

LETTER

Do edge responses cascade up or down a multi-trophic food web?

Gina M. Wimp,^{1*} Shannon M. Murphy,² Danny Lewis¹ and Leslie Ries³

¹*Biology Department, Georgetown University, Washington, DC 20057, USA*

²*Department of Biological Sciences, University of Denver, Denver, CO 80208, USA*

³*Department of Biology, University of Maryland, College Park, MD 20742, USA*

*Correspondence: E-mail:

gmw22@georgetown.edu

Abstract

Despite nearly 100 years of edge studies, there has been little effort to document how edge responses ‘cascade’ to impact multi-trophic food webs. We examined changes within two, four-tiered food webs located on opposite sides of a habitat edge. Based on a ‘bottom-up’ resource-based model, we predicted plant resources would decline near edges, causing similar declines in specialist herbivores and their associated predators, while a generalist predator was predicted to increase due to complementary resource use. As predicted, we found declines in both specialist herbivores and predators near edges, but, contrary to expectations, this was not driven by gradients in plant resources. Instead, the increase in generalist predators near edges offers one alternative explanation for the observed declines. Furthermore, our results suggest how recent advances in food web theory could improve resource-based edge models, and *vice versa*.

Keywords

Ecological boundary, ecotone, edge effects, habitat fragmentation, predictive model, resource distribution.

Ecology Letters (2011) **14**: 863–870

INTRODUCTION

Understanding how habitat fragmentation impacts individual species and communities has been a major topic in landscape and conservation biology for decades (Saunders *et al.* 1991; Laurance 2008). More recently, there has been an attempt to understand how food web dynamics may be influenced by fragmentation (reviewed in Tscharntke & Brandl 2004; van Nouhuys 2005; Martinson 2009), which is part of an effort to understand spatial food web dynamics in general (Gripengberg & Roslin 2007; Amarasekare 2008; McCann & Rooney 2009). Many studies have documented that species losses or shifts due to fragmentation can vary based on trophic position (e.g. Turner 1996; Didham *et al.* 1998; Zabel & Tscharntke 1998; Krauss *et al.* 2010), but examinations of specific species interactions are almost always restricted to two-species models (Martinson 2009). The few studies that have examined multi-trophic interactions focused on isolation and/or area effects (e.g. Komonen *et al.* 2000; Cronin 2004; Cagnolo *et al.* 2009; Fenoglio *et al.* 2010). To date, however, the impacts of edge effects on multi-trophic interactions have been ignored. This has happened despite the fact that habitat edges have been a topic of research for nearly a century because they are a key component in understanding fragmentation (Cadenasso *et al.* 2003; Ries *et al.* 2004; Laurance 2008), and are also ubiquitous features of both natural and managed landscapes (Lidicker 1999). Furthermore, current theory developed to understand the mechanisms that cause edge effects specifies the importance of understanding species interactions (Fagan *et al.* 1999; Ries *et al.* 2004). Indeed, one of the fundamental assumptions within the edge literature is that a single species’ response to an edge may ‘cascade’ throughout a community and has the potential to impact all species connected throughout a web of interactions (Fagan *et al.* 1999; Cadenasso *et al.* 2003).

Despite the presumed importance of multi-trophic cascades to the ecology of habitat edges, they have never been described empirically (Martinson 2009). Previous research has demonstrated that herbivores

can track the edge responses of their host plants (e.g. Bergman 1999; Cadenasso & Pickett 2000) and predators and parasitoids can track the edge responses of their prey base (e.g. Zabel *et al.* 1995; Cronin 2009). Other studies have examined rates of herbivory or predation with respect to edges (e.g. Jules & Rathcke 1999; McGeoch & Gaston 2000; Ries & Fagan 2003; Valladares *et al.* 2006), and have found that predator abundance (as reviewed in Chalfoun *et al.* 2002) and rates of predation (as reviewed in Batary & Baldi 2004) either increase or show no response to habitat edges; rarely were decreases in predators found near edges. However, a cascade suggests that impacts should be observed throughout multiple tiers of a complex food web and, to date, this has never been described (Martinson 2009). Thus, it is currently unknown how readily cascades of edge response occur and how deeply they can proliferate throughout a food web. Notably, it is also unknown how the strength of an edge response may change in each successive level of the food web. Here, we offer the first empirical study of whether and how edge effects cascade throughout a complex, multi-tier food web.

One recent development in edge research is the synthesis of multiple mechanisms that underlie observed edge effects (Cadenasso *et al.* 1997; Fagan *et al.* 1999; Lidicker 1999) into a single framework (Ries *et al.* 2004). This framework summarises four dominant mechanisms that underlie edge effects: ecological flows, access to complementary resources, organisms mapping onto resource gradients and species interactions (Ries *et al.* 2004). The first three mechanisms (flows, complementary resources and resource mapping) have been incorporated into a general resource-based model (Ries & Sisk 2004; hereafter RS) that predicts when positive, negative or neutral edge responses are most likely to occur (Fig. 1). To allow this model to be general, predictions are based solely on known habitat associations (columns in Fig. 1), augmented by any information on resources gained from adjacent habitats (rows in Fig. 1) that are not available in the focal habitat (‘complementary’ resources). These complementary resources are contrasted with resources that may be present in the adjacent habitat, but are redundant to those already found in the focal

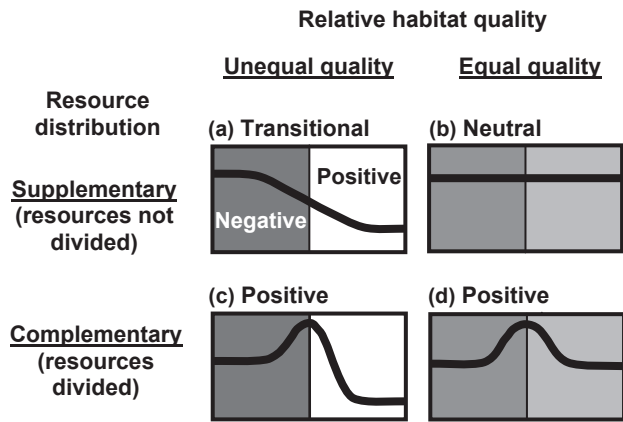


Figure 1 Model predictions of edge responses are Transitional (a), Neutral (b) or Positive (c and d) based on relative habitat quality and resource distribution. Lower habitat quality is indicated by a white box while habitats of higher or equal quality are shaded. The same resources are either available in both habitats (supplementary) or different resources are divided between habitats (complementary). Reprinted, with permission, from Ries & Sisk 2008.

habitat ('supplementary' resources). For species whose resources are available in only a single habitat, a transitional response is predicted (Fig. 1a) based on the assumption that there is a gradient in resources near the edge (see Ries *et al.* 2004 for a detailed explanation). Such transitional responses might be expected to cascade upward, resulting in similar patterns among higher-level consumers, particularly specialists. In contrast, when resources are complementary, the RS model always predicts an increased abundance near the edge (Fig. 1c,d) because the edge offers maximum access to required resources from both habitats. The simplicity of the model allows it to be widely applied by using prior knowledge of the resources an organism uses without having to collect detailed data on the fine-scale distribution of these same resources, data which are usually not available. One limitation of the RS model, however, is that it ignores potential species interactions, especially top-down pressures from natural enemies such as predators or parasitoids (Ries *et al.* 2004) because such interactions require data that are rarely available such as local community composition and species' numerical responses to natural enemies. Despite these strong assumptions, the model has successfully predicted the direction of observed edge responses by birds, mammals, plants and butterflies (Ries *et al.* 2004; Ries & Sisk 2008) as well as communities in aquatic systems (Macreadie *et al.* 2010).

Herein, we examine two parallel four-tiered relationships among plants, herbivores, meso- and top-predators that occur on adjacent sides of an edge between two marsh grasses (Fig. 2). This nine-species system has the advantage not only of being well studied (Denno 1980; Denno *et al.* 2002; Finke & Denno 2002, 2005; Wimp *et al.* 2010 and references therein), but also outside the most common targets of studies on edge effects, vertebrates at forest edges, so that we may continue to test the generality of the model's predictions. We had three primary goals for our research. First, we sought to quantify edge responses of the two dominant grasses and their associated arthropod species and compare them to RS model predictions. Second, to use the observed edge responses to evaluate a key assumption of the RS model that a gradient in resources near the edge (in this case, food quantity and quality) can cause cascades up the trophic food web and

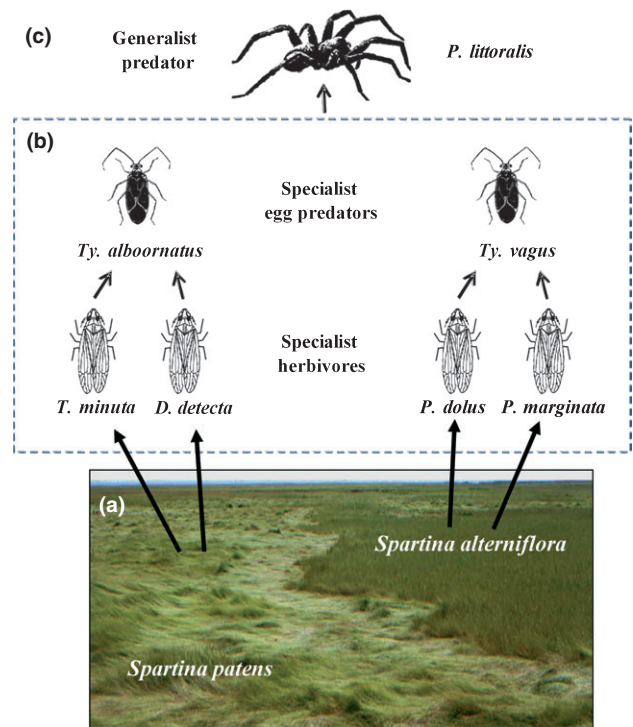


Figure 2 Monoculture patches of the primary producers (*Spartina patens* and *Spartina alterniflora*) show distinct edges (a). Each species has an associated group of two planthopper herbivores that are specialists and one specialist egg predator (b). In *S. patens*, *Tumidagena minuta* and *Delphacodes detecta* are the herbivores and *Tytthus* (abbreviated *Ty.* to distinguish it from *Tumidagena alboornatus*) is the egg predator. In *S. alterniflora*, *Prokelisia dolus* and *Prokelisia marginata* are the herbivores and *Tytthus vagus* is the egg predator. The generalist hunting spider *Pardosa littoralis* is found in both habitats and feeds on all associated members of the community (c). The dotted box contains all potential prey species for *Pardosa littoralis*.

result in similar edge responses among herbivores and their enemies. Third, if cascades across multiple trophic levels are observed, we sought to determine how the magnitude of the effect changed across different trophic levels.

MATERIALS AND METHODS

Study site and organisms

We studied the edge responses of seven arthropod species at an expansive salt marsh near Tuckerton, New Jersey (39°30.8' N, 74°19.0' W) that is dominated by natural monocultures of two grasses in the genus *Spartina*: *S. patens* and *S. alterniflora*. Although each species grows in monoculture, these two *Spartina* species frequently occur together; often *S. patens* is found growing in isolated patches that are completely surrounded by a 'matrix' of *S. alterniflora*. Where these two species meet, they form a distinct 'edge' that is readily observed in the field (Fig. 2). Previous studies in other systems have found that the density of native primary producers often declines along habitat edges (e.g. Jules & Rathcke 1999); we therefore predicted that the quality (% Nitrogen) and quantity (biomass) of *S. patens* and *S. alterniflora* would show a transitional response (Fig. 1a) to the habitat edge.

Spartina alterniflora and *S. patens* each have their own unique arthropod communities that are, for the most part, specialised on

each grass species. *Spartina alterniflora* is associated with a diverse arthropod fauna and this community has been well studied and thoroughly characterised (e.g. Denno *et al.* 2002; Finke & Denno 2002; Wimp *et al.* 2010). The community associated with *S. patens* is also described, but less well known (Denno 1980 and references therein). For this study, we focused on seven arthropod species, all of which are abundant species known to play key roles in the ecology of the salt marsh ecosystem (Finke & Denno 2005). Within patches of *S. patens*, we studied two specialist herbivore species (*Tumidagena minuta* and *Delphacodes detecta*) and one specialist predator, the mirid bug *Tytthus alboornatus* (Fig. 2). Within patches of *S. alterniflora*, we studied two specialist herbivore species (*Prokelisia dolus* and *Prokelisia marginata*) and one specialist predator, the mirid bug *Tytthus vagus*. Both *Tytthus* species are voracious predators of planthopper eggs. We also studied one generalist intraguild predator that is found in both habitats, the wolf spider *Pardosa littoralis* (Please see Appendix S1 for a complete description of each of our study species and their position in this arthropod foodweb).

Because all four herbivores are habitat specialists with no known resources used from adjacent habitats, we expected all to show a transitional response to edges (Fig. 1a). In contrast, *Pardosa* obtains critical resources from each habitat. *Spartina patens* has a much deeper litter layer (i.e. thatch) than *S. alterniflora* and this accumulated litter has been shown to reduce cannibalism among *Pardosa* (Langellotto & Denno 2006). However, *S. alterniflora* has been shown to have a higher density of planthoppers (Lewis & Denno 2009) and their escape strategies from *Pardosa* have been demonstrated to be ineffective (Denno *et al.* 2003), so planthoppers in *S. alterniflora* may be preferred prey. It is important to note that the predicted edge response for *Pardosa* according to the RS model is similar to the response predicted by spatial food web theory, which asserts that generalist predators utilise (or couple) spatially distinct resources (Rooney *et al.* 2006). Because the egg predators are specialists but *Pardosa* is a generalist whose preferred resources are divided between habitats, we predict different responses for the specialist and generalist predators: a transitional response (Fig. 1a) for the egg predators and a positive response (Fig. 1d) for *Pardosa*.

Survey design and sample collection

In spring 2007, we established seven transects with four habitat/edge classes that were separated from one another by an average of 333 m (ranging from 71 to 576 m). The first sample site on each transect was located in the centre of a *S. patens* patch (referred to as 'patens interior', hereafter 'pi') and ranged from 6 to 18 m from the edge of the patch (Figure S1). The second and third sample sites were located within a metre of the patch edge; the second site near *S. patens* edges (hereafter, 'pe') and the third site on the *S. alterniflora* side of the edge ('ae'). The fourth sample site for each transect was located within *S. alterniflora*, the same distance from the edge as the associated first 'center' site in *S. patens* ('ai').

To examine the effects of habitat edges on plant quality, we measured the nitrogen content of *Spartina* by collecting 15–20 *Spartina* culms per sample site in June, washed them with deionised water, dried them in a drying oven at 60 °C for 3 days, ground them in a Wiley Mill, and then sent our plant samples to the Cornell Stable Isotope Laboratory (Cornell University, Ithaca, NY, USA) for analyses. We measured peak plant biomass and thatch on either July

13, 2007 or July 17, 2007 using 0.047 m² quadrats (Denno *et al.* 2002). We then sorted quadrat samples into live and dead plant material and measured the height of living culms. Because the marsh is dominated by monocultures, either *S. patens* or *S. alterniflora* constituted 97–100% of the total biomass at a site, even for edge habitats. However, we included only the dominant *S. patens* or *S. alterniflora* plants in our biomass calculations for each site. We washed live plant material and thatch with deionised water, dried the samples in a drying oven at 60 °C for 3 days, and then weighed them. We then measured the nitrogen content of live plant samples using the methods described above for *Spartina* culms.

We assessed arthropod density three times during the growing season (June 26, July 17 and August 4, 2007) using a D-vac suction sampler (Rincon-Vitova Insectaries, Ventura, CA, USA) with an aperture diameter of 21 cm. At each sample site, we collected arthropods with three 5-second placements of the D-vac head on the marsh surface. We sampled the two sites adjacent to the edge on each transect simultaneously to avoid driving arthropods from one side of the edge to the other with the D-vac. We stored all arthropods in ethanol and later sorted, counted and identified all individuals to genus and species.

Statistical analyses

We analysed live plant biomass and thatch from *S. patens* and *S. alterniflora* edge and interior habitats using an ANCOVA (proc mixed, SAS 2002) with habitat (pi, pe, ai, ae) as a fixed factor and transect as a random factor. The remaining response variables (per cent nitrogen and arthropod densities) were analysed similarly, but using a repeated measures ANCOVA with the addition of month as a second random factor. It was necessary to drop *S. alterniflora* edge and interior habitats from our analysis of *T. alboornatus* densities because we did not find this species in *S. alterniflora*. It was also necessary to drop July data from our analysis of *T. vagus* because we collected only three individuals in that month. We log transformed densities of *T. vagus* and *D. detecta* to achieve normality and square-root transformed densities of the remaining taxa with the exception of *Pardosa*, which were normally distributed. Even after a transformation, variance differed among habitats for three taxa: *D. detecta*, *P. marginata* and *T. minuta*. Thus, for analyses of these species we used separate estimates of variance in each habitat instead of a single, pooled estimate. Because we performed multiple tests using arthropod data obtained from the same D-vac samples, the Hochberg method was used to control for family wise error rate (SAS Proc Multtest).

To examine the relative strength of edge effect and examine whether edge effects increase or decrease in magnitude up the food chain, we calculated relative effect size (Denno *et al.* 2003), as the natural log of the ratio of untransformed species abundances in edge habitat relative to interior habitat (Relative effect size = ln[edge value/interior value]). A value of zero indicates equal edge and interior values, a negative value indicates lower edge values than interior values (i.e. a negative edge response) and a positive value indicates a positive edge response. While we did not perform a different set of statistical tests for this comparison, if edge differed from the interior, then the edge to interior ratio would differ from one and the log of this ratio would differ from zero. Edge responses were measured as per cent nitrogen and live biomass for *Spartina* plants and density for arthropod herbivores and predators.

RESULTS

Effects of habitat edge on plant quality, live biomass and thatch

We found significantly higher host plant per cent nitrogen ($F_{3,18.1} = 34.29$, $P < 0.0001$, Fig. 3a) in *S. alterniflora* than in *S. patens* habitats, but no difference between interior and edge habitats in *S. patens* ($t_{18.4} = 1.38$, $P = 0.18$) or *S. alterniflora* ($t_{17.8} = 0.25$, $P = 0.81$) (Fig. 3a). Conversely, we found significantly less live biomass ($F_{3,24} = 19.6$, $P < 0.0001$, Fig. 3b) and thatch ($F_{3,18} = 22.21$, $P < 0.0001$, Fig. 3c) in *S. alterniflora* relative to *S. patens* habitats. However, similar to our results for per cent nitrogen, there was no difference in live biomass among edge and interior habitats in *S. patens* or *S. alterniflora* (Fig. 3b,c).

Arthropod responses to the habitat edge

Specialist herbivores demonstrated transitional responses (Fig. 1a) to the habitat edge in both *S. patens* and *S. alterniflora* (Fig. 4c–f). In *S. patens*, the herbivore *T. minuta* was most abundant in the habitat interior and declined significantly along the *S. patens/S. alterniflora* habitat edge ($t_{36.6} = 3.26$, $P = 0.0024$, Fig. 4e). Similarly, the herbivore *D. detecta* was most abundant in *S. patens* habitat interior and declined significantly along the *S. patens/S. alterniflora* habitat edge ($t_{5.77} = 2.51$, $P = 0.047$, Fig. 4c). For the *S. alterniflora* habitat specialists, the herbivore *P. dolus* was most abundant in the habitat interior and declined significantly along the *S. patens/S. alterniflora* habitat edge ($t_{21.1} = 2.54$, $P = 0.019$, Fig. 4d). In contrast, although the *S. alterniflora* specialist herbivore *P. marginata* was more abundant in *S. alterniflora* relative to *S. patens*, we found no difference in abundance among interior and edge habitats ($t_{10.4} = 1.33$, $P = 0.21$, Fig. 4f).

The specialist egg predator *T. alboornatus* was more abundant in *S. patens* interior habitats and declined significantly along the *S. patens/S. alterniflora* edge ($t_{52} = 2.58$, $P = 0.013$, Fig. 4a). The specialist egg predator *T. vagus* was more abundant in *S. alterniflora* relative to *S. patens*, but we found no difference in abundance between interior and edge habitats within *S. alterniflora* ($t_{45} = 1.12$, $P = 0.27$, Fig. 4b). Densities of the generalist predator *Pardosa* differed among habitats ($F_{3,72} = 4.49$, $P = 0.006$, Fig. 5a), increasing along the edge in *S. patens* habitat ($t_7 = 2.51$, $P = 0.014$). When we analysed total available prey by combining the six potential prey species for *Pardosa* (species contained within the dotted box in Fig. 2) and counted both the adults and nymphs, the difference among habitats only approached significance ($F_{3,9.83} = 3.49$, $P = 0.059$, Fig. 5b), although prey densities tended to be lower near the *S. patens/S. alterniflora* edge compared to habitat interiors.

Relative strength of edge effects

We found no systematic change in the magnitude of edge response with trophic level. In *S. patens*, edge responses in the specialist herbivores *T. minuta* and *D. detecta* were not consistent with the response of their host plant (Fig. 6a). Further, the magnitude of edge avoidance was similar among the two herbivores and their specialist predator (Fig. 6a). In *S. alterniflora*, only the relative effect size of the specialist herbivore *P. dolus* was significantly different from zero (Fig. 6b). As in *S. patens*, edge effects in herbivores were not related to changes in their *S. alterniflora* host plants, and the response of specialist predators was amplified relative to herbivores, but not significantly

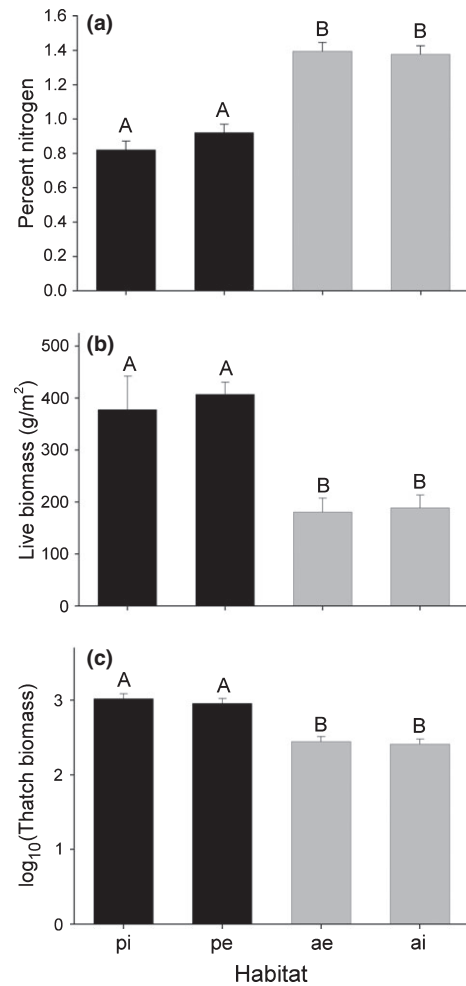


Figure 3 Effects of habitat edges on host plant per cent nitrogen (a), live biomass (b) and thatch (c) in *Spartina patens* and *Spartina alterniflora*. Live plant samples and thatch were collected from *S. patens* interior (pi), *S. patens* edge (pe), *S. alterniflora* edge (ae) and *S. alterniflora* interior (ai) plots. *Spartina patens* samples (interior and edge) contained only *S. patens* plant material and *S. alterniflora* samples (interior and edge) contained only *S. alterniflora* plant material. The distinct border between these two habitats meant that there was very little incursion of *S. alterniflora* into *S. patens* and vice versa. Means are given \pm 1 SE and different letters denote significant differences among groups.

(Fig. 6b). Finally, for both food webs, the shared top generalist predator *Pardosa* showed an edge response in the opposite direction compared to its prey base, and response magnitude was lower in *S. alterniflora* relative to *S. patens* (Fig. 6a,b).

DISCUSSION

Our results show that the abundances of the dominant arthropods in a multi-tier food web all shift relative to habitat edges. Importantly, the direction of all responses within the consumer tiers were predictable based simply on habitat associations and known resource distribution, which suggests that understanding shifts in food web dynamics in fragmented systems is a tractable goal. All seven arthropod species measured showed edge responses in the predicted direction (Fig. 4) whereas only the grasses failed to respond as predicted (Fig. 3). Similar to results from other edge studies, a neutral edge response was

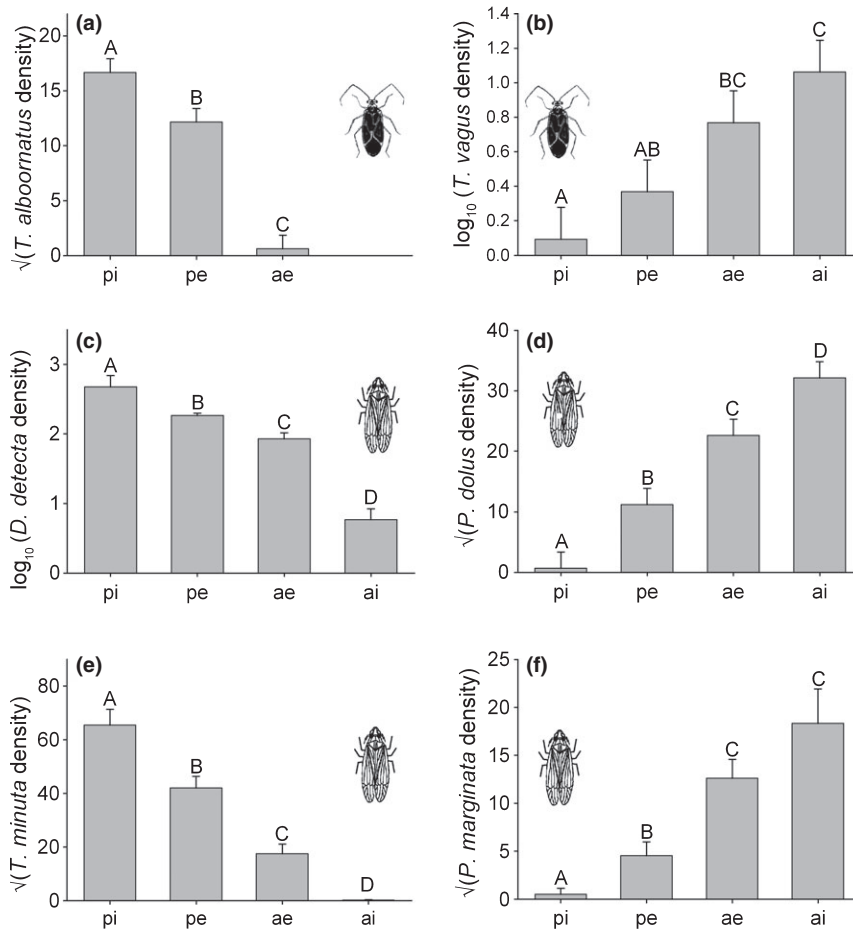


Figure 4 Effects of habitat edges on specialist herbivores and predators. Species are arranged to also represent their trophic position (similar to Fig. 2); herbivores are found in the lower four panels and predators are in the top two panels. Effects of habitat edges on adult densities of the specialist egg predators *Tytthus alboornatus* (a) and *Tytthus vagus* (b), as well as the specialist herbivore planthoppers *Delphacodes detecta* (c), *Prokelisia dolus* (d), *Tumidagena minuta* (e), and *Prokelisia marginata* (f). Herbivores were collected from *Spartina patens* interior (pi), *S. patens* edge (pe), *Spartina alterniflora* edge (ae) and *S. alterniflora* interior (ai) plots. The associated communities of herbivores and specialist predators are separated into the left and right panels for *S. patens* and *S. alterniflora*, respectively. Means are given \pm 1 SE and different letters denote significant differences among groups.

observed instead of observing a response opposite of that predicted (Ries & Sisk 2010). Despite our success in predicting the direction of observed responses, the evidence for the putative mechanisms assumed by the RS model was mixed. Evidence of resource mapping was only demonstrated by specialist predators, and we did not find evidence of cascades that extended beyond two-species interactions. On the other hand, the prediction based on complementary resource use was supported. This mixed support for the mechanisms assumed by the RS model identifies an important direction for future modelling efforts; the RS model is exclusively driven by bottom-up factors such as resource quality or quantity and does not consider top-down effects on edge communities.

The most common herbivores in both *Spartina* habitats all become less abundant near habitat edges despite the fact that host plant per cent nitrogen, live biomass and thatch did not decline near edges (Fig. 3). These four herbivores are extreme habitat specialists without any known complementary resources (Denno 1980), so a transitional edge response was both predicted (Fig. 1a) and observed (Fig. 4), but the basis for that prediction, a gradient in *Spartina* resources, was not found. On the other hand, specialist egg predators of these herbivores declined near habitat edges, by roughly the same amount as their prey,

which was consistent with resource mapping assumed by the RS model (Ries *et al.* 2004).

Also as predicted, the top predator in this system, the hunting spider *Pardosa*, increased in density near habitat edges. *Pardosa* are known to be voracious consumers of both planthoppers and *Tytthus* (Finke & Denno 2002 and references therein) and so this offers an alternate mechanism to explain the decline in middle-tier species along the habitat edge. Planthoppers are known to shift their distribution in response to predators (Denno *et al.* 2002, 2003) and although the decline seen in *Tytthus* is consistent with mapping onto their prey resources, we cannot eliminate the possibility that they too may be avoiding *Pardosa*. It is therefore possible that the decline in both planthoppers and meso-predators that we found along the habitat edge could be driven by *Pardosa* consumption or non-consumptive prey responses to edge zones where *Pardosa* density is greater. Although *Pardosa* has been shown to induce trophic cascades that benefit host plant resources in other marsh contexts (Finke & Denno 2005), it is possible that plants showed no response to habitat edges (Fig. 3a,b) because simultaneous bottom-up and top-down forces were cancelling each other out. To determine the extent to which trophic cascades could be influential throughout the food web,

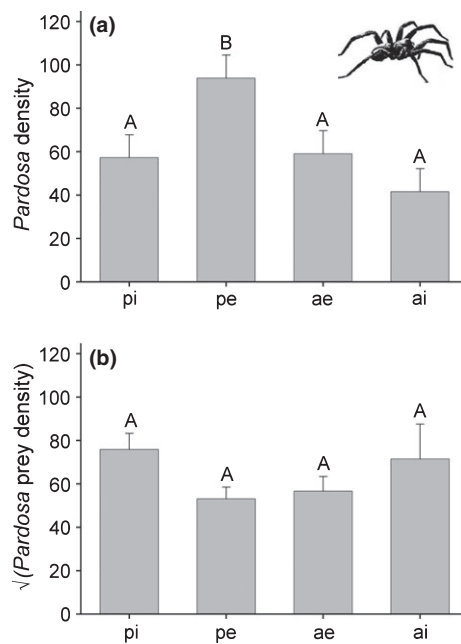


Figure 5 Effects of habitat edges on densities of the generalist predator *Pardosa littoralis* (a) and all potential prey (b). This complete measure of potential prey was calculated by summing the abundances of all dominant species from Fig. 4, which includes only adults, and by also including nymphs (which cannot be determined to species and were therefore not included in Fig. 4). Specimens were collected from *Spartina patens* interior (pi), *S. patens* edge (pe), *Spartina alterniflora* edge (ae) and *S. alterniflora* interior (ai) plots. Means are given \pm 1 SE and different letters denote significant differences among groups.

predator exclusions (*sensu* Denno *et al.* 2002; Finke & Denno 2002) should be performed along habitat edges.

At least two mechanisms other than selective pressure by *Pardosa* may explain the observed decline in planthopper density along the habitat edge. First, there may have been a decline in resources or habitat quality that was not measured in this study. However, the measures of host plant quality and quantity included in this study have been repeatedly demonstrated to drive planthopper density responses in this system (Denno *et al.* 2002 and references therein), so we believe this is an unlikely explanation. A second possibility is that planthopper movement behaviours near habitat boundaries may cause patterns that are independent of resources. We have no specific information that could support or refute this idea, but theoretical models suggest that edge-independent movements may result in lower edge densities (Olson & Andow 2008). Alternatively, behavioural cues to turn away from edges could cause lower densities near edges that are unrelated to resources and more associated with an unwillingness to cross into neighbouring habitat (Haddad & Baum 1999; Ries & DeBinski 2001). This type of dynamic could explain planthopper distributions across the edge, and may be especially pronounced in the two *S. patens* planthoppers in this study that are flightless (Denno 1980) and may have difficulty re-locating their host plants if they venture too far into *S. alterniflora* habitat.

The generalisation that predators tend to be more abundant near edges (Chalfoun *et al.* 2002) comes largely from a focus on studies of generalist predators (Martinson 2009). Herein we show that two specialist predators show sharp declines near edges within their preferred habitat (Fig. 4a,b). That specialist predators can map onto the distribution of their prey base has been shown previously for the

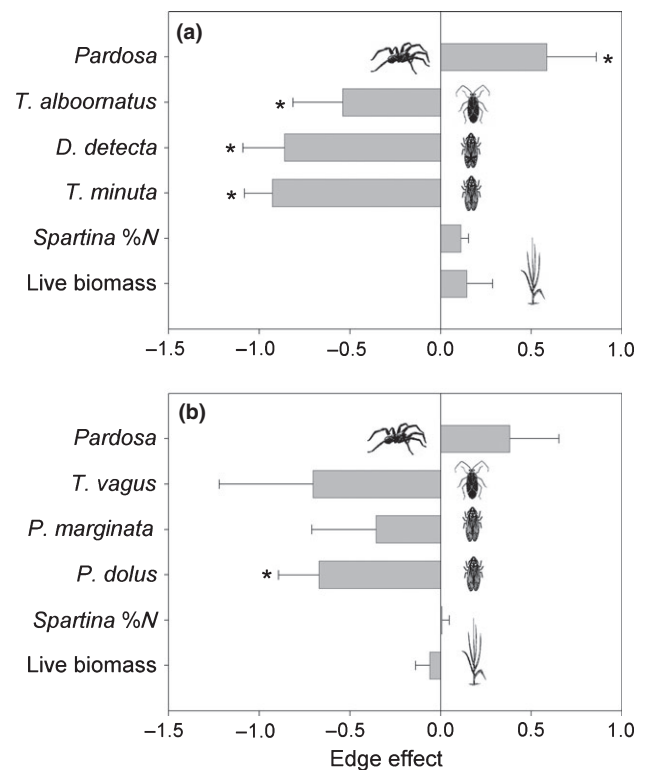


Figure 6 Edge effect ($\ln[\text{edge value}/\text{interior value}]$) for plant measures, herbivore densities and predator densities in *Spartina patens* (a) and *Spartina alterniflora* (b). Negative effects signify lower values at the edge relative to the interior. Asterisks indicate values significantly different from zero at $\alpha = 0.05$ and significant differences are the same as in Figs 3–5. Error bars display the standard error of the mean effect size.

specialist parasitoid *Anagris columbi*, which also feeds upon planthoppers (Cronin 2003). The specialist predators in the *Spartina* system, however, are also subject to predation by the dominant predator in the system, *Pardosa* (Finke & Denno 2002), so we cannot eliminate the possibility that their decline at the edge may be to avoid predation by *Pardosa*, especially in *S. patens*.

Although we found evidence that specialist predators tracked prey resources, we did not find evidence that resources at one trophic level ‘cascade’ to affect non-adjacent trophic levels. The two specialist predators were the only organisms in our study that showed evidence consistent with mapping onto the distributional patterns of their food resources, indicated by their abundances tracking the densities of their prey resources (Fig. 4). The magnitude of changes in both herbivores and specialist predators was roughly comparable for both (Fig. 6) so there was no obvious magnification or dampening of effects seen across trophic levels. In *S. patens*, where both planthoppers and their egg predator showed significant edge responses, the magnitudes were similar for all (Fig. 6a). In *S. alterniflora*, both planthoppers and the associated egg predator also showed declines near the edge, but these declines were not significant for all species. The magnitude of the edge effect was highest for the egg predator relative to the planthoppers, but this effect did not differ significantly from zero (Fig. 6b).

Determining the strength of top-down effects on food webs in a landscape will therefore require knowledge of the mechanisms that lead to higher densities of generalist predators. We found that the generalist hunting spider *Pardosa* showed a positive response to

the habitat edge (Fig 5a). For a generalist species, the mechanism assumed by the RS model is complementary resource distribution (Fig. 1d), which is consistent with what is known about *Pardosa* and its resource use. Past research in the same system has shown that the significantly greater density of thatch in *S. patens* relative to *S. alterniflora* offers greater protection for *Pardosa* against intraguild predation and cannibalism (Denno *et al.* 2002; Langelotto & Denno 2006 and references therein). On the other side of the edge, *S. alterniflora* may offer a preferred prey base compared to *S. patens* because *S. alterniflora* consistently has higher prey densities over multiple years (Lewis & Denno 2009), although that was not the case in this study (Fig. 5b). Furthermore, *Pardosa* in *S. alterniflora* have been shown to grow larger than *Pardosa* in *S. patens*, possibly because of higher quality prey (Lewis & Denno 2009) or due to higher capture probabilities (as per Denno *et al.* 2003). Thus, *Pardosa* may be tracking the distribution of two independent resources, thatch and prey in two different habitats, and thus cannot be mapped directly onto a single gradient. Instead, the magnitude of the edge response may be dependent on the relative importance of each resource (see Ries & Sisk 2008), which is currently unknown for *Pardosa*.

Future directions

Our study shows that a general model of edge responses based on habitat associations and knowledge of complementary resources (Ries & Sisk 2004) continues to successfully predict the direction of many observed edge responses. However, the evidence that multiple organisms in a well-studied food chain map onto changes in the distribution of their resources, one fundamental assumption of this model, is mixed. While the utility of the Ries & Sisk (2004) model lies in its ability to predict species edge responses based on general knowledge of resource use, the focus of the model on bottom-up resources ignores the possibility that an aggregation of generalist predators along habitat edges may drive responses at lower trophic levels. Herein lies the opportunity for a synthesis between landscape ecology and the burgeoning field of spatial food web ecology.

Recent theory in spatial food web ecology has demonstrated that generalist predators often utilise (or couple) spatially separated prey resources (Rooney *et al.* 2006; McCann & Rooney 2009). While organisms at lower trophic levels may respond to resources at a microhabitat scale (especially when their resources are static in space during their lifetime), predators often utilise resources on a larger, macrohabitat scale in order to meet their energy demands (McCann & Rooney 2009). Empirical research has also demonstrated that higher order generalist predators and parasitoids spatially track multiple prey resources (Eveleigh *et al.* 2007) and often couple spatially distinct resources, such as benthic and pelagic prey (Rooney *et al.* 2006). Such resource coupling by generalist predators could easily explain one of the common patterns found in edge studies: higher abundance of generalist predators (reviewed in Chalfoun *et al.* 2002; Martinson 2009) and higher predation rates (reviewed in Batary & Baldi 2004) along habitat edges. This suggests that complementary resources may have been defined too narrowly in the original RS model; specifically, the RS model would not describe two different prey species as complimentary resources if they do not represent two qualitatively different categories of resources for the predator. In contrast, spatial food web theory would predict that access to different prey resources (on either a temporal or spatial scale) would benefit generalist predator populations. It therefore becomes important for the RS model to

re-examine the definition of complementary resources in light of insights from spatial food web theory.

Not only does edge ecology have much to gain from theory in spatial food web ecology, but the reverse is also true. When considering the resources that lead to spatial coupling by organisms, spatial food web ecologists primarily focus on food resources. However, many organisms require access to non-consumptive resources such as nesting or oviposition sites, shelter and habitats that provide protection from cannibalism and/or predation. These resource requirements should be more fully integrated into our understanding of the factors that drive the spatial distribution of a species. Furthermore, the wealth of literature on generalist predators found along edge boundaries can provide spatial food web ecologists with a vast array of empirical studies by which they may evaluate their predictions on the effects of predator coupling on prey abundance and stability.

Despite years of study on edge effects, quantification of the specific mechanisms that underlie observed edge patterns is still lacking for most systems and thus makes it difficult to evaluate the success of recent models in predicting those patterns. Edge response studies that pinpoint causal mechanisms through experimental designs are therefore essential. The design of observational studies can also be strengthened by independently establishing which factors are most important for driving species distributions (e.g. Kristan *et al.* 2003). Finally, the integration of theory from spatial food web and landscape ecology may improve both our understanding of common patterns observed in the edge literature and enhance our ability to predict spatial patterns in food web dynamics, a current focus of research.

ACKNOWLEDGEMENTS

This research would not have been possible without the guidance of our esteemed mentor, Bob Denno, who always provided us invaluable feedback and support until his untimely death (GMW, SMM, and DL). We thank Martin Brabson, Maggie Douglas, Brian Crawford, Doug McCaskill, Edgardo Parilla, Rachel Pearson and Lillian Power for help with both fieldwork and lab work. We thank the University of Denver Ecology Group and three anonymous reviewers for comments on a previous version of this manuscript that greatly improved it. Ken Able at the Rutgers University Marine Station facilitated our research at the Tuckerton field site. Erik Denno provided the line drawings used in our figures. This research was supported by the Strategic Environmental Research and Development Program (SI-1597) for LR and the National Geographic Society (Award #8496-08) for GMW.

REFERENCES

- Amarasekare, P. (2008). Spatial dynamics of foodwebs. *Annu. Rev. Ecol. Syst.*, 39, 479–500.
- Batary, P. & Baldi, A. (2004). Evidence of an edge effect on avian nest success. *Conserv. Biol.*, 18, 389–400.
- Bergman, K.O. (1999). Habitat utilization by *Lopinga achine* (Nymphalidae: Satyriinae) larvae and ovipositing females: implications for conservation. *Biol. Conserv.*, 88, 69–74.
- Cadenasso, M.L. & Pickett, S.T.A. (2000). Linking forest edge structure to edge function: mediation of herbivore damage. *J. Ecol.*, 88, 31–44.
- Cadenasso, M.L., Traynor, M.M. & Pickett, T.A. (1997). Functional location of forest edges: gradients of multiple physical factors. *Can. J. For. Res.*, 27, 774–782.
- Cadenasso, M.L., Pickett, S.T.A., Weathers, K.C. & Jones, C.G. (2003). A framework for a theory of ecological boundaries. *Bioscience*, 53, 750–758.

- Cagnolo, L., Valladares, G., Salvo, A., Cabido, M. & Zak, M. (2009). Habitat fragmentation and species loss across three interacting trophic levels: effects of life-history and food-web traits. *Conserv. Biol.*, 23, 1167–1175.
- Chalfoun, A.D., Thompson, F.R. & Ratnaswamy, M.J. (2002). Nest predators and fragmentation: a review and meta-analysis. *Conserv. Biol.*, 16, 306–318.
- Cronin, J.T. (2003). Matrix heterogeneity and host-parasitoid interactions in space. *Ecology*, 84, 1506–1516.
- Cronin, J.T. (2004). Host-parasitoid extinction and colonization in a fragmented prairie landscape. *Oecologia*, 139, 503–514.
- Cronin, J.T. (2009). Habitat edges, within-patch dispersion of hosts, and parasitoid oviposition behavior. *Ecology*, 90, 196–207.
- Denno, R.F. (1980). Ecotope differentiation in a guild of sap-feeding insects on the salt marsh grass, *Spartina patens*. *Ecology*, 61, 702–714.
- Denno, R.F., Gratton, C., Peterson, M.A., Langellotto, G.A., Finke, D.L. & Huberty, A.F. (2002). Bottom-up forces mediate natural-enemy impact in a phytophagous insect community. *Ecology*, 83, 1443–1458.
- Denno, R.F., Gratton, C., Döbel, H. & Finke, D.L. (2003). Predation risk affects relative strength of top-down and bottom-up impacts on insect herbivores. *Ecology*, 84, 1032–1044.
- Didham, R.K., Lawton, J.H., Hammond, P.M. & Eggleton, P. (1998). Trophic structure stability and extinction dynamics of beetles (Coleoptera) in tropical forest fragments. *Phil. Trans. R. Soc. B*, 353, 437–451.
- Eveleigh, E.S., McCann, K.S., McCarthy, P.C., Pollock, S.J., Lucarotti, C.J., Morin, B. et al. (2007). Fluctuations in density of an outbreak species drive diversity cascades in food webs. *Proc. Natl. Acad. Sci. USA*, 104, 16976–16981.
- Fagan, W.E., Cantrell, R.S. & Cosner, C. (1999). How habitat edges change species interactions. *Am. Nat.*, 153, 165–182.
- Fenoglio, M.S., Salvo, A., Videla, M. & Valladares, G.R. (2010). Plant patch structure modifies parasitoid assemblage richness of a specialist herbivore. *Ecol. Entomol.*, 35, 594–601.
- Finke, D.L. & Denno, R.F. (2002). Intraguild predation diminished in complex-structured vegetation: implications for prey suppression. *Ecology*, 83, 643–652.
- Finke, D.L. & Denno, R.F. (2005). Predator diversity and the functioning of ecosystems: the role of intraguild predation in dampening trophic cascades. *Ecol. Lett.*, 8, 1299–1306.
- Gripenberg, S. & Roslin, T. (2007). Up or down in space? Uniting the bottom-up versus top-down paradigm and spatial ecology. *Oikos*, 116, 181–188.
- Haddad, N.M. & Baum, K.A. (1999). An experimental test of corridor effects on butterfly densities. *Ecol. Appl.*, 9, 626–633.
- Jules, E.S. & Rathcke, B.J. (1999). Mechanisms of reduced trillium recruitment along edges of old-growth forest fragments. *Conserv. Biol.*, 13, 784–793.
- Komonen, A., Penttilä, R., Lindgren, M. & Hanski, I. (2000). Forest fragmentation truncates a food chain based on an old-growth forest bracket fungus. *Oikos*, 90, 119–126.
- Krauss, J., Bommarco, R., Guardiola, M., Heikkinen, R.K., Helm, A., Kuussaari, M. et al. (2010). Habitat fragmentation causes immediate and time-delayed biodiversity loss at different trophic levels. *Ecol. Lett.*, 13, 597–605.
- Kristan, W.B., Lynam, A.J., Price, M.V. & Rotenberry, J.T. (2003). Alternative causes of edge-abundance relationships in birds and small mammals of California sage scrub. *Ecology*, 26, 29–44.
- Langellotto, G.A. & Denno, R.F. (2006). Refuge from cannibalism in complex-structured habitats: implications for the accumulation of invertebrate predators. *Ecol. Entomol.*, 31, 575–581.
- Laurance, W.F. (2008). Theory meets reality: how habitat fragmentation research has transcended island biogeographic theory. *Biol. Conserv.*, 141, 1731–1744.
- Lewis, D. & Denno, R.F. (2009). A seasonal shift in habitat suitability enhances an annual predator subsidy. *J. Anim. Ecol.*, 78, 752–760.
- Lidicker, W.Z. (1999). Responses of mammals to habitat edges: an overview. *Landscape Ecol.*, 14, 333–343.
- Macreadie, P.I., Connolly, R.M., Jenkins, G.P., Hindell, J.S. & Keough, M.J. (2010). Edge patterns in aquatic invertebrates explained by predictive models. *Mar. Freshw. Res.*, 61, 214–218.
- Martinson, H. (2009). *Critical patch sizes and the spatial structure of salt marsh communities*. Doctoral Dissertation, University of Maryland College Park, pp. 184.
- McCann, K.S. & Rooney, N. (2009). The more food webs change, the more they stay the same. *Phil. Trans. R. Soc. B*, 364, 1789–1801.
- McGeoch, M.A. & Gaston, K.J. (2000). Edge effects on the prevalence and mortality factors of *Phytomyza iliis* (Diptera: Agromyzidae) in a suburban woodland. *Ecol. Lett.*, 3, 23–29.
- van Nouhuys, S. (2005). Effects of habitat fragmentation at different trophic levels in insect communities. *Ann. Zool. Fenn.*, 42, 433–447.
- Olson, D. & Andow, D. (2008). Patch edges and insect populations. *Oecologia*, 155, 549–558.
- Ries, L. & DeBinski, D.M. (2001). Butterfly responses to habitat edges in the highly fragmented prairies of Central Iowa. *J. Anim. Ecol.*, 70, 840–852.
- Ries, L. & Fagan, W.F. (2003). Habitat edges as a potential ecological trap for an insect predator. *Ecol. Entomol.*, 28, 567–572.
- Ries, L. & Sisk, T.D. (2004). A predictive model of edge effects. *Ecology*, 85, 2917–2926.
- Ries, L. & Sisk, T.D. (2008). Edge effects are predicted by a simple model in a complex landscape. *Oecologia*, 156, 75–86.
- Ries, L. & Sisk, T.D. (2010). What is an edge species? The implications of sensitivity to habitat edges. *Oikos*, 119, 1636–1642.
- Ries, L., Fletcher, R.J., Battin, J. & Sisk, T.D. (2004). Ecological responses to habitat edges: mechanisms, models, and variability explained. *Ann. Rev. Ecol. Evol. Syst.*, 35, 491–522.
- Rooney, N., McCann, K., Gellner, G. & Moore, J.C. (2006). Structural asymmetry and the stability of diverse food webs. *Nature*, 442, 265–269.
- Saunders, D.A., Hobbs, R.J. & Margules, C.R. (1991). Biological consequences of ecosystem fragmentation: a review. *Conserv. Biol.*, 5, 18–32.
- SAS (2002). SAS Version 9.1. SAS Institute Inc., Cary, NC, USA.
- Tscharntke, T. & Brandl, R. (2004). Plant–insect interactions in fragmented landscapes. *Annu. Rev. Entomol.*, 49, 405–430.
- Turner, I.M. (1996). Species loss in fragments of tropical rain forest: a review of the evidence. *J. Appl. Ecol.*, 33, 200–209.
- Valladares, G., Salvo, A. & Cagnolo, L. (2006). Habitat fragmentation effects on trophic processes of insect–plant food webs. *Conserv. Biol.*, 20, 212–217.
- Wimp, G.M., Murphy, S.M., Finke, D.L., Huberty, A.F. & Denno, R.F. (2010). Increased primary production shifts the structure and composition of a terrestrial arthropod community. *Ecology*, 91, 3303–3311.
- Zabel, J. & Tscharntke, T. (1998). Does fragmentation of *Urtica* habitats affect phytophagous and predatory insects differentially? *Oecologia*, 116, 419–425.
- Zabel, C.J., McKelvey, K. & Ward, J.P. (1995). Influence of primary prey on home-range size and habitat-use patterns of northern spotted owls (*Strix occidentalis caurina*). *Can. J. Zool.*, 73, 433–439.

SUPPORTING INFORMATION

Additional Supporting Information may be found in the online version of this article:

Appendix S1 Choice of focal species and trophic relationships among these species.

Figure S1 Design of sampling transects.

As a service to our authors and readers, this journal provides supporting information supplied by the authors. Such materials are peer-reviewed and may be re-organised for online delivery, but are not copy edited or typeset. Technical support issues arising from supporting information (other than missing files) should be addressed to the authors.

Editor, Ferenc Jordan

Manuscript received 17 February 2011

First decision made 23 March 2011

Second decision made 26 May 2011

Manuscript accepted 13 June 2011