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# Complex community and evolutionary responses to habitat fragmentation and habitat edges: what can we learn from insect science?

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Habitat fragmentation is the primary factor leading to species extinction worldwide and understanding how species respond to habitat edges is critical for understanding the effects of fragmentation on insect diversity in both natural and managed landscapes. Most studies on insect responses to the habitat edge focus on bottom-up changes in resources. Only a few recent studies have examined multi-trophic responses to habitat edges; the results of these studies highlight the problem that we lack a conceptual framework to understand the complex results observed when a single species' response to an edge 'cascades' throughout the food web in ways that are currently not predictable. Recent research from insect systems suggests that habitat edge responses cascade both up and down multi-trophic foodwebs and these altered species interactions may affect evolutionary processes. Future studies that investigate the effects of habitat edges on both ecological and evolutionary dynamics can help to fill these knowledge gaps and we suggest that insects, with short generation times, present an ideal opportunity to do so.

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## Introduction

Habitat loss and fragmentation is widely considered to be the primary factor leading to species extinction worldwide. Although multiple mechanisms contribute to species losses in fragmented habitats, fragmentation is usually associated with increased edge habitat [1], and most effects of fragmentation attributed to patch area are actually scaled-up edge effects [2]. Compared with core (interior) habitat, edge habitats are subject to different abiotic conditions, such as variation in solar radiation, temperature, wind, soil moisture and humidity [3••]. The severity of the changes in abiotic conditions can depend on how 'soft' or 'hard' the contrast is between the two abutting habitats. Understanding how species respond to habitat edges is critical for understanding the effects of fragmentation on diversity in both natural and managed landscapes [3••]. Yet, despite recent advances in understanding single species responses to habitat edges, we lack a framework to understand more complex interactions or evolutionary processes. Here, we synthesize the literature on ecological and evolutionary responses to edges with a focus on empirical examples from insect science; these well-studied systems provide a gateway to understand mechanisms, interactions and, where generation times are short, evolutionary changes in real time.

## Ecological responses to habitat edges

### Bottom-up drivers of insect responses to habitat edges

The factors underlying single-species edge responses have been formalized into an Edge Resource Model (ERM) that created a simple set of predictions for any species at any edge type based on resource quality and distribution in adjoining habitats [4]. The model was based on two fundamental mechanisms that are unique to edges: (1) ecological flows of species/energy/material from one adjoining habitat into another creating a gradient of habitat quality near the edge and (2) better access to spatially separated resources is maximized at edges (also known as 'cross-boundary subsidies'). The ERM has been a useful model for studying insect responses to habitat edges because many edge responses result from bottom-up changes in resources. The typical prediction is that microclimatic changes near edges impact plant distribution or quality, and variation in these key resources then cascades to alter herbivore and predator distributions. Notably, changes in the physical environment along the habitat edge can change habitat structure, which may increase the interception of allochthonous nutrients (e.g. through increased deposition [5]) and thereby increase plant quality for herbivores. For example, although density of a key host plant declined in patch edges during colonization after the Mt. St. Helen's eruption, higher nutritive quality was shown to lead to insect herbivore outbreaks [6]. Such increases in plant quality along the habitat edge may explain why a recent meta-analysis found an overall increase in insect herbivore abundance, richness, and plant herbivory along habitat edges relative to core habitats [7]. The ERM provides a mechanistic explanation for many edge responses reported in the literature [3••], but it is limited to single species responses and does not incorporate multi-species interactions or predict how shifts in the community along a habitat edge alters species interactions or top-down effects.

## Top-down drivers of insect responses to habitat edges

The consequences of fragmentation for top-down control of species have also been considered in the literature. A recent meta-analysis found increased consumption in edge habitats compared to interiors [8••]. Notably, this increased top-down effect was driven primarily by herbivores feeding on plants, and in particular by dietary generalists, not specialists. Further, this meta-analysis found no evidence that higher trophic level organisms such as predators or parasitoids increased consumption in edge habitats (but see [9••], discussed below in 'multi-trophic interactions and community patterns'). Although herbivory rates change near edges, top-down mechanisms such as changes in predation rate have not been integrated into formal predictions of edge responses and the edge literature is conflicted about how predators respond to edges. Theory related more generally to habitat fragmentation, not just habitat edges, predicts that higher-trophic-level consumers should be particularly vulnerable to habitat fragmentation (e.g. [10]); the predicted negative impact of fragmentation on predators is based on Island Biogeographic Theory [11] and the idea that patch size and isolation have greater impacts at higher trophic levels [10,12]. Despite the fact that edge effects dominate in fragmented habitats, a common generalization has emerged from the edge literature that generalist predators increase along habitat edges [13]. The belief that predators respond positively to edges may persist because the edge effect literature is biased towards generalist predators of avian nests [14], which makes it difficult to ascertain whether this edge-predator effect is widely applicable to other taxa. Thus, the conflicting views of predators (that they often thrive at edges, but are especially vulnerable to fragmentation) may come from focusing on different predator communities and may be biased towards generalist, vertebrate mesopredators. In support of this assertion, studies of insects in agricultural systems have primarily demonstrated that predators track transitional gradients in prey resources across the edge (e.g. [15]), and positive edge responses are relatively rare. A better understanding of how top-down interactions disrupt species mapping onto critical resources is essential for predicting population and community responses to habitat edges.

## Multi-trophic interactions and community patterns

Landscape and conservation ecologists have studied how habitat fragmentation affects individual species as well as communities for decades [16] and recent studies have tried to understand how fragmentation affects food web dynamics [reviewed in 8••,17]. However, most examinations of species interactions in fragmented habitats are restricted to two-species models [8••] and the few studies that have examined how habitat fragmentation affects multi-trophic interactions focused on isolation and/or area effects (e.g. [18–20]), not the effects of habitat edges *per se* (but see [9••]). Only two studies have examined responses to habitat edges from a community perspective, and both found top-down effects on herbivores. For example, Evans *et al.* [21•] found decreased herbivore consumption near edges, a result of trophic interactions among ants, aphids, and a defoliating herbivore. In another multi-trophic study, Wimp *et al.* [9••] demonstrated that predicted declines of planthopper herbivores near edges were not explained by bottom-up effects on resources, which did not vary in quality or quantity between edge and core habitats, but instead were likely due to predator avoidance. Predators may also 'spillover' into natural fragments from managed habitat at higher rates than other trophic levels [22•] and bias in dispersal patterns may concentrate parasitoids at edges [23] thereby increasing top-down control along edges. These results suggest that top-down selective pressures can drive species responses to habitat edges and argue for incorporating predator/parasitoid densities as an additional resource that may drive herbivore edge responses.

Most studies that examined the impact of habitat edges on insect communities have quantified changes in abundance or species richness, but did not examine changes in community structure, critical resources or trophic interactions that may have led to those responses [17]. These studies have largely examined the prediction that insect diversity and abundance will be greater along habitat edges relative to the interior because edges represent the convergence of two distinct habitats. While some studies have found higher arthropod diversity in edge relative to interior habitats, others have found no response, or the reverse, often with inconsistent results among different taxa in the same study [24–27,28•]. It may therefore be useful to consider how feeding specialization and functional group might influence insect community responses to the habitat edge. Previous studies have found that specialist herbivores are more likely to be negatively impacted by the habitat edge relative to generalist herbivores [7]. For example, specialist planthoppers are negatively affected by edges due to the absence of food in the adjacent habitat [9••,29], and this negative response intensifies when there is a high degree of environmental dissimilarity (or contrast) between the two adjoining habitats [24,29]. However, because these specialist herbivores are unwilling to cross from suitable to unsuitable habitat, they are often found in aggregations near the edge, and this can lead to increased rates of parasitism, despite declines in parasitoid abundance along