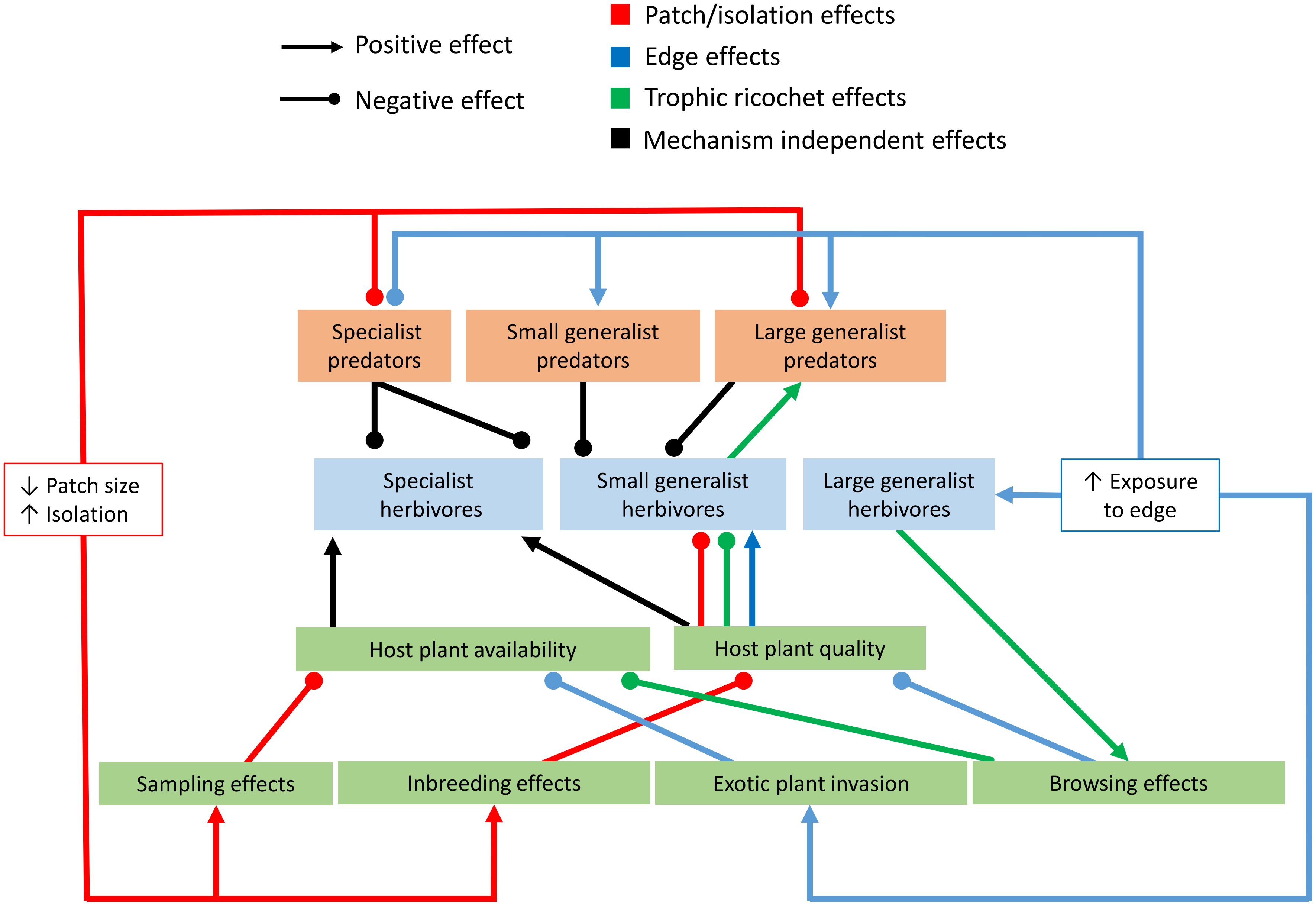

Positive effect
Negative effect
Patch/isolation effects
Edge effects
Trophic ricochet effects
Mechanism independent effects
Specialist predators
Small generalist predators
Large generalist predators
↓ Patch size
↑ Isolation
Specialist herbivores
Small generalist herbivores
Large generalist herbivores
↑ Exposure to edge
Host plant availability
Host plant quality
Sampling effects
Inbreeding effects
Exotic plant invasion
Browsing effects

Figure 2

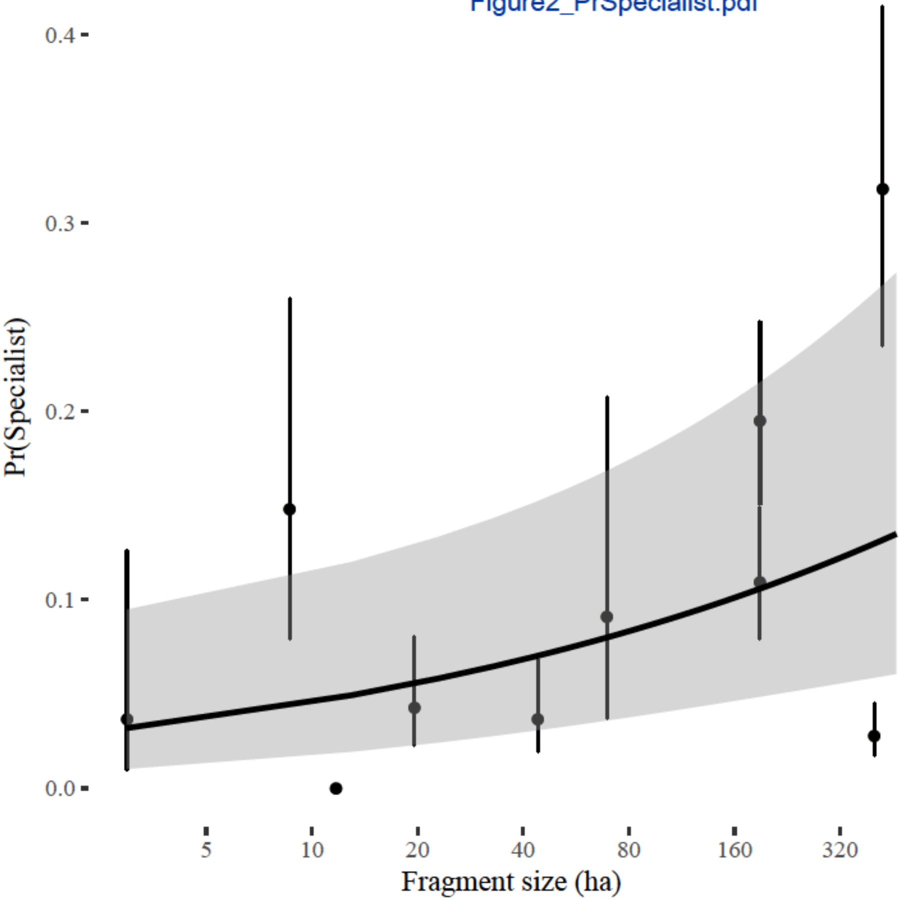
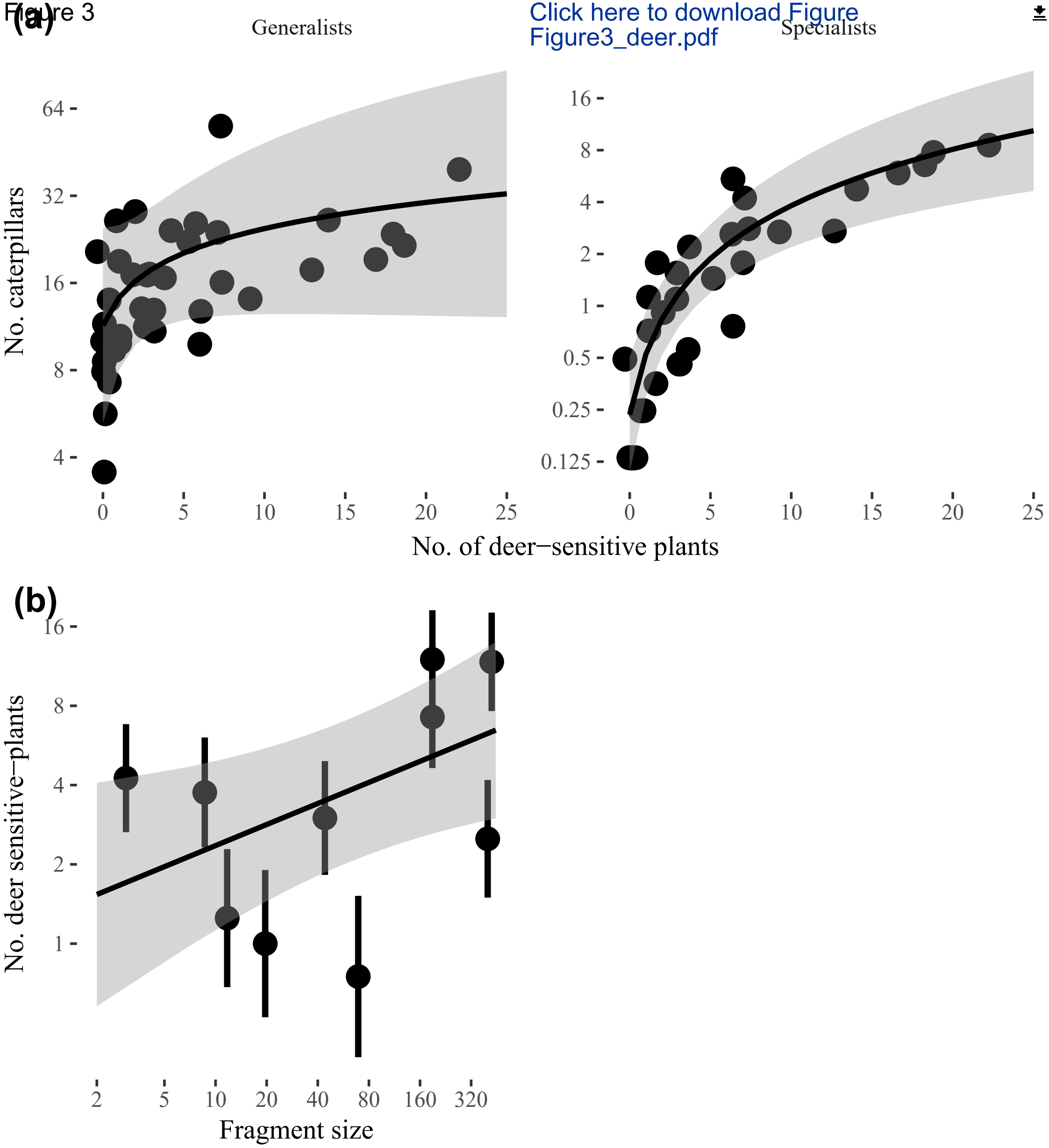

0.4
0.3
0.2
0.1
0.0
Pr(Specialist)
5
10
20
40
80
160
320
Fragment size (ha)

Figure 3


(a)
Generalists
Specialists
No. caterpillars
64
32
16
8
4
16
8
4
2
1
0.5
0.25
0.125
0
5
10
15
20
25
0
5
10
15
20
25
No. of deer−sensitive plants
(b)
16
8
4
2
1
No. deer sensitive−plants
2
5
10
20
40
80
160
320
Fragment size