Fragment size affects plant herbivory via predator loss

Lucy Genua, Denon Start and Benjamin Gilbert

L. Genua, D. Start (orcid.org/0000-0003-3036-9880)(denon.start@mail.utoronto.ca) and B. Gilbert, Dept of Ecology and Evolutionary Biology, Univ. of Toronto, Toronto, ON, M5S 3B3, Canada.

Fragmentation and resultant changes in patch size are predicted to alter species diversity and community composition, yet the consequences of these differences for species interactions are poorly understood. Theory predicts that predators are more sensitive to fragmentation than their prey, resulting in greater predator loss in small patches. Predator loss, in turn, is predicted to 1) increase herbivory rates overall, and 2) cause herbivores to shift feeding from plants that act as refugia to those that are preferred forage. We tested these predictions in an old-field community using two experiments. The first was a large-scale experiment that included hundreds of arthropod species in fragments of various sizes, and used goldenrod and switchgrass to assess herbivory. Our second experiment manipulated densities of a focal predator species and a focal prey species to determine if changes in densities, rather than other characteristics of fragments, were sufficient to cause the trends observed in the first experiment. We found that predator densities declined in small fragments whereas herbivore densities showed the opposite trend. Total herbivory mirrored herbivore densities by increasing in small patches, and this mean increase was driven by large increases in goldenrod herbivory but declines in switchgrass herbivory. Experimental manipulation of densities confirmed that herbivores preferentially feed on goldenrod, and that predators depress herbivory on goldenrod but have a negligible effect on switchgrass. Our results suggest that fragmentation alters trophic interactions by causing declines in predator densities and increases in herbivore densities, but that feeding preferences of herbivores may generate unequal impacts among plant species.

Habitat fragmentation can alter patterns of species occurrence and ultimately create differences in community composition (MacArthur and Wilson 1967, Tscharntke et al. 2002). These differences are of particular concern because human activity has increased the rate of habitat fragmentation, contributing to the current extinction crisis (Wilcox and Murphy 1985). A common consequence of habitat fragmentation is a reduction in average patch size (Andrén 1994). The small patches created by habitat fragmentation typically support depauperate communities, owing to higher extinction rates and lower rates of colonization (MacArthur and Wilson 1967, Tscharntke et al. 2002). While we can predict that small communities will support fewer species, the identity of the species composing those communities should also change. For example, dispersive (Vanschoenwinkel et al. 2007, Start and Gilbert 2016), fecund (Dupré and Ehrlén 2002), small (Öckinger et al. 2010) and diet generalist (Gravel et al. 2011) species are all disproportionately common in small communities. An additional factor that explains the distribution of species across patch sizes is trophic level. Trophic levels differ in their sensitivity to patch size (Holt et al. 1999), but the implications of these differences are poorly understood.

Predators are predicted to be absent or rare in small patches for several reasons, ranging from low regional abundances to trophic constraints. For example, predators are frequently less abundant than their prey and random sampling from this abundance distribution can cause predators to be excluded from the smallest patches ('sampling effects' sensu Srivastava et al. 2008). When predators do manage to colonize small patches, they typically have much smaller populations than their prey and thus are at greater risk of stochastic extinction than their prey, an effect that is exacerbated in small patches (Elton 1927, Lande 1993). Predators may also be sensitive to patch size because of trophic dependency, the reliance of predators on their prey and the reliance of prey on plants (Holt et al. 1999). Trophic dependencies can cause extinctions in the prey or basal resource (plants) to cascade up food chains, causing predators to also become extinct. Trophic dependency is most important for diet specialized predators (Gravel et al. 2011, Start and Gilbert 2016) or predators requiring multiple prey species as prey switching cannot prevent predator extinction in the event of the extinction of a single prey species (Holt et al. 1999). For example, Gravel et al. 2011 showed that in both aquatic and terrestrial systems predators are poorly represented in small patches, presumably due to stochastic extinction and sampling effects, and that specialist predators are particularly affected by changes in patch size. While researchers are accumulating evidence of why predators are lost from small patches, we have only begun to explore the implications of these differences for species interactions.

The loss of predators from patches can have important implications for interactions between other species, notably plants and herbivores. Predator loss is commonly linked to stronger plant-herbivore interactions measured as increased herbivory, decreased plant biomass, and ultimately reduced plant fitness (Terborgh et al. 2001, Spiller and Schoener 2007, Estes et al. 2011). An increased effect of herbivory following predator loss is termed trophic release (Crooks and Soulé 1999, Heithaus et al. 2008, Brodie and Giordano 2013) and can result from two mechanisms. First, predator declines reduce predation rates, increasing the density of herbivores and ultimately herbivory (density-mediated effects). Second, predator loss can affect herbivore behavior such that herbivores decrease vigilance, increase time spent foraging, and forage in riskier but more nutritious areas (behaviorally-mediated effects, Schmitz et al. 1997). These processes can occur simultaneously and, while density-mediated effects are necessarily ubiquitous, behavioral effects are also common and may be of equal or greater importance (Turner and Mittelbach 1990, Schmitz et al. 1997). Combining information from biogeographic studies demonstrating predator loss in small patches (Gravel et al. 2011) and studies of trophic release (Schmitz et al. 1997), we predict that reduced patch size should be associated with greater herbivory and that these differences are caused by both behaviorally- and density-mediated effects on the prey.

Increased herbivory at lower predator densities is likely to be a general pattern, but these patterns can be reversed under some conditions. If increasing predator density causes greater interference competition among predators, it can increase herbivore abundance by reducing predator efficiency (Case and Gilpin 1974, Polis et al. 1989). Cannibalism, an extreme form of predator interference, can reduce the effect of predators on prey and ultimately plants by causing predators to forage more cautiously when at high density (Rudolf 2008). Resource-switching by herbivores can also cause some plant species to benefit from predator loss. For example, Schmitz (2003) found that the presence of a predacious spider caused grasshoppers to switch from feeding primarily on grass to almost exclusively feeding on goldenrod, generating a negative indirect effect on goldenrod but a positive indirect effect on grass. This type of resource switching is likely to be common and occurs when two resources represent a tradeoff between nutritive quality and predation risk (Schmitz et al. 1997). In large patches that support more predators, high quality (more nutritive) plant species that benefit from predator presence should be favored, whereas the opposite pattern is expected to occur in small patches. In other words, while we can predict that the effect of herbivory will typically be greater in small patches, predator interference and herbivore specific responses to predation risk can alter these patterns for particular plant species.

In our study we used two experiments to explore the effects of patch size on predator and herbivore densities and ultimately herbivory. We first used arthropod sampling and herbivory data from experimental old-field fragments to test our predictions for predator loss, herbivore release and increased herbivory using a full invertebrate food web. We then coupled these observations with a density manipulation experiment using a common spider–grasshopper species pair

to separate the effects of density from other effects of fragmentation (Didham et al. 1998). We used data from both experiments to address four specific predictions: 1) predators are more sensitive to patch size than their prey, 2) predator loss in small fragments increases rates of herbivory, 3) predator loss shifts the relative amount of herbivory on different plant species, and 4) the changes in predator and herbivore densities within fragments are sufficient to generate patterns of herbivory observed.

Material and methods

Field methods

Fragmentation experiment
In summer 2015 we utilized an established experimental old-field metacommunity along with individual focal plants to test for differences in trophic interactions among fragments differing in size. The metacommunity was established in fall 2012 by seeding 168 patches with either old-field or tall grass prairie species at the Koffler Scientific Reserve, Ontario, Canada (Supplementary material Appendix 1 Table A1). We divided the 168 communities equally into 14 blocks separated by 10 meters of mowed field, with patches in each block being split equally between old-field and tall grass prairie species (Supplementary material Appendix 1 Fig. A1). The field was mowed approximately monthly and dominated by invasive grasses such as *Bromus inermis*, with both grasshoppers and jumping spiders being among the arthropods present. Each block consisted of twelve 0.25-m², 1-m², and 4-m² patches (four each) separated by 1 m of 'weed barrier', a polyethylene cloth that prevents plants from growing but allows rainfall to enter the soil. Previous research in arthropod communities indicates that this separation is sufficient to limit movement even of winged arthropods (Kareiva 1987). The spatial arrangement of patches was consistent across blocks but seed treatments were randomly assigned within each block. Since establishing the communities, many species have recruited from nearby old-fields such that old-field and tall grass prairie communities now share most species (approximately 60 of 74 plant species are shared), and have become dominated by goldenrod and grass species.

Within each block, we randomly selected one patch of each size that was seeded with old-field species and one patch of each size seeded with tall-grass prairie species for our sampling. To control for potential among-patch variation in plant species and quality, we planted one stiff goldenrod *Solidago rigida* and one switchgrass *Panicum virgatum* into each focal patch (n = 84 patches). We chose these species because they were common in our metacommunities, represent different growth forms, are fed on by many of the same herbivores, and similar species have been shown to respond differently to predators (Schmitz et al. 1997). Prior to planting, we germinated all individuals from commercially available seed, then grew them in a greenhouse for ~2 months. We planted all individuals in early July 2015, placing plants in one corner of each plot to negate potential differences in edge effects among patches differing in size.

Beginning in early July we conducted four weekly surveys of the arthropod community associated with each focal plant (goldenrod and switchgrass). During each survey we recorded all arthropods on each plant, surveying only on sunny days with little wind (< 10 km h⁻¹). Arthropods were considered part of the focal plant community if they were either on the plant or, in the case of web building spiders, had some portion of their web connected to the plant. During surveys, we categorized each arthropod by morpho-species while collecting voucher specimens, later identifying each morpho-species to family level and categorizing each species as a predator or herbivore (Supplementary material Appendix 1 Table A2). To test for relationships between arthropod abundance and herbivory, we also estimated percent herbivory (hereafter referred to as herbivory). A single observer (DS) estimated herbivory across all leaves on both goldenrod and switchgrass as the percent of all leaf area that had been removed by leaf chewers. Herbivory was not measured when plants had been destroyed by deer or small mammals. Previous research on methods to estimate percent leaf loss to chewing herbivores has shown that this type of visual estimate provides fast and accurate measures of herbivory that are unbiased and only slightly more variable than digital methods (Johnson et al. 2016).

Density experiment

We used a density manipulation experiment to separate the effect of predator and prey density on herbivory from the other effects of fragmentation (such as altered shading, plant community composition, or plant–plant competition; Didham et al. 1998, Tuff et al. 2016). We tested for these differences by manipulating both herbivore and predator abundances in artificial plots and recording the effects on herbivory of stiff goldenrod *Solidago rigida* and switchgrass *Panicum virgatum*. We grew both species from seed for ~2 months before transplanting them into the ground prior to the experiment.

Rather than manipulating the abundance of entire trophic guilds, we focused on a common predator-prey pair which disproportionately affects herbivory (Ruhren and Handel 1999): predatory jumping spiders *Phidippus clarus* and the nymphs of a generalist red-legged grasshopper *Melanoplus femurrubrum*. We collected all individuals of both species from old-field areas near our fragments, and then kept spiders in 50 ml Falcon tubes and grasshoppers in outdoor cages over natural vegetation prior to the beginning of the experiment. Spiders were fed ad libitum with collected insects prior to the start of the experiment.

To isolate the effects of herbivore and predator density, we factorially manipulated the densities of both spiders and grasshoppers in caged plots. We planted goldenrod and switchgrass into a plowed field before erecting triangular mesh cages over each pair of plants (32 × 32 × 42 cm base by 91 cm tall). We then introduced 0, 1 or 2 predators and 0, 3, 5 or 9 grasshoppers (12 total treatments) to randomly assigned plots. Spider and grasshopper densities represent a range of the densities we found in the field. All density combinations were replicated ten times with the exception of zero predators – five herbivores (n = 9) and one predator – five herbivores (n = 11).

Following the introduction of spiders and grasshoppers a single observer (LG) surveyed predator and prey survival and visually estimated (as above) percent herbivory of each plant. We repeated these surveys daily for eight days and then did final, exhaustive surveys (Royauté and Pruitt 2015). We terminated the experiment at that point both because some grasshoppers had molted into adults which are too large to be consumed by jumping spiders (Hawlena et al. 2011), and because some predators had died. To be confident of final abundances we opened cages and removed all spiders and grasshoppers over the three days following the end of the experiment. We used final abundances to correct surveys from previous days in cases where either spiders or grasshoppers were not visible or missed during counts.

Statistical methods

We used a series of mixed models to test for differences in patterns of abundance and trophic interactions among fragment patches differing in size. We first used generalized linear mixed effects models (GLMM) with a Poisson link function to test for differences in arthropod abundance. We ran separate models to estimate predator and herbivore abundance, including patch size and plant species and their interaction as main effects. We included date and plot nested in block as random effects to control for temporal and spatial variation in herbivory, respectively. We also tested for changes in the proportion of herbivores and predators choosing to occupy switchgrass or goldenrod. We estimated these proportions using a GLMM with a binomial error distribution, including patch size as a main effect and date and plot nested in block as random effects. In all cases we sequentially dropped non-significant interaction terms until only significant predictors remained in the final model. We then compared residual variance to the mean to test for over- and under-dispersion. We tested all models using maximum likelihood methods.

Next we aimed to link patterns of herbivory and arthropod abundance across patch sizes. We first tested for differences in herbivory among patches differing in size using another GLMM with a Poisson distribution. We used a Poisson distribution because we modeled herbivory as the integer value of percent herbivory, which never approached the maximum of 100 and upon inspection was consistent with a Poisson distribution (variance was equal to the mean). This model again included plant species and patch size and their interaction as main effects with date and plot nested in block as random effects. Finally we aimed to explicitly link changes in herbivore and predator abundance among patches differing in size to patterns of herbivory. We estimated herbivory using a GLMM with a Poisson distribution while including predator and herbivore abundance as main effects, and date and plot nested in block as random effects.

For the density experiment, we used a series of linear models to test for the effects of predator and herbivore abundance and their interaction on final herbivory measurements. We first estimated herbivory using a linear mixed-effects model with plant species, initial herbivore abundance, initial predator abundance, and all two- and three-way interactions included as fixed effects and plot included as a random effect (since both plant species were in each plot). To account for differences in variance between goldenrod and switchgrass

herbivory we used the 'weights' function (in lme4, nlme library). In all analyses, we began with all terms and sequentially dropped higher order, non-significant terms until all remaining terms were statistically significant.

Because herbivores died during the density experiment, initial herbivore abundance is not fully representative of a plant's total exposure to herbivores. To measure total exposure to herbivores, we calculated 'total herbivore days' for each plot by summing the number of grasshoppers observed in each plot across all eight days of the experiment. Put otherwise, total herbivore days represents the sum of the number of days each individual grasshopper survived during the experiment. Calculation of total herbivore days allows us to separate two causes of herbivory: the per capita rate of herbivore consumption (i.e. percent plant consumed per herbivore per day), and the behavioural effect that predators have on herbivore feeding beyond their influence on herbivore numbers. To understand the per capita rate of herbivore consumption, we examine the slope of the line fitting plant herbivory to total herbivore days – this slope describes the effect of herbivore abundance over time. The intercepts of the lines at different predator abundances describe the non-consumptive impacts of predators (the change in herbivory that results from a change in herbivore behavior). Differences among treatment intercepts represent differences in herbivory at constant herbivore abundance, meaning that behavior rather than abundance must be creating these differences. Calculating 'total days' was not necessary for predators, as predator abundances did not show large changes during the experiment, so we used our initial treatment for predators in our analyses. To avoid detecting significant differences in herbivory among treatments owing to a lack of herbivores, we repeated the above analysis of total herbivore days while excluding zero-herbivore treatments.

To relate patterns of herbivory to predation of grasshoppers we subsequently tested for the effects of predator abundance on total herbivore days. We employed a linear model using initial herbivore abundance, initial predator abundance, and their interaction as predictors and the natural logarithm of total herbivore days as the response. We tested for overdispersion in all GLMs to determine if a quasi-likelihood estimation was more appropriate. We also tested the assumptions of all linear models by visually inspecting residual variance. We conducted statistical analyses in R ver. 3.2.2 (<www.r-project.org>) using the base package and the 'lme4'and 'nlme' packages (Bates et al. 2015).

Data deposition

Results

Fragmentation experiment

Herbivore and predator densities changed across patch sizes, but the direction and magnitude of changes in abundance differed between plant species. Small patches supported fewer predators and more herbivores averaged per plant (Fig. 1A; both $p < 0.001$). The proportion of predators and herbivores on each plant species also depended on
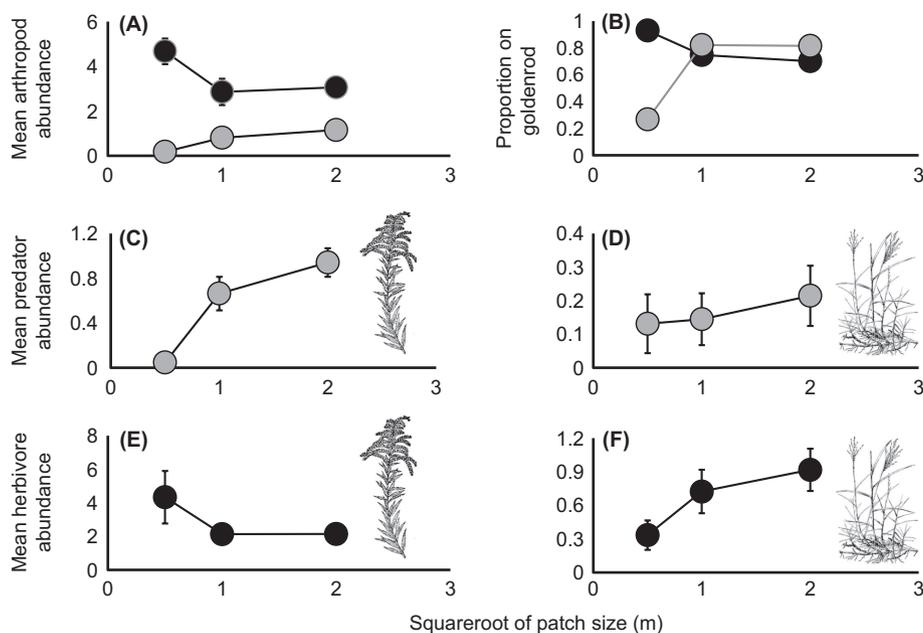

Figure 1. Patterns of herbivore and predator density in old-field fragments differing in size. Predators (grey) and herbivores (black) increased and decreased in density with patch size, respectively (A). Within a patch, the proportion of herbivores on goldenrod was always greater than on switchgrass, but decreased with patch size. The proportion of predators on goldenrod (relative to switchgrass) increased with patch size (B). Predator density was highest in large patches on both goldenrod (C) and switchgrass (D). Small patches conferred higher densities of herbivores on goldenrod (E) but fewer herbivores on switchgrass (F). Mean densities represent the mean density calculated across four insect surveys. Error bars denote ± 1 SE. While analyses used patch area, we plotted results using the square-root of patch area which represents the length of one side of the patch.

patch size, with smaller patches having a higher proportion of herbivores on goldenrod (Fig. 1B, p < 0.001). Predator abundance per plant showed consistent patterns between plant species, increasing with patch sizes for both goldenrod (Fig. 1C; p < 0.001) and switchgrass (Fig. 1D; p = 0.004). However, herbivore abundance decreased with increasing patch size on goldenrod plants, whereas it increased with patch size on switchgrass plants (Fig. 1E–F; both p < 0.001).

The effect of patch size on herbivory differed between species, increasing herbivory on goldenrod in small patches (Fig. 2A) and decreasing it on switchgrass (Fig. 2B; both p < 0.001). The ultimate causes of changes in herbivory appeared to differ between species. Increased herbivore abundance per plant had no detectable effect on goldenrod herbivory (Fig. 2C; p = 0.967), whereas it increased herbivory on switchgrass (Fig. 2D; p < 0.001). Conversely, high predator abundance per plant reduced goldenrod herbivory (Fig. 2E; p < 0.001) without affecting herbivory of switch grass (Fig. 2F; p = 0.569).

Density experiment

Treatments lacking herbivores experienced virtually no herbivory on either goldenrod (0.3% ± 0.1% SEM) or switchgrass (0%). After removing these no-herbivore treatments, herbivory was greater on goldenrod than on switchgrass (13.5% versus 0.7%, p < 0.001). Herbivory on both species was affected by initial herbivore and predator abundances, but these effects differed between goldenrod and switchgrass (initial herbivore abundance × plant species, p < 0.01; initial predator abundance × plant species, p < 0.001). The presence of predators decreased herbivory on both switchgrass (p < 0.05) and goldenrod (p < 0.001). High initial herbivore abundance was associated with greater herbivory on goldenrod (p < 0.01), and a marginal increase of herbivory on switch grass (p = 0.051).

In order to separate consumptive and behavioral effects of predators on herbivores, we calculated the total herbivore days that each plot experienced, and related this measure to herbivory. The total number of herbivore days was greater when starting at high initial herbivore abundance and in the absence of predators (both p < 0.001, Supplementary material Appendix 1 Table A3). Introducing a single predator reduced total herbivore days by almost half (to 0.56 herbivores per predator), and two predators reduced total herbivore days to about a third (to 0.31; Supplementary material Appendix 1 Eq. A2, Table A3).

In cages with fewer total herbivore days, both goldenrod and switchgrass experienced reduced herbivory (Fig. 3; p < 0.001), but the magnitude of this effect was greater for goldenrod (plant species × total herbivore days p < 0.001). The abundance of predators had a marginally negative effect on goldenrod herbivory even after accounting for the numeric (consumptive) effect of reducing herbivore abundances (different intercepts in Fig. 3A; p = 0.051), but predators had
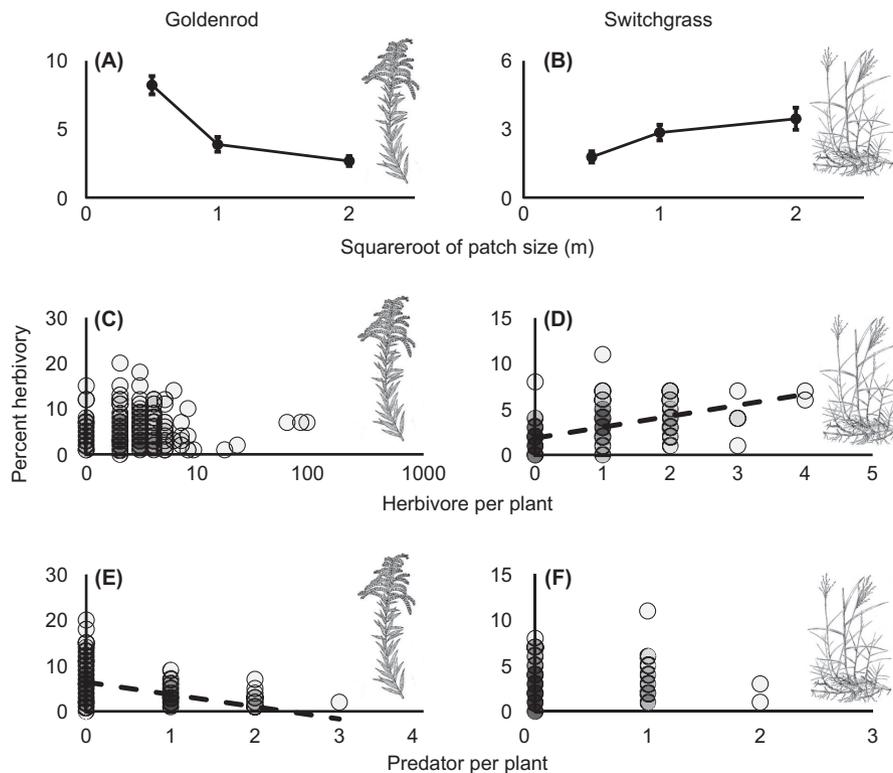

Figure 2. Patterns of herbivory on goldenrod and switchgrass. Herbivory decreased and increased with patch size on goldenrod (A) and switchgrass (B), respectively. Herbivore density had no effect on goldenrod herbivory (C) but increased switchgrass herbivory (D). However, herbivory occurred on goldenrod even when very few herbivores were observed. Conversely, predator density decreased goldenrod herbivory (E) but did not affect switchgrass herbivory (F). The error bars in (A) and (B) are ± 1 SE. The trend lines in (D) and (E) are predicted values generated from GLMMs. Note the differences in y-axis values between pairs of plots representing data from goldenrod and switchgrass. We measured herbivory to the nearest whole number.
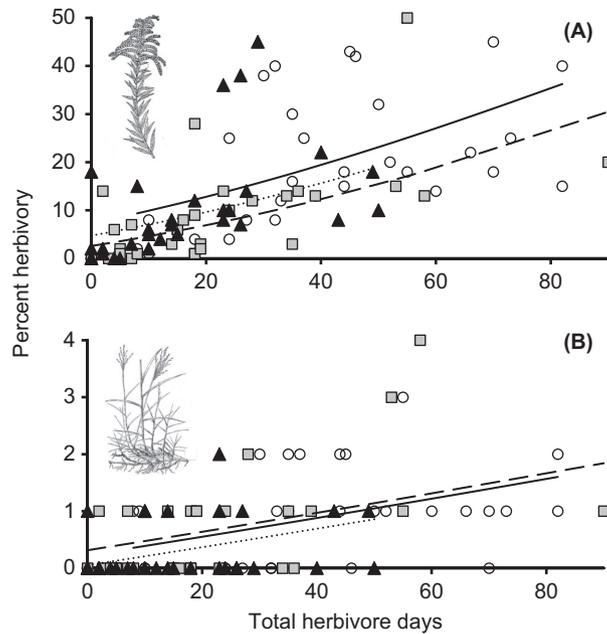
Figure 3. Total herbivore days increase herbivory on both goldenrod (A) and switchgrass (B). Predators reduced herbivory on goldenrod (A) but not switchgrass (B). Predator abundances per plot are denoted as follows: zero predators (white circle, solid line), one predator (grey square, dashed line), two predators (black triangles, dotted line). The lines show back-transformed fitted values generated from linear models. Note that the panels have different y-axes as switchgrass experienced much less herbivory on average.

no effect on switchgrass herbivory other than their reduction of herbivore numbers (Fig. 3B; $p > 0.1$).

Discussion

Our study demonstrates that habitat fragmentation affects the trophic structure of communities, but that feeding preferences of herbivores interact with predator loss in small fragments to generate unequal impacts among plant species. As predicted, predator density declined with shrinking patch size, while herbivore density showed the opposite pattern (Fig. 1). However, the change in herbivory in response to fragment size differed between plant species (Fig. 2), suggesting that the relationship between herbivore density and herbivory may be influenced by species-specific mechanisms, including behavioral switching. Herbivory on goldenrod declined in large patches, with these patterns apparently driven by increases in predator density rather than declines in herbivore density (Fig. 2). Conversely, changes in switchgrass herbivory were driven by differences in herbivore density, which increased in larger patches (Fig. 2). In the density experiment, herbivore and predator densities altered patterns of herbivory in a similar manner, and revealed that goldenrod herbivory is both more sensitive to increases in herbivore abundance and to changes in herbivore behavior due to the absence of predators. The results of our density experiment show that changes in arthropod density could contribute to differences in herbivory in fragmented habitats. As a whole, our results suggest that while trophic levels respond predictably to fragmentation, the effects of these changes on plant communities are species-specific and can be altered by herbivore behavior.

Our results provide support for the prediction that higher trophic level species are more sensitive to fragmentation than herbivores (Fig. 1A). A number of mechanisms, including trophic dependency and small population sizes making extinction more likely, have been proposed for this pattern, suggesting that it is likely to be commonly found in nature (Lindeman 1942, Srivastava et al. 2008). The corollary to this result, that herbivore density increases in small fragments, has received less attention despite the literature on trophic release (Heithaus et al. 2008, Brodie and Giordano 2013, Harvey and MacDougall 2015). Predator loss from small patches appears to cause trophic release whereby herbivore density increases in the absence of predation (Fig. 1), creating an overall increase in herbivory (Fig. 2A–B). This contrasts with general findings which suggest that herbivory typically declines in fragmented habitats, but these declines were not significant in quantitative reviews of old-field habitats (Martinson and Fagan 2014). Opposing effects of fragmentation in our experiment and other systems suggest that different mechanisms might be driving each trend. If patterns of herbivory are driven by top–down processes such as trophic release, then herbivory should increase in small fragments. Conversely, if small fragment size creates depauperate communities lacking plants that sustain a diversity of herbivores, then herbivory should increase with fragment size (Chávez-Pesqueira et al. 2015). One factor which may affect our divergent result is scale, with some researchers suggesting that top–down trophic cascades may be more important at small spatial scales such as those in our experiments (Borer et al. 2005). In sum, multiple mechanisms can alter patterns of herbivory in fragmented habitats, but our results show that predator loss in small fragments leads to trophic release and increased herbivory.

While trends in total predator and herbivore density were consistent with theory, switchgrass and goldenrod communities were impacted differently by fragmentation. Predator density increased with fragment size on both switchgrass and goldenrod but did so much more quickly and to higher absolute densities on goldenrod (Fig. 1C–D). These patterns mean that, if predation risk is directly related to predator density (Holling 1959), predation risk will increase with fragment size for herbivores regardless of which species of plant they are occupying. However, herbivores can choose to forage on either species within a single fragment, a decision that is largely mediated by predation risk (Charnov 1976, Brown 1988, Schmitz et al. 1997, Lima and Bednekoff 1999). Goldenrod and switchgrass harbor greater predator densities and are therefore riskier (relative to the other species) in large and small fragments, respectively (Fig. 1B). The observed patterns of predator density were mirrored by opposite patterns of herbivore density. In other words, herbivores were more common in small patches on goldenrod (Fig. 1E) and more rare in the same patches on switchgrass (Fig. 1F). These patterns of predator and herbivore density are consistent with adaptive resource switching by herbivore species (Brown 1988, Schmitz et al. 1997, 2004). Herbivores forage on the relatively less risky switchgrass in large patches, but switch to goldenrod in small patches when predation risk is lower. Similar patterns of resource switching have been well characterized (Lima and Valone 1986, Brown 1988) including in old-field systems (Schmitz et al. 1997, 2004), but, to our knowledge, have not been shown to result from fragmentation.

While the results of our fragmentation experiment were consistent with predictions for arthropod density underlying the effects of fragmentation on herbivory, it is possible that other mechanisms could in fact generate these patterns. Our second experiment aimed to test whether changes in density were the mechanism driving these patterns by isolating density from other factors that vary with fragment size. Despite the potential for other fragment-induced changes, such as edge effects, to influence correlative tests, our separate density manipulation experiment gave surprisingly consistent results (Fig. 3). As in the fragmentation experiment, predator density had a negative effect on herbivory of goldenrod (Fig. 3A) but no effect on switchgrass herbivory (Fig. 3B) other than to reduce herbivore densities (Supplementary material Appendix 1 Fig. A2). These patterns are indicative of a behavioral effect, where increased predation risk reduces herbivory on goldenrod without a detectable effect on switchgrass, thereby increasing the proportion of switchgrass in herbivore diets (Lima et al. 1985, Lima and Valone 1986, Schmitz et al. 1997). The apparent resource switch observed in the density experiment was in the same direction as that detected in the fragmentation experiment, suggesting that the simple spider–grasshopper system captured important processes that occurred in the more diverse fragmentation experiment. For example, herbivory rates on goldenrod in the density experiment fell by approximately 10% when a predator was present, and fell by approximately 6% in the fragmentation experiment when predators were present, whereas predators did not change per capita herbivory of switchgrass in either experiment (Fig. 2, 3). However, high herbivore densities also had a much larger impact on goldenrod than switchgrass in the density experiment (Fig. 3), with herbivory increasing by approximately 30% on goldenrod but only 2% on switchgrass from low to high herbivore densities. This direct effect of herbivore density on goldenrod herbivory was not observed in our fragments (Fig. 2C), possibly due to the confounding of herbivore and predator densities in fragments, the more complex arthropod communities in the experimental fragments, or our particular choice of arthropod species (Schmitz et al. 2004). Whatever the cause, the combined evidence of the fragmentation and density experiments indicates that both behavioral effects induced by predators, as well as different plant sensitivities to herbivore density, underlie the shift from goldenrod herbivory to switchgrass herbivory as fragment size increases.

Species-specific shifts in herbivory with fragment size can have important implications for both coexistence and plant community dynamics in fragmented landscapes. If herbivory reduces plant fitness (Strauss et al. 1996, Strauss 1997, Agrawal 1999, Strauss and Agrawal 1999), then we expect goldenrod to gain an advantage in large patches and switchgrass to have a greater advantage in small patches (Fig. 2). Although the end result of such advantages depends on fitness differences between these species (Chesson 2000), they likely lead to shifts in relative abundance with patch size (Schmitz 2003). This suggests that variation in patch size on a landscape could alter trophic dynamics (Holt et al. 1999), resultant competitive dynamics (Holt 1977), and ultimately long term coexistence of plant species (Holt and Lawton 1994). More generally, our results suggest that some species can benefit from fragmentation through indirect advantages that result from shifts in trophic dynamics in these environments. Mesopredators have similarly been shown to benefit from reduced predation in small patches, increasing their density and their impact on resource species (Crooks and Soulé 1999). Notably, this increased fitness in small patches from altered trophic dynamics could be offset or reinforced by other environmental conditions (Henle et al. 2004, Cushman 2006), or by direct effects on competitor species (Yeaton and Cody 1974, Jutila and Grace 2002). Our results suggest that species-specific responses to the trophic effects of fragmentation are likely to contribute to the effects of fragment size on community structure.

In summary, by incorporating well-understood trophic processes into spatial ecology, we have shown that small fragments reduce predator density and increase herbivore density. These changes increase overall herbivory on plants, but the effect of fragment size on herbivory rates varies among plant species. Differential herbivory in response to fragment size results from changes in herbivore behavior when predators are lost, as well as species-specific rates of increase in herbivory with increasing herbivore density. Our study demonstrates that while the response of predators and herbivores to fragmentation is generally predictable, numeric and behavioral effects of herbivores can create unexpected cascades with potentially important implications for species coexistence.

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