



Habitat edges alter arthropod community composition

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Abstract

Context Historically, habitat edges were thought to increase diversity by combining communities from two habitats, but empirical results are mixed. Variation in edge responses may be driven by lumping specialists and generalists with divergent responses.

Objectives We examined arthropod communities associated with a habitat edge in an intertidal salt marsh in New Jersey. We predicted that herbivores, largely specialists, would decline along the habitat edge due to their failure to expand across the boundary, and specialist natural enemies should track prey. Generalists should be less impacted by the edge if they use resources from both sides. Thus, habitat edges should affect species composition more than species diversity.

Methods We studied the edge responses of 115 arthropod species to the habitat edge formed between

Spartina patens (SP) and *Spartina alterniflora* (SA) throughout the growing season.

Results We found that the edge between SA and SP affected the abundance and composition of the associated arthropod community, but not species richness. Composition of herbivores, epigeic feeders, specialist natural enemies, and generalist predators shifted not only between SA and SP interiors, but also the edges. Compositional shifts were driven by dietary or habitat specialists.

Conclusions We found that edges change community composition via divergent responses by species with different resource requirements. This change in composition is not between two disparate habitat types but two congeneric grass species. Our results demonstrate that biodiversity losses due to edge effects associated with habitat fragmentation will not be random but will be driven by specialization and resource use.

Keywords Arthropod · Community · Diversity · Ecological boundary · Edge effects

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Introduction

Habitat loss is widely considered to be the key factor leading to species extinction worldwide, and a major contributor to the erosion of species diversity (Fahrig

2003). Natural vegetation on every continent except Antarctica has been removed by human activities, leaving fragmented patches of suitable habitat across the landscape (Saunders et al. 1991). Edge habitats form at the boundary between two habitat patches that differ in resource availability, quality, and/or structure (Fagan et al. 1999; Ries and Sisk 2004), and are thus critical landscape features that influence population and community responses to fragmentation (Murphy et al. 2016). Most species' density responses to habitat area are driven by edge rather than area effects (Fletcher et al. 2007; Pfeifer et al. 2017).

Historically, habitat edges were assumed to have higher species diversity relative to habitat interiors (Leopold 1933). Odum (1953) suggested two mechanisms that might lead to higher species richness along edge relative to interior habitats: (1) spillover of organisms from the adjacent habitat, and (2) the appearance of species in edge habitats that are not found in either of the two abutting habitats. While numerous studies assume higher diversity at edges because of this historical context, community metrics such as richness and diversity tend to show variable responses to habitat edges (Ries et al. 2017), which may be explained in part by the condition of the adjacent habitat (Ewers and Didham 2006; De Carvalho Guimarães et al. 2014). For example, when the abutting habitat has been degraded or altered by human activity, diversity along the habitat edge is unlikely to be greater in the natural habitat (Alignier et al. 2014). In addition to changes in species diversity, changes in community composition along habitat edges seem likely, given the differential perception of habitat edges by organisms with divergent resource requirements (Fagan et al. 1999; Ries et al. 2004; Ries and Sisk 2004; Ries and Sisk 2008; Peyras et al. 2013) or life history characteristics (Ewers and Didham 2006), which may in turn lead to changes in species abundance or susceptibility to extirpation with fragmentation. For example, edge responses in herbivores are thought to be driven by dietary specialization (Bagchi et al. 2018). Moreover, studies that have separately examined generalist and specialist dung beetle responses to the habitat edge have shown that specialized species demonstrate stronger edge responses (Peyras et al. 2013); this highlights the importance of separating generalists and specialists to reduce variability and better explain overall patterns.

Decades of research have demonstrated that animal communities are driven by both bottom-up and top-down forces and that these forces may vary with dietary specialization (Vidal and Murphy 2018 and references therein); this research may help us understand larger animal community patterns at habitat edges. Plants and other primary producers are the foundation on which animal communities are built (Hutchinson 1959). Thus, animal community responses to habitat edges will be driven, at least in part, by plant responses to habitat edges. If plant communities exist in edge habitats that are compositionally distinct from interior habitats (e.g., Krishnadas et al. 2019), then this unique plant community can attract a distinct animal assemblage (Peyras et al. 2013). While this would not necessarily lead to higher species richness or diversity at the habitat edge, it would lead to a shift in overall composition. However, if we do not find a unique plant community at the edge, but simply two adjacent habitats, community responses may still be driven by changes in plant resources due to spillover from one habitat to the other (Rand et al. 2006). For example, shifts from forest to grassland habitats alter beetle composition in edge habitats, and these shifts in beetle composition are detectable over large spatial scales (Ewers and Didham 2008). Plants living along the edge may also experience a different set of abiotic conditions, which may affect plant biomass and quality (Ries and Sisk 2004). This change in plant quality or quantity may lead to bottom-up effects on dependent herbivores, which may in turn affect higher trophic levels (Frost et al. 2015). What we might expect under this set of circumstances is a change in overall animal abundance near the habitat edge. Since there is a positive relationship between abundance and species richness (Gotelli and Colwell 2001), a change in abundance might also be associated with a change in species richness.

Even if plant quality, quantity, or composition do not change along the habitat edge, animals may still demonstrate behavioral responses to the habitat edge that result in lower edge densities. Such behavioral responses may be even more pronounced for dietary specialists that use cues to search for the proper host plant, and/or organisms with limited mobility that may not be able to relocate the proper host plant if they venture too far into the adjacent habitat (e.g., Cronin 2009; Wimp et al. 2011, 2019).

Finally, while some organisms may decline near habitat edges, generalist predators have actually been shown to couple different habitats in order to maximize their potential to find prey (Rooney et al. 2006; McCann and Rooney 2009). Thus, we might expect a positive response of generalist predators to the habitat edge (Rand and Lauda 2006; Rand and Tscharrntke 2007; Wimp et al. 2011; Blitzer et al. 2012; Frost et al. 2015). Indeed, we might even expect a decline in organisms that represent prey for higher trophic level predators. Importantly, whether an organism is defined as a specialist or generalist not only depends on diet, but also habitat. For example, organisms can be dietary generalists, but habitat specialists that require particular plants for web scaffolding (e.g., web builders) or particular micro-environments (Langelotto and Denno 2004). Specialization across either axis (diet or habitat) has previously been shown to restrict the distribution of these organisms and lead to negative edge responses (Wimp et al. 2019). Some organisms are dietary and habitat generalists, and these organisms will either be unaffected by habitat edges (if resources exist in both habitats) or positively affected by habitat edges (if adjacent habitats provide complementary resources; Ries et al. 2004).

We examined arthropod communities associated with the two foundation plant species found in an intertidal salt marsh, *Spartina alterniflora* Loisel (Poaceae) and *Spartina patens* (Aiton) Muhl (Poaceae). Our system is ideal for testing community-wide responses to habitat edges because edges naturally form between *S. alterniflora* and *S. patens* and there is not a transition zone, but rather a sharp boundary between the lowland grass species (*S. alterniflora*) and the upland grass species (*S. patens*). Thus, we can examine the impacts of edges on animal communities without the confounding effects of shifts in plant species composition along the habitat edge. Moreover, our previous research has shown that host plant quality does not decline along the habitat edge (Wimp et al. 2011), so we can examine animal community responses without the confounding effects of changing host plant quality. Because our herbivores are largely specialists in either *S. alterniflora* or *S. patens*, we predicted they would decline in abundance along the habitat edge due to their failure to expand across the boundary, and specialist predators and parasitoids that feed on these herbivores would follow prey or host distribution. However, generalists (epigeic feeders and

predators) might be less impacted by the habitat edge, especially if they are able to use resources in each habitat equally well. Overall, we predicted that differential responses to habitat edges among specialists and generalists will lead to an overall decline in species abundance near the habitat edge, but no effect on species richness. Similarly, we expected an overall change in arthropod composition in edge relative to interior habitats, and this change should be driven again by specialist organisms.

Methods

Study site and organisms

We studied the edge responses of 115 arthropod species (Supplementary Appendix A) at a salt marsh located in Sheepshead Meadows, which is part of the New Jersey Department of Environmental Protection's Great Bay Wildlife Management Area and the Jacques Cousteau National Estuarine Research Reserve (39°33'09.5"N 74°20'09.1"W). This salt marsh is predominantly composed of two grasses: *S. patens* (SP commonly known as marsh hay) and *S. alterniflora* (SA commonly known as smooth cordgrass). SA dominates the landscape (Wimp et al. 2011), and SP exists in patches within the larger SA matrix. These two species form a hard edge, with very little mixing of grass species (Wimp et al. 2011). The arthropod community (Supplementary Appendix A) consists of insects, spiders, mites, amphipods, isopods, and pseudoscorpions. In the salt marsh system, there are two distinct food webs on the marsh platform. One food web is based on live plant material (SA or SP) and the other food web we collectively refer to as "epigeic" because members use a mixture of material found on the marsh surface such as algae, detritus, and associated microbes. The two habitats also differ in structure. SP has a greater layer of dead material (or thatch) and lays more flatly on the marsh surface relative to SA, which has erect culms. Lastly, SA and SP each have their own unique arthropod communities that are, for the most part, specialized on each grass species (Denno 1977, 1980). Previous studies in this system have determined trophic relationships among the dominant species and whether they were trophic specialists/generalists (Döbel and Denno 1994; Finke and Denno 2002, 2004; Ferrenberg and Denno 2003;

Gratton and Denno 2003; Wimp et al. 2013; Murphy et al. 2020). For the purposes of our analyses here, we group these species into one of the following functional groups: (1) herbivores, (2) epigeic feeders, (3) generalist predators, and (4) specialist predators and parasitoids. Specialist predators and parasitoids are grouped together because there is only one specialist predator species found in each *Spartina* habitat (*Tytthus vagus* in *S. alterniflora* and *Tytthus alboornatus* in *S. patens*), so we grouped them with the parasitoids based on their similar specialist diets.

Experimental design

We established 7 study areas in the spring of 2007 using some of the largest SP patches found on the salt marsh, so that we could capture unique interior and edge dynamics in both habitats (finding expansive areas of SA is not an issue). The different areas we chose were separated from one another (71–576 m, 333 m on average; Supplementary Appendix B, Figure B1). Each study area had a large SP patch abutting SA, and we established 2×2 m plots in each of the 4 habitats (SP interior, SP edge, SA interior, and SA edge), for a total of 28 plots (Supplementary Appendix B, Figure B2). The interior plots in SP patches ranged from 6–18 m from the edge of the patch, depending on the overall size of the patch. Thus, we matched this distance for the SA interior plot, such that SA and SP interior plots in a given area were the same distance from the habitat edge; these two plots represent the habitat interiors for these two *Spartina* species. The two edge plots were located 0.5 m from the habitat edge, one in SP and one in SA, and were adjacent to one another.

We collected arthropods three times during the growing season (June 26, July 17, and August 4) using a D-vac suction sampler (Rincon-Vitova Insectaries, Ventura, California, USA), and a hose diameter of 21 cm. We placed the hose on the marsh surface three times in each plot, and each placement was for 5-s. We stored arthropods from each plot in ethanol and later sorted, counted, and identified each individual to genus and species with the help of experts when needed. We collected a total of 210,742 individuals. All analyses were performed on seasonal totals.

Statistical analyses

We performed a Two-Way ANOVA to examine the response of both arthropod species richness and abundance (number of arthropods per m^2) to two factors: edge versus interior, and plant species (SA or SP) in two separate ANOVA analyses. As mentioned in the previous section, all analyses were performed on seasonal totals. Additionally, we examined the response of each feeding group to edge versus interior, and plant species (SA or SP) using a Two-way ANOVA. Arthropod abundance data were transformed to meet equality of variance assumptions (square root or natural log), but species richness data met assumptions. Pairwise differences among groups were measured with a Tukey's test. All analyses were performed in R environment 3.4.1 (R Development Core Team 2020) using the packages *compute.es*, *car*, and *pastecs*, and using the functions “aov”, “leveneTest”, “shapiro.test” and “TukeyHSD.”

In addition to impacts on species richness and abundance, we also examined the impact of habitat edges on arthropod species composition using NMDS (Non-Metric Multidimensional Scaling). We performed NMDS for both the overall community and each feeding group. We used the overall abundance of each species across all time periods for our analysis, which allowed us to examine patterns of species assortment among our treatments across the entire growing season. We used the Bray–Curtis dissimilarity coefficient (Faith et al. 1987) to create a dissimilarity matrix, and the ordination was performed in DECODA (database for ecological community data, Minchin 2001). Overall differences among habitat types (SA and SP interior and edge habitats) were examined using ANOSIM (analysis of similarity, Warwick et al. 1990) and pairwise comparisons among habitat types were made using posthoc comparisons in DECODA that were adjusted using a Sequential Bonferroni. We determined the percent contribution that each arthropod species made to the overall dissimilarity among habitat types using similarity percentages in Primer-E (SIMPER, Clarke and Warwick 2001), for both overall arthropod composition and composition within each feeding group.

Results

Species richness and abundance

We did not find a difference in species richness between SA and SP ($F_{1,24} = 2.781$, $P = 0.11$, Fig. 1A). We found a slight increase in species richness in edge versus interior habitats ($F_{1,24} = 4.13$, $P = 0.053$, Fig. 1A), but did not find an interaction between plant species and edge habitats ($F_{1,24} = 0.011$, $P = 0.92$, Fig. 1A). Arthropod abundance was greater in SP compared to SA ($F_{1,24} = 54.475$, $P < 0.0001$, Fig. 1B), and declined in SP edge relative to SP interior habitats ($F_{1,24} = 8.479$, $P = 0.0076$, Fig. 1B). We also found an interaction between edge and plant species ($F_{1,24} = 6.097$, $P = 0.02$, Fig. 1B) since arthropod abundance declined in SP edge relative to interior

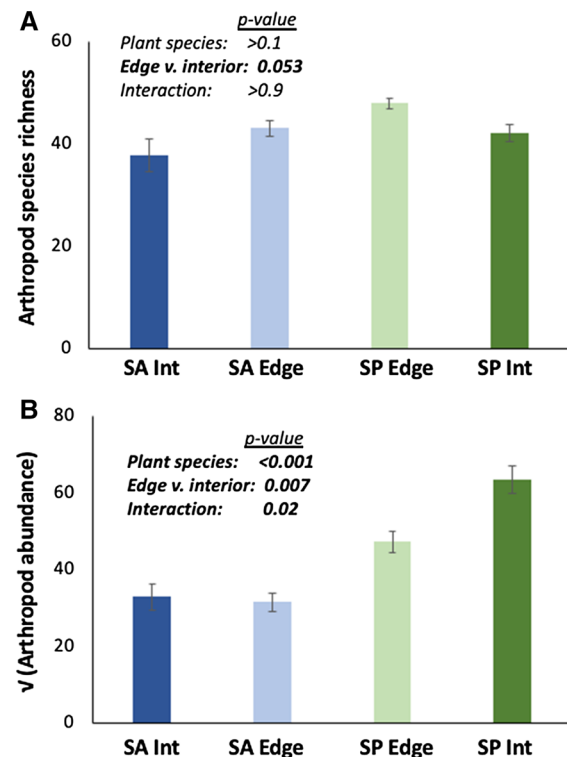


Fig. 1 Arthropod response to the habitat edge between *Spartina alterniflora* and *Spartina patens* as measured by **A** arthropod species richness and **B** arthropod species abundance (square root transformed to meet assumptions of normality and equality of variances). Shown are mean \pm 1 SE (alt int = *S. alterniflora* interior; alt edge = *S. alterniflora* edge; pat edge = *S. patens* edge; pat int = *S. patens* interior) and letters above bars indicate significant differences among habitat types

habitats but did not change in SA edge versus interior habitats. Thus, while species richness peaked along the habitat edge, abundance was greatest in the SP interior and declined along the SP edge and in SA habitats. These different patterns found for species richness and abundance are driven by different feeding groups, as explained below.

Not only did we find an overall response in arthropod abundance, responses to habitat type differed across feeding groups. While herbivore abundance was not affected by plant species ($F_{1,24} = 0.17$, $P = 0.68$, Fig. 2A), or the interaction between plant species and edge versus interior habitats ($F_{1,24} = 0.689$, $P = 0.42$, Fig. 2A), there was a slight decrease in herbivores in edge versus interior habitats ($F_{1,24} = 4.007$, $P = 0.056$, Fig. 2A). The abundance of epigeic feeders was greater in SP relative to SA ($F_{1,24} = 110.439$, $P < 0.0001$, Fig. 2B), decreased slightly along the habitat edge ($F_{1,24} = 4.239$, $P = 0.0505$, Fig. 2B), and we did not find an interaction between plant species and edge versus interior habitats ($F_{1,24} = 0.88$, $P = 0.36$, Fig. 2B). Generalist predators were not affected by plant species ($F_{1,24} = 0.000$, $P = 0.99$, Fig. 2C) or edge versus interior habitats ($F_{1,24} = 2.394$, $P = 0.14$, Fig. 2C). However, we found an interaction between plant species and edge versus interior habitats ($F_{1,24} = 4.431$, $P = 0.046$, Fig. 2C) whereby generalist predator abundance declined along the SA edge versus interior but did not change in SP edge versus interior habitats. The abundance of specialist predators and parasitoids was greater in SP relative to SA ($F_{1,24} = 7.402$, $P = 0.012$, Fig. 2D), but was not affected by edge versus interior habitats ($F_{1,24} = 3.478$, $P = 0.075$, Fig. 2D), or the interaction between plant species and edge versus interior habitats ($F_{1,24} = 0.129$, $P = 0.72$, Fig. 2D).

Community responses

We found that habitat type altered arthropod community composition (Overall ANOSIM $R = 0.6483$, $P < 0.0001$, Fig. 3). After adjusting for multiple comparisons using a Sequential Bonferroni, we found that these differences in arthropod community composition were not only driven by differences between the two grass species (SA interior versus SP interior ANOSIM $R = 0.9378$, $P < 0.0001$), but also by differences in community composition between the

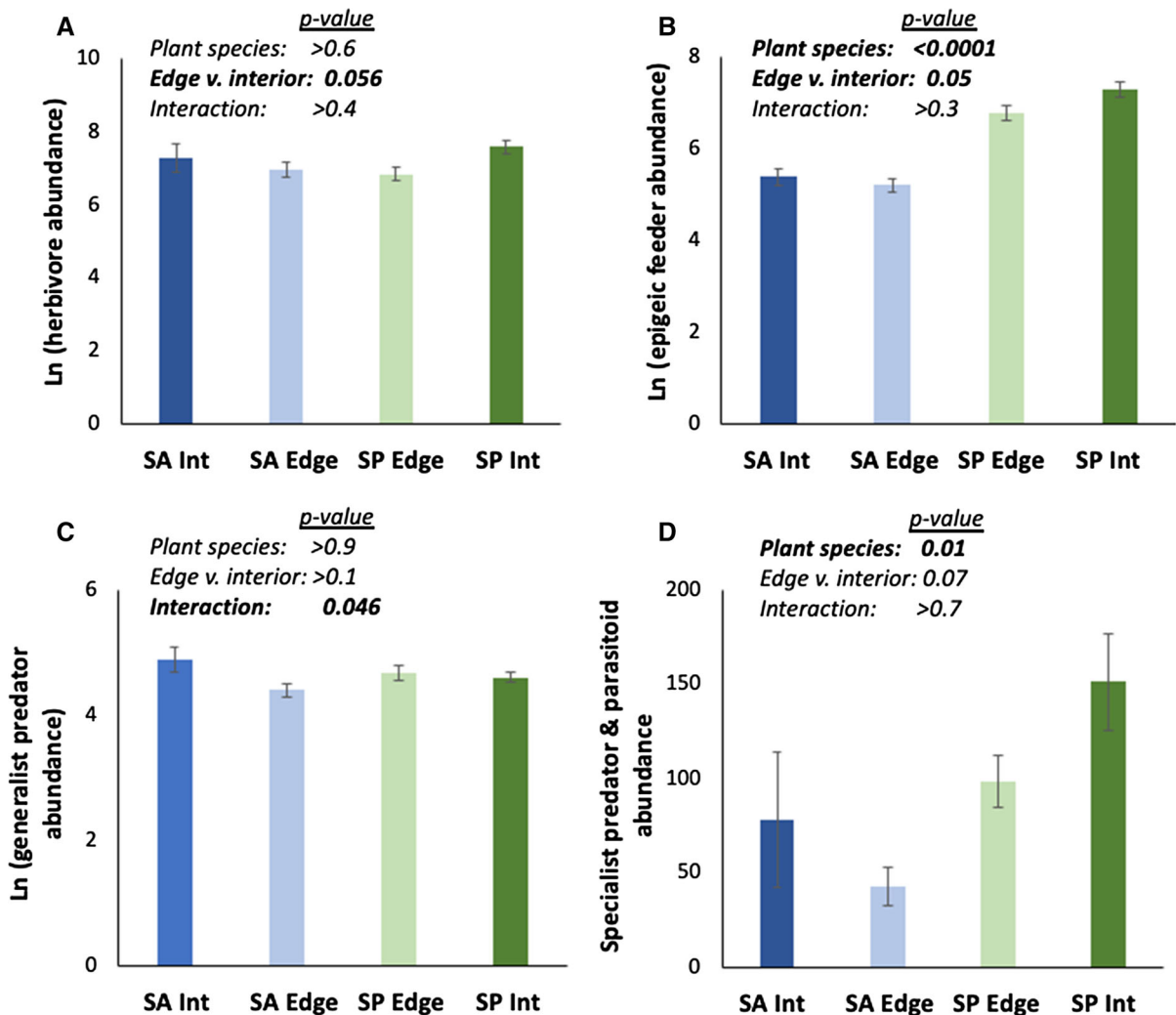


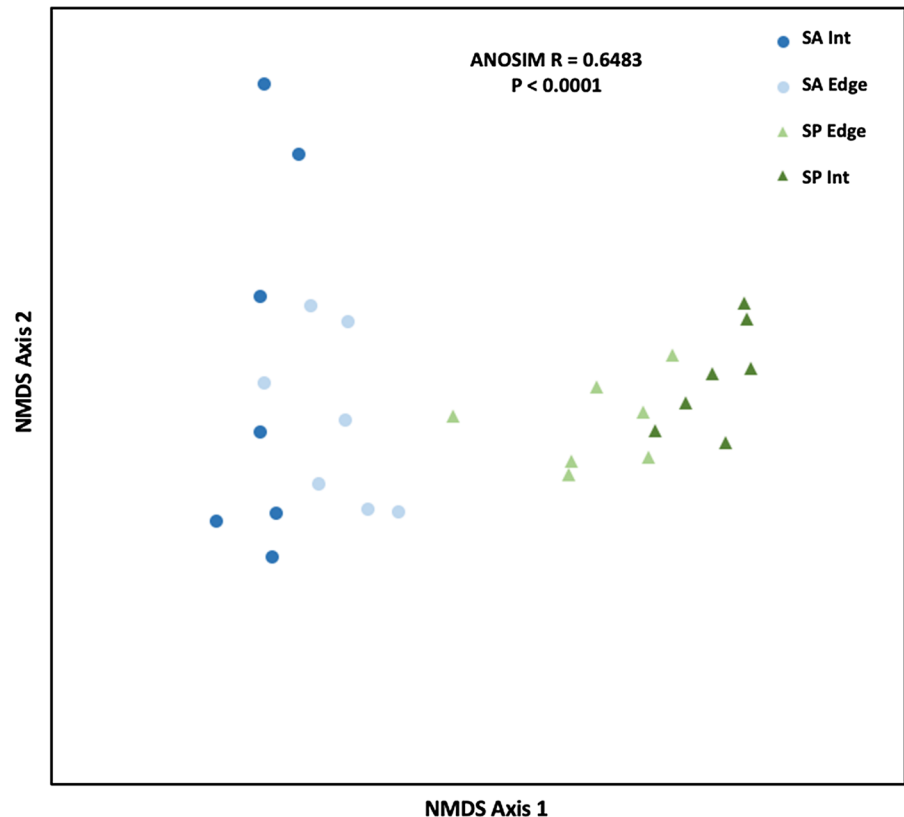
Fig. 2 Arthropod abundance (number of arthropods per m²) by feeding groups across *Spartina alterniflora* and *S. patens* interior and edge habitats for: **A** herbivores, **B** epigeic feeders, **C** generalist predators, and **D** specialist predators and parasitoids (transformed data are shown in cases where we had to do

so to meet assumptions of normality and equality of variances). Shown are mean \pm 1 SE (alt int = *S. alterniflora* interior; alt edge = *S. alterniflora* edge; pat edge = *S. patens* edge; pat int = *S. patens* interior) and letters above bars indicate significant differences among habitat types

two edge habitats (SA edge versus SP edge ANOSIM $R = 0.8834$, $P < 0.0001$). According to SIMPER, differences between the two interior habitats (SA and SP) were driven not only by specialist herbivores (*Tumidagena minuta*, *Delphacodes detecta*, and *Prokelisia* nymphs), but also by epigeic feeders (*Diapterobates* sp.) (Supplementary Appendix C). Similarly, differences between the two adjacent edge habitats were driven not only by specialist herbivores (*T. minuta*, *D. detecta*, *Delphacodes penedetecta*, *Prokelisia* nymphs, and *Prokelisia dolus*), but also by

epigeic feeders (*Diapterobates* sp.) (Supplementary Appendix C). Notably, we found a difference in arthropod community composition between SP interior and SP edge habitats (ANOSIM $R = 0.312$, $P = 0.017$), but not between SA interior and SA edge habitats (ANOSIM $R = 0.1672$, $P = 0.063$). According to SIMPER, the difference between SP interior and edge habitats is once again driven by specialist herbivores (*T. minuta* and *D. detecta*) and epigeic feeders (*Diapterobates* sp.) (Supplementary Appendix C).

Fig. 3 Arthropod composition differed according to habitat type (alt int = *S. alterniflora* interior; alt edge = *S. alterniflora* edge; pat edge = *S. patens* edge; pat int = *S. patens* interior). Arthropod composition differed between the *Spartina* species (*S. alterniflora* and *S. patens*) as well as between edge and interior habitats within *S. patens*. Points represent the arthropod community found in each of the 28 plots (7 per habitat type), and the placement of points is a Euclidean measure of Bray–Curtis dissimilarities among plots. ANOSIM stands for analysis of similarity



When we examined compositional shifts across the different feeding groups, we found that arthropod composition consistently differed between SP and SA habitats, but edge responses varied across the different groups. We assessed multiple comparisons across habitat types (SA interior, SA edge, SP interior, and SP edge) for each feeding group after a Sequential Bonferroni.

Herbivores

Herbivore composition changed across the four habitat types (ANOSIM $R = 0.4253$, $P < 0.001$, Fig. 4A). We found differences in herbivore composition between the interiors of both SA and SP habitats (ANOSIM $R = 0.6822$, $P = 0.001$), and between the edges of SA and SP habitats (ANOSIM $R = 0.3751$, $P = 0.009$). Herbivore composition was different between SP interior and edge habitats (ANOSIM $R = 0.171$, $P = 0.042$), but did not differ between SA interior and edge habitats (ANOSIM $R = 0.0525$, $P = 0.2$). These changes in herbivore composition are driven by strong, negative responses of specialist

herbivores in SP compared to the specialist herbivores in SA (Supplementary Appendix C).

Epigeic feeders

Habitat type had a significant effect on the composition of epigeic feeders (ANOSIM $R = 0.6675$, $P < 0.001$, Fig. 4B). We found differences in epigeic feeder composition between the interior of SA and SP habitats (ANOSIM $R = 1.0$, $P = 0.001$), and between the edges of SA and SP habitats (ANOSIM $R = 0.9747$, $P = 0.001$); however, epigeic feeder composition did not differ between either the SP interior and edge habitats (ANOSIM $R = 0.1263$, $P = 0.13$), or between the SA interior and edge habitats (ANOSIM $R = -0.797$, $P = 0.9$) (Supplementary Appendix C).

Generalist predators

Habitat type had a significant effect on the composition of generalist predators (ANOSIM $R = 0.3842$, $P < 0.0001$, Fig. 4C). We found differences in

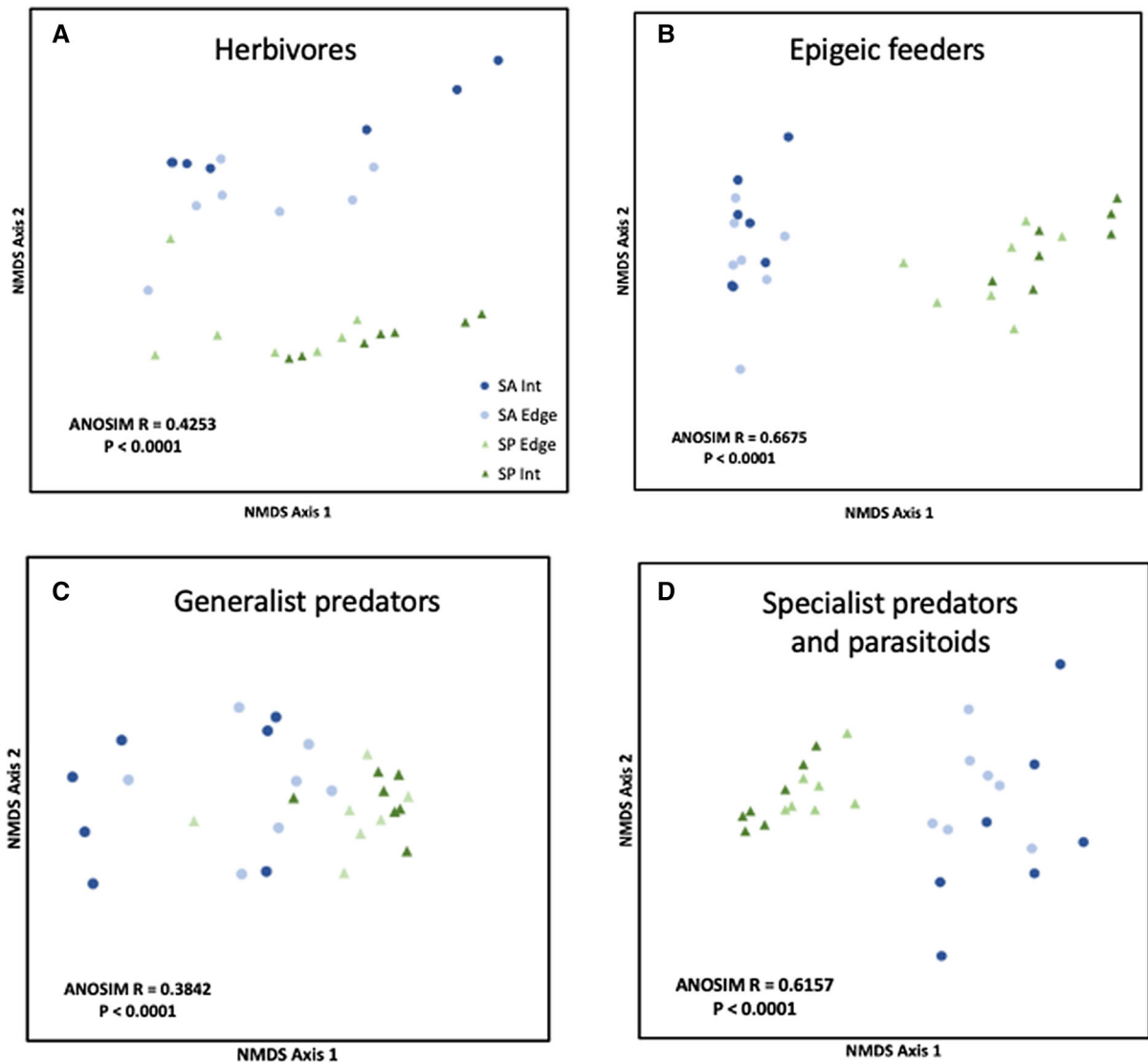


Fig. 4 Arthropod composition according to habitat type (alt int = *S. alterniflora* interior; alt edge = *S. alterniflora* edge; pat edge = *S. patens* edge; pat int = *S. patens* interior). Overall data were separated by feeding group: **A** herbivores, **B** epigeic feeders, **C** generalist predators, and **D** specialist predators and

parasitoids. The symbol legend in **A** applies to all figures. Points represent the arthropod community found in each of the 28 plots (7 per habitat type), and the placement of points is a Euclidean measure of Bray–Curtis dissimilarities among plots. ANOSIM stands for analysis of similarity

generalist predator composition between the interior of SA and SP habitats (ANOSIM $R = 0.7269$, $P < 0.0001$), and between the edges of SA and SP habitats (ANOSIM $R = 0.5112$, $P = 0.006$). While we found a difference in generalist predator composition between the edge and interior of SA (ANOSIM $R = 0.2371$, $P = 0.026$), there was no difference in composition between the edge and interior of SP habitats (ANOSIM $R = 0.1950$, $P = 0.2$). These

patterns are driven by differential responses to the habitat edges by different groups of spiders and mites (Supplementary Appendix C).

Specialist predators and parasitoids

Habitat type had a significant effect on the composition of specialist predators and parasitoids (ANOSIM $R = 0.6157$, $P < 0.001$, Fig. 4D). We found

differences in specialist predator composition between the interiors of both SA and SP habitats (ANOSIM $R = 0.9145$, $P < 0.001$) and between the edges of SA and SP habitats (ANOSIM $R = 0.9436$, $P < 0.001$). There was a trend towards different specialist predator and parasitoid communities between the SP interior and edge habitats (ANOSIM $R = 0.1837$, $P = 0.065$), but not between SA interior and edge habitats (ANOSIM $R = 0.1103$, $P = 0.107$). These patterns are driven by the strong, negative response of specialist predators and parasitoids in SP, tracking their SP herbivore prey (Supplementary Appendix C).

Discussion

We found that habitat edges between congeneric grasses (SA and SP) affected the abundance and composition of the associated arthropod community. We did not find differences in species richness between SA and SP, nor any interaction between plant species and edge habitats. In contrast with numerous studies that have predicted an increase in animal diversity along habitat edges (e.g., Wirth et al. 2008), we only found a slight increase in species richness in edge relative to interior habitats. While spillover from adjacent habitats often leads to an increase in arthropods along edges, this phenomenon may be biased towards pest species found in agricultural systems (as reviewed by Nguyen and Nansen 2018). Even without a change in species richness, we still found compositional differences between two abutting edge communities. Moreover, this change in composition happened not between two disparate habitat types (e.g., a forest and a meadow, Ewers and Didham 2008), but a habitat edge between two congeneric grass species. Arthropod composition was consistently different between the SA and SP edge habitats, so there was relatively little spillover in arthropods from the adjacent habitat type even though species might have been expected to be able to use these congeneric habitats more easily than disparate habitats.

Arthropod abundance was higher in SP relative to SA and affected by the habitat edge. We also found an interaction between plant species and edge habitat, whereby arthropod abundance declined along the SP edge relative to interior habitats, but there was no edge response in SA. When we examined arthropod

responses across feeding groups, we found that responses to edge habitat and plant species differed by feeding group. Herbivore abundance was not affected by plant species, but declined slightly along the habitat edge relative to the interior. The abundance of epigeic feeders was greater in SP relative to SA, and also decreased slightly along the habitat edge relative to the interior. This response by epigeic feeders was driven largely by the oribatid mite *Diapterobates* sp., which feeds on the fungi found in SP litter (Val Behan-Pelletier, personal communication). Specialist and generalist predators also responded to edge habitat and plant species in different ways. Specialist predator and parasitoid abundance was greater in SP relative to SA, but not affected by habitat edges. In contrast, generalist predator abundance was not affected by plant species or habitat edges, but we did find an interaction between plant species and edge habitat whereby generalist predator abundance declined along the SA edge relative to the interior, but did not change along the habitat edge in SP. Thus, responses differed by trophic group and we did not find an “edge-biased distribution” (Nguyen and Nansen 2018) either for overall arthropod abundance, or for any arthropod group; when arthropods responded to habitat edges, they were more likely to exhibit declines rather than increases.

While species richness did not vary across habitats, the species that composed the community were different among habitat types. Arthropod community composition differed not only between the interiors of both habitats, but also between the edges. This may partially explain why we did not find a significant difference in arthropod species richness across habitats; arthropods found primarily in one habitat do not spill-over to the adjacent habitat, particularly if they are dietary or habitat specialists (also see Cronin and Haynes 2004). The species that drove these differences between SA and SP (in both edge and interior habitats) were primarily specialized herbivores found either in SP (*T. minuta* and *D. detecta*) or SA (*P. dolus*, *Prokelisia* nymphs, *D. penedetector*), as well as a detritivorous oribatid mite (*Diapterobates* sp.) in SP. Similarly, previous studies on dung beetles have found stronger edge responses in specialists relative to generalists (Peyras et al. 2013). Furthermore, while we did not find differences in the arthropod community between SA interior and SA edge habitats, we did find such differences in SP. These differences in the

arthropod community between the SP interior and SP edge habitats were driven by specialist herbivores (*T. minuta* and *D. detecta*) as well as the detritivorous oribatid mite, *Diapterobates* sp. Thus, the heightened response to habitat type and habitat edges displayed by specialists drove the overall compositional responses. This highlights the importance of using diet and habitat specialization as a mechanism to understand species responses to habitat edges, similar to previous studies that have found different edge sensitivities among specialists and generalists (Peyras et al. 2013; Frost et al. 2015). Importantly, the arthropod community with the strongest response to habitat edges was in SP, which is also the grass that has become increasingly fragmented due to its sensitivity to sea level rise (Nyman et al. 1993; Donnelly and Bertness 2001), and thus has an increasing edge-to-interior ratio.

Importantly, we found changes in arthropod composition among habitat types across all feeding groups. Herbivore composition was different not only between the interior of SA and SP, but also between the edges of these habitats. Furthermore, herbivore composition in SP differed between the interior and edge habitats. The herbivore edge responses we found were primarily driven by SP specialists, and we found negative edge responses in the dominant SP herbivores previously (Wimp et al. 2011), possibly due to the fact that these specialists have trouble relocating the proper host plant if they venture too far into the adjacent habitat. Thus, the idea that herbivore specialists are likely to be strongly impacted by habitat edges seems to be substantiated in our study, as also suggested by Bagchi et al. (2018). Similarly, the composition of epigeic feeders differed between both the interior of SA and SP, as well as SA and SP edge habitats. This pattern likely has to do with the fact that algal and detrital resources are quite different among SA and SP. Filamentous algal resources are greater in SA due to tidal influx (Sullivan and Currin 2000), while SP has a thick, persistent layer of thatch that provides consistent detrital resources (Denno et al. 1996). Generalist predator composition differed not only between the interior of SA and SP, but also between SA and SP edge habitats. Interestingly, generalist predator composition differed between SA interior and edge habitats, which is the opposite pattern relative to herbivores that differed between SP interior and edge habitats. This pattern for generalist predators is driven by web-building spiders that are found predominantly

in the interior of SA habitat, and show a strong, consistent negative response to the SA edge. Even though web-building spiders can feed on both grazing and epigeic prey (Wimp et al. 2013), they need the coarse, upright culm structure found in SA in order to provide scaffolding for web attachment (Döbel et al. 1990; Wimp et al. 2019). Finally, the composition of specialist predators and parasitoids differed between both the interior of SA and SP, and along SA and SP edge habitats, which is not surprising since these predators and parasitoids track specialist herbivores that are habitat-specific. Notably, the composition of specialist predators and parasitoids also differed between the interior and edge of SP, similar to the herbivores found in this habitat. Thus, while generalist predators showed the opposite edge response pattern relative to herbivores, specialist predators and parasitoids tracked their SP prey. Such differential responses by specialists and generalists have also been found in previous studies of arthropod predators (e.g., Frost et al. 2015).

Overall, the changes in arthropod composition we found could be explained by resource and habitat specialization. The herbivores in our system were largely specialists, and their specificity to either SA or SP led to compositional shifts in the dominant group of herbivores on the different grass species. Similarly, the specialist predators and parasitoids that fed on these herbivores mapped to their prey distribution. While generalist predators can feed on diverse prey, it was notable that the extreme habitat specialization by web-building spiders drove the compositional shifts in this group even though they are not dietary specialists. Perhaps the most surprising result is the high habitat specificity of epigeic feeders. While many of these species can feed on both algae and detritus, the species that drove compositional patterns were oribatid mites that fed on SP fungus. While it has often been difficult to predict arthropod community responses to habitat edges, here we demonstrate that dietary and habitat specialization, a topic insect ecologists have examined for decades (e.g. Ehrlich and Raven 1964, Futuyama and Moreno 1988; Mooney et al. 2012; Vidal and Murphy 2018), can help us understand the mechanisms driving arthropod community responses to habitat edges, and make sense of seemingly disparate results. Moreover, viewing arthropod responses to habitat edges through the lens of dietary and habitat specialization may also help unify edge studies in

natural and managed systems. For example, extreme diet and habitat specialization in the naturally fragmented salt marsh led to compositional shifts in the overall community with relatively little spillover, whereas the “edge-biased distribution” often found in managed systems may be driven by generalist pest species (Nguyen and Nansen 2018).

Previous studies speculated that habitat edges could restructure communities and here we demonstrate that edges do indeed change community composition via differential responses by species with different resource requirement (Fagan et al. 1999; Ries et al. 2004; Ries and Sisk 2004; Ewers and Didham 2006; Ries and Sisk 2008; Peyras et al. 2013). Among the many functional traits that likely affect edge responses (e.g. dispersal ability, hunting mode; Galle et al. 2020), understanding whether a species is a habitat or dietary specialist is essential to make predictions about its response to a habitat edge (Wimp et al. 2011, 2019, Bagchi 2018). Biodiversity losses due to habitat fragmentation are primarily caused by edge effects (Fletcher et al. 2007), and our results suggest that these declines in biodiversity from edge effects will not be random but will be driven by specialization and resource use. Furthermore, any declines of specialist species could lead to dramatic declines in biodiversity. For example, previous studies have found that specialists comprise roughly 90% of insect herbivore species (Forister et al. 2015); thus, the negative impacts of habitat edges on this group could lead to overall biodiversity losses. Further, we found that the arthropod community with the strongest edge response resided in SP, which is the grass that is also most threatened by habitat fragmentation and sea level rise (Nyman et al. 1993; Donnelly and Bertness 2001), suggesting that SP specialists will be the first to be lost in the face of global change. Insects, which are the dominant group of animals on earth, may be undergoing massive declines referred to by some authors as the “insect apocalypse” (Hallmann et al. 2017, Sanchez-Bayo and Wyckhuys 2019, van Klink et al. 2020; but see Thomas et al. 2019, Willig et al. 2019). Managing habitats in ways that reduce the impact of edge effects could be a way to prevent declines of arthropods, which play key roles in ecosystem function.

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