ABSTRACT

Title of Document: CRITICAL PATCH SIZES AND THE SPATIAL STRUCTURE OF SALT MARSH COMMUNITIES.

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The size, connectivity, and quality of habitat patches can have multifaceted impacts on species and communities. In this dissertation, I combined a multi-year field survey, manipulative field experiments, and a literature review to investigate how spatial structure influences species and their trophic interactions in fragmented habitats. For all empirical work, I used as a study system the arthropod assemblage found on patches of the salt marsh grass *Spartina patens*.

In **Chapter 1**, I conducted seven surveys of habitat patches over three years to examine the effects of patch size, connectivity, and local environmental conditions on a guild of specialist sap-feeding herbivorous insects and their natural enemies. I found striking differences among species in the effects of both patch size and connectivity, which led to differences in species' relative abundances and trophic structure among these patches. In **Chapter 2**, I manipulated host plant quality and

predator density to experimentally examine mechanisms that might structure this arthropod community. I found that positive responses of herbivores to experimentally-elevated patch quality were limited by dispersal constraints and that predation by abundant generalist spiders may constrain the spatial distribution of certain species.

Investigating systems beyond the marsh, I conducted a literature review and analysis in **Chapter 3** wherein I examined whether the spatial structure of habitats generally influences trophic interactions. From the literature, I identified 171 studies of trophic interactions in fragmented habitats and found that the influence of fragmentation and related variables on the occurrence or strength of trophic interactions was largely predictable based on the habitat affinity of interacting species. With this dataset, I also identified key gaps in the fragmentation literature, including a heavy bias towards the study of two-species interactions. Therefore, in **Chapter 4** I took advantage of my data from the salt marsh to identify how, in addition to the two-species interactions of parasitism and egg predation, more complex food web interactions might depend on variation in the size of habitat patches.

Overall, my findings show that variation in patch size can have varied, but predictable, effects on patch occupancy, population density, and interactions between species in fragmented habitats.

CRITICAL PATCH SIZES AND THE SPATIAL STRUCTURE OF SALT MARSH COMMUNITIES

By

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Dissertation submitted to the Faculty of the Graduate School of the
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Dedication

I dedicate this work to two men who inspired me

to work hard, seek learning, and appreciate all things great and small,

my grandfather William Johnson,

and my mentor, Bob Denno.

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I would like to thank many people and organizations that have helped me along the way and without whom this work would not be possible. First, I am fortunate to have had the distinct pleasure of coming to the University of Maryland to work with Bob Denno and Bill Fagan as my co-advisors. They were the two guiding voices through the years of developing this project, and I am sincerely grateful for their mentoring and for helping me develop as a scientist and critical thinker. I am deeply saddened by Bob's passing mid-way through my dissertation, but I will never forget all I learned from him or his joy for life, even in its most drizzly forms.

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good friends. I'd like to thank all the Faganites, especially: Justin Calabrese, Frances Sheller, Leslie Ries, Heather Lynch, James Gilbert, Chris Che-Castaldo, Evan Grant, Elise Larsen, Paula Cassanovas, Sarah Kingston, Sara Zeigler, and Elise Zipkin. All the Denno-ites: Ian Kaplan, Danny Lewis, Rachel Goeriz Pearson, Jes Hines, Gina Wimp, and Shannon Murphy, with special thanks to the latter three for help with arduous field work after an injury.

I want to especially thank my parents, who have always been supportive of my dreams and goals, even when that means I spend a lot of time shin-deep in muck. And most of all, I want to thank my wonderful husband, James Phongsuwan, whose constant love, support, and good humor have buoyed me throughout my graduate work and who stuck with me despite some of our first 'dates' being to the marsh. A special thanks also to our dog, Maggie, who stayed patiently by my side as I wrote this dissertation.

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Introduction

The size, connectivity, and quality of habitat patches can have multifaceted impacts on species and communities. Species' ecological traits, such as trophic position, dispersal ability, body size, and habitat specificity, may mediate the effects of patch size and connectivity such that species respond differently to spatial heterogeneity in the same landscape. Additionally, although spatial structure may be of great importance in patchy or fragmented systems, the quality of the local environment can impact the probability of patch occupancy and the density of individuals on a patch. In this dissertation, I investigate how patch size, connectivity, and quality impact species and their interactions, using field studies of arthropods on patches of salt marsh grass and a literature review of trophic interactions in fragmented habitats. In Chapter 1, I identify patterns of patch occupancy and population density among species that depend on patch size, connectivity, and local patch quality and lead to changes in trophic structure across patches. In Chapter 2, I investigate the mechanisms that might lead to such patterns through manipulative field experiments. I examine the generality and predictability of how spatial structure may impact trophic interactions through a literature review and analysis in Chapter 3, and investigate the impact of patch size on the occurrence and strength of specific trophic interactions in the salt marsh in Chapter 4.

I decided to study the differential effects of patch size, connectivity, and quality across species of salt marsh arthropods inhabiting patches of the high marsh grass *Spartina patens* for several reasons. Mid-Atlantic intertidal marshes are characterized by extensive meadows of *Spartina alterniflora* punctuated by discrete patches of *S. patens* at higher elevations. At my study site in Tuckerton, New Jersey, the two *Spartina* grasses dominate the landscape, with few other plant species present and little mixing between them. Because both the patches and the matrix in which they are embedded are monocultures, I eliminated, to a great extent, the often confounding effects of matrix quality and within-patch vegetation diversity.

Assemblages of insect herbivores and specialist predators on each *Spartina* grass are mutually exclusive. On *S. patens*, a guild of six phloem-feeding plant- and leaf- hoppers are the dominant herbivores. These species, like many herbivorous insects, are wing dimorphic, with a characteristic proportion of macropterous (long winged and flight capable) and brachypterous (short winged and flightless) adults in a population. Natural enemies of these species include specialist egg predators and parasitoids as well as hunting spiders. Therefore, species in this system vary in trophic position, wing morphology, and body size, and any differences among species in response to patch size and connectivity can be interpreted in relation to these traits. Studies of the effects of patch size and connectivity on occupancy and population densities rarely investigate differential effects among species and across multiple trophic levels.

Although simple density-patch size relationships were previously investigated among these species, major questions remain unanswered, such as the influence of patch connectivity and local site characteristics on population densities, the effects of patch size and connectivity on patch occupancy, and the emergent effects on trophic structure. Additionally, the mechanisms leading to such patterns are rarely investigated in any field system, and the relative simplicity of this system, combined with the knowledge of the natural history of these species, made it an ideal system with which to test competing hypotheses about structuring mechanisms. This work continues decades of basic ecological research in this model ecological system and may provide insight into the impacts of the habitat destruction that threatens many coastal marshes. Because many other habitats are either naturally patchy or become fragmented due to anthropogenic influences, the processes we identify here may find broader application in understanding the effects of spatial structure on other species and food webs.

I conducted replicated surveys of habitat patches over three years to address the hypothesis that species respond to variation in patch size and connectivity depending on their ecological traits (Chapter 1). Such differences among species have largely been compared across systems, and rarely have a suite of herbivorous species and the predators with which they interact been investigated in the same system. With logistic regressions, I tested whether species differed in occupancy-patch size relationships and determined the patch sizes required for the occurrence of species in this system. Such critical patch sizes may differ systematically among species based on trophic position and may be a useful index of the relative sensitivity of species to changes in patch size. I examined whether species also differed in density-patch size relationships, as predicted by theory, and investigated how such variability may scale up to impact species' relative abundances and trophic structure.

The mechanisms underlying the spatial structure of populations and communities can include local factors such as abiotic conditions, resource quality, and trophic interactions, as well as spatial factors, such as movement between patches and effects of patch size. Seldom are such factors experimentally manipulated in a field system to investigate the relative importance of different mechanisms or how mechanisms might interact to influence population density across patches. In Chapter 2, I addressed several potential mechanisms underlying the metacommunity structure of salt marsh arthropods. I examined how dispersal may structure this arthropod assemblage with a defaunation experiment, in which I manually removed all arthropods from small patches and from plots within large patches in order to investigate colonization patterns among species. Due to the high absolute and relative abundance of spiders on small patches, I next manipulated spider densities in field enclosures to test whether high predation levels on small patches might contribute to the consistent pattern of lower prey population densities on small patches. I investigated predation pressure on the most abundant herbivore as well as its specialist egg predator to determine the relative sensitivity of these species to spider predation. Using stable isotope analysis, I also investigated whether generalist spiders feed disproportionately on different types of prey on small and large patches.

That patch size can influence food web interactions has been observed by other authors in a widely-scattered literature on the effects of habitat fragmentation on trophic interactions. However, generalities on whether trophic interactions are more likely to be lost or gained in fragmented habitats are still lacking. I thus undertook a literature review of trophic interactions in fragmented habitats, presented in Chapter 3. In this study, I investigated how fragmentation has been shown to impact species interactions and tested the prediction that, as for single species, the habitat affinity of interacting species may be a major determinant of whether a trophic interaction will occur more or less frequently in fragmented habitats. I identified the ways in which patch scale (patch size, patch connectivity, and distance from an edge) and landscape scale (fragmentation per se, proportion habitat in the landscape) factors may impact trophic interactions involving habitat specialists and habitat generalists differently and examine whether results from studies in the literature were consistent with these predictions.

A distinguishing feature of the studies found by this review was that most studies were conducted on trophic interactions involving only two species. More complex food web modules, or sets of interacting species, were scarcely studied, despite their frequency in real food webs. Based on the natural history of species in the salt marsh, I next investigated how the occurrence and strength of trophic interactions might vary with patch size among salt marsh arthropods. Thus, as a step towards understanding the complex ways in which spatial structure and habitat fragmentation may influence biological systems, I examined how the critical patch size concept might be applied not only to individual species but to entire food web modules in patchy habitats.

Chapter 1: Differential effects of patch size and connectivity in a salt marsh arthropod metacommunity

Co-authored with: *W. F. Fagan and R. F. Denno*

Abstract

The size and connectivity of habitat patches can influence patterns of species occupancy and population density. Species may differ, however, in the direction or strength of these relationships due to variation in trophic position, habitat affinity, movement ability, body size, and other ecological traits. Additionally, while spatial structure may be of great importance in patchy or fragmented systems, the quality of the local environment can also influence populations of species on those patches. In this study, we examined the effects of patch size, connectivity, and local environmental conditions on a guild of sap-feeding herbivores and their natural enemies occupying patches of the salt marsh grass *Spartina patens*. From seven surveys of habitat patches over three years, we found striking differences among species in the patterns of patch occupancy, leading to variation in the threshold patch size and connectivity required for a high probability of occurrence. Population density also varied among species and between trophic levels, such that species' relative abundances and the ratios of predators to prey were also functions of patch size, connectivity, or the interaction between patch size and connectivity. More generally, we demonstrate that even among taxonomically-similar species feeding on the same resources, density-area and density-connectivity relationships differed greatly and were related to the suite of ecological traits that characterize these species.

We conclude that this arthropod assemblage can best be described as a metacommunity and discuss how variation among species in response to spatial and local characteristics of the landscape might impact trophic interactions on the marsh.

Introduction

Island biogeographic and metapopulation theories are classic frameworks for investigations of how species richness and patch occupancy are influenced by island or patch size and isolation (MacArthur and Wilson 1967, Levins 1969, Hanski 1994). In addition to focusing on patch characteristics, advances in metapopulation theory have found that species may differ in patch occupancy requirements based on their movement ability (Hanski 1994), trophic position (Holt 1996), diet breadth (van Nouhuys and Hanski 2002), and susceptibility to variation in patch quality (Thomas et al. 2001). Together, the two theories predict that small and isolated islands or patches have fewer overall species and a lower probability of patch occupancy, leading to "critical patch sizes" in which certain patches may be too small or isolated for birth and immigration rates to compensate for high mortality or emigration (Kierstead and Slobodkin 1953, Ludwig et al. 1979, Cantrell and Cosner 1994, 2001a).

In addition to patch occupancy, population density can also vary with patch size (Bowers and Matter 1997, Bender et al. 1998, Connor et al. 2000, Hambäck and Englund 2005). Several ecological theories have made predictions about the sign of such a density-area relationship (DAR). The classical resource concentration hypothesis of Root (1973) predicts positive density-area relationships, inspired by observations of higher densities of host-specific insect herbivores in monocultures rather than polycultures. Several mechanisms are hypothesized to account for such a positive DAR, including high colonization or low emigration rates on large patches, and a higher diversity or abundance of natural enemies on smaller patches (Root 1973). In contrast, negative density-area relationships are predicted based on certain patch-locating behaviors, such as when the rate that individuals encounter patches is proportional to their edge to area ratio or when individuals otherwise have imperfect knowledge of the full patch network (Schooley and Wiens 2005 and references therein). Lastly, the passive sampling hypothesis (Haila et al. 1993, Bowers and Matter 1997) presumes that patches receive colonists from a regional pool proportional to their sizes and predicts no systematic variation in the density-area relationship. A recent contribution by Hambäck and Englund (2005) demonstrated theoretically that the full range of density-patch size relationships are possible based on differences in movement mechanisms among species (see also Hambäck et al. 2007).

Although theory predicts the sign of the DAR slope, the strength of this relationship might also vary among species and spatially within a metacommunity due to such factors as patch size, connectivity, and patch quality. For example, variation in resource quality can be very important in determining the distribution and abundance of insect herbivores (Awmack and Leather 2002) and has been incorporated into models of metapopulation dynamics, with varying success (Moilanen and Hanski 1998, Thomas et al. 2001). The physical structure of the habitat, such as vegetation density or three-dimensional structure, can also impact microclimate and trophic interactions within a patch (Langellotto and Denno 2004).

In this study, we examined whether patch size, connectivity, and local habitat characteristics influenced patch occupancy and population density for a guild of sap-feeding herbivores and their natural enemies. Using three years of arthropod surveys across patches of the salt marsh grass *Spartina patens*, we tested the hypothesis that patch occupancy is an increasing function of patch size and that species at higher trophic levels are more sensitive to such spatial heterogeneity than their herbivorous prey. We then tested the extent to which local factors also influenced density across patches and investigated the degree to which the impact of patch size and connectivity may be predictable based on species' ecological traits. Finally, we examined whether patterns based on single species responses might lead to systematic differences in trophic structure across patches.

We selected this salt marsh study system of host plants and arthropods for several reasons. First, because both the patches and the matrix in which they are embedded are monocultures, we eliminated, to the greatest extent possible in a natural system, the often confounding effects of matrix quality and within-patch vegetation diversity (Ewers and Didham 2006). Second, species in this system vary in trophic position, wing morphology, and body size, and any differences in responses among species can be interpreted in relation to these traits. Third, although simple density – patch size relationships were previously investigated among these species (Raupp and Denno 1979, Denno 1981, Hines et al. 2005), major questions remain unanswered, such as the influence of patch connectivity and local site characteristics on DARs, the effects of patch size and connectivity on patch occupancy, and the emergent effects on trophic structure.

Methods

Study System

We conducted this study on an extensive marsh in the Mullica River–Great Bay estuarine system in Tuckerton Township, Ocean County, New Jersey, USA. Mid-Atlantic marshes are characterized by extensive meadows of *Spartina alterniflora* (SA) punctuated by discrete patches of *S. patens* (SP) at higher elevations (Blum 1968, Denno 1980). At this study site, the two *Spartina* grasses dominate the landscape, with few other plant species present and little mixing between them. Assemblages of insect herbivores and specialist predators on each *Spartina* grass are mutually exclusive (Denno 1977). On SP, a guild of six phloem-feeding plant- and leaf- hoppers are the dominant herbivores (Denno 1980; Table 1.1). These species, like many herbivorous insects (Denno 1994), are wing dimorphic, with a characteristic proportion of macropterous (long winged and flight capable) and brachypterous (short winged and flightless) adults in a population. Natural enemies of these species include the specialists *Tytthus alboornatus*, an egg predator, and the parasitoid *Haplogonatopus sp.* (Hines et al. 2005, Chapter 4), as well as abundant generalist spiders (Döbel et al. 1990). We selected two spider species for this investigation, the habitat generalist *Pardosa littoralis* and the habitat specialist *Thanatus striatus* (Döbel et al. 1990), as they represent ends on the continuum of habitat specificity, were both abundant enough for statistical analysis, and are reliably identifiable as juveniles and adults in our samples.

Spatial Characteristics

We surveyed all accessible patches of SP at this study site with a handheld global positioning device (Garmin GPS 72 model). Patch size and orientation were recorded in the field, and all data were imported into an ArcView Geographic Information System (ArcView GIS 3.3). Inaccessible patches were identified on a 1 m^2 resolution aerial photograph (USGS digital orthophoto quadrangle) and manually digitized. While measures of patch isolation that are simply based on the distance to the nearest patch can be descriptive, these measures are rarely realistic enough to make adequate predictions of patch occupancy (Moilanen and Nieminen 2002). Composite scores of patch connectivity, or the inverse of isolation, can provide much more biological realism and predictability by incorporating the area and distance of potential donor patches to a focal patch. We therefore used a modified measure of connectivity derived from incidence function models (Hanski 1994). This measure is a patch-level connectivity measure, $S_i = \sum_{j}^{n} A_j \exp(-\alpha d_{ij})$, where *i* is the focal patch and d_{ij} is the distance between patch *i* and any other patch *j*. In this measure, the potential for colonists from patch *j* is a negative exponential function of the distance between the patches and is weighted by the size of patch *j*. Thus large and nearby patches contribute most to total patch connectivity. A dispersal parameter, α, governs the steepness of the exponential function. Among species in this system, actual levels and mechanisms of dispersal are unknown. Given the scale of patchiness, we selected the value of $\alpha = 0.1$ for this study, representing an average dispersal distance of 10 m. S_i calculated with alternative values of α within a reasonable range of average dispersal distances (1 – 20 m) were highly correlated with S_i for 10 m dispersal. We then log-transformed this IFM connectivity measure to improve the distribution of values across patches. Although this measure is much more biologically realistic than assuming all potential dispersal originates from a patch's nearest neighbor (Moilanen and Nieminen 2002), because we do not have measures of actual dispersal ability this measure should be considered one of relative, not absolute, connectivity.

Local Patch Characteristics

We measured total above ground live and dead biomass and grass culm density for each patch, harvesting all material within one randomly placed 0.047 m^2 quadrat frame per patch (Wiegert 1962, Denno et al. 2002). Additionally, we collected 10 – 20 culms of SP from the centers of these patches at the peak of plant biomass in 2005 to assess plant nitrogen and carbon content. Each of these local factors is hypothesized to influence population densities on a patch. In combination with the density of culms, the three-dimensional structure of the habitat may vary greatly across patches. The amount of dead grass, or thatch, at a site can be an important factor mediating trophic interactions (Finke and Denno 2002, Langellotto and Denno 2004). In SP, thatch can build up for up to 7 years and the layer can be up to 20 cm thick (Blum 1968, Denno 1980). Additionally, as insect herbivores are often N-limited (Mattson 1980, Awmack and Leather 2002, Huberty and Denno 2006), we expect that plants with higher %N may support higher densities of herbivores. We thus use these three factors (culm density, thatch biomass, and %N) as potentially important local factors (Table 2). As the elevation of the marsh surface is fundamental in determining where SP can occur, we also measured relative elevation among patches using the dissolution of plaster casts by tidal inundation (Agrandi and Hood 1998, Gratton and Denno 2005). We placed plaster casts in the centers of patches for 45 days, then transported them to the lab, and rinsed them gently of dirt. After air-drying, we weighed the casts and used the proportion of initial plaster remaining as the measure of elevation.

Arthropod Sampling

We sampled arthropods three times per year from the centers of SP patches in 2004 (n = 60 patches) and twice in 2005 (n = 62) and 2006 (n = 62) with a D-Vac insect suction sampler with a 0.031 m^2 sampling nozzle (D-Vac, Ventura, California, USA). Slight differences in patch numbers over the years were due to the encroachment of SA into several small patches after 2004; these patches were replaced with others. Overall, 55 patches were sampled for all 7 dates; for multivoltine herbivore species, this sampling effort can span up to six generations (Denno 1980). Arthropods were killed with ethyl acetate, transferred to 70% ethanol, and sorted in the lab.

Statistical Analysis

All statistical tests were conducted in R (version 2.8.1; R Development Core Team 2008), with packages specified below.

Patch occupancy as a function of patch size and connectivity

We first examined whether patch occupancy of adults differed between species as a function of patch size and connectivity. We used repeated measures multiple logistic regression, with the presence of a species on a patch as the response variable, and species, $\log_{10}$ transformed patch size (hereafter, patch size), $\log_{10}$ transformed connectivity (hereafter, connectivity), and all two- and three-way interactions as explanatory variables, specifying date and site as random factors (lmer function in the lme4 package in R, Bates et al. 2008). We tested the significance of model terms with likelihood ratio tests, comparing models with and without the specific term of interest. This repeated measures analysis incorporates information on patch occupancy from all 7 sample dates. We conducted a second multiple logistic regression with the same explanatory variables but with a more conservative response variable. For this second analysis, we considered a species to occupy a patch if it was ever observed on the patch through the duration of the study (we refer to this as the 'Any Date' model).

Because of species differences in the relationships between patch size, connectivity, and patch occupancy (see Results), we next modeled the occupancy of single species with multiple logistic regression and used the parameters from significant models to investigate whether critical patch sizes or levels of connectivity are required for these species. From the logit transformation, $ln\left(\frac{p}{1-p}\right) = \beta_0 + \beta_1 X$, we calculated the patch size threshold, X, that would be required for a probability, p, of 0.9 for the occurrence of a given species, a value that has been used elsewhere to quantify relative sensitivity of insect species in fragmented habitats (Kruess and Tscharntke 2000).

We investigated whether differences among species in occupancy – patch size relationships were predictable based on any of the known ecological traits in Table 1.1. We used a derived variable approach (p 475, Crawley 2007), calculating a summary statistic and using this as the response in a subsequent linear model. For each species, this summary variable was the repeated measures estimates of the slope of the occupancy-patch size relationship, as this parameter, β_1, governs the steepness of the relationship and was available for all 9 of the patch-restricted species. We used stepwise multiple regression to test whether this occupancy-patch size relationship depended on species' trophic position, body size, and wing morphology and retained the most parsimonious model based on AIC values.

Finally, we tested whether patch size or connectivity influenced the consistency of patch occupancy through time. We used generalized linear models with binomial errors to examine whether patch size or connectivity significantly influenced the proportion of total surveys a patch was occupied by each species. Seven survey dates were available for 8 of the 10 species; four survey dates were available for *T. striatus* and *Haplogonatopus sp.* Only models without overdispersion were considered to have adequate goodness of fit (Crawley 2007).

Population density as a function of spatial and local factors

For an analogous comparison with the presence-absence data, we next evaluated whether species differed in density – patch size and density – connectivity relationships, first testing the full model of density as a function of patch size x connectivity x species, with the random effects of site and date (lmer package). We evaluated model terms, from most to least complex, with likelihood ratios tests and retained terms if their interactions were significant.

To understand how spatial (patch size, connectivity, elevation) and local (culm density, thatch, and %N) variation influenced population density among species, we used the response variable "time-averaged density," the average density of a species across all surveys. We used this time-averaged density for the multiple regression analysis for the following reasons: 1) phenology throughout the season and differences among years led to wide variation among dates, and we were most interested in the overall effects of each potential explanatory variable, regardless of sample date, 2) the resulting time-averaged density variable was well-distributed without transformation with respect to potential explanatory variables, leading to more easily interpretable results, and 3) with these data, we were able to employ a stepwise model selection approach to iteratively test the importance of each term. We used maximum likelihood multiple regression models, specifying first a full model and reducing based on a backwards stepwise technique that removes and tests each term iteratively and selects the most parsimonious model that does not lead to increases in model AIC (stepAIC, package MASS, Venables and Ripley 2002). The full model specified for each species was a linear model of time-averaged density as a function of the additive effects of patch size, connectivity, elevation, thatch, culm density, %N, and the interaction between patch size and connectivity. We chose to use the backwards selection technique to simplify models because we had *a priori* hypotheses for the importance of each term in the full model.

We also investigated how species' relative abundances within a trophic level varied with patch size and connectivity, using the time-averaged species densities and categorical levels of patch size and connectivity. We categorized patches smaller than the median patch size as small and those more isolated than the median connectivity value to be far (as in Cronin et al. 2004). We next constructed contingency tables with spatial categories as columns (small-far, small-near, large-far, large-near) and species within a trophic category as rows, and populated the table with the species' mean density for that category. Because species differed in relative abundance, we asked whether variation in mean species' density differed among categories compared to each species' average density across categories, using a log-likelihood ratio test of homogeneity for each trophic level separately (g.test function in R, author Peter Hurd; Sokal and Rohlf 2003). This approach is analogous to that used by Mikkelson (1993) to compare species richness among trophic levels in fragmented habitats. To illustrate differences in relative abundance for each trophic level separately, we plotted the proportional density of each species (time-averaged density of species / total time-averaged density of species in the trophic level) against patch size and connectivity categories.

Effects of patch size and connectivity on trophic structure

To understand how overall trophic structure might vary based on patch size and connectivity, we employed two techniques. First, we compared whether the total average herbivore load (the sum of the time-averaged densities across species) was a function of patch size and connectivity and if it differed from that of natural enemies (summed across 4 species). Because we expected that the only habitat generalist, *P. littoralis*, might respond differently to patch size and connectivity, we conducted this trophic-level density comparison with and without *P. littoralis* data. Second, we calculated specific predator to prey ratios to investigate how spatial factors might influence the potential for trophic interactions. Eggs of the dominant herbivore, *T. minuta*, are fed upon by the specialist mesopredator *T. alboornatus*, and both are likely prey of *P. littoralis* (see Chapter 4). We therefore calculated the predator: prey ratio for each of the three predator: prey combinations to investigate how the trophic context in which species are engaged might vary with patch size and connectivity. We square-root transformed these ratios to improve homogeneity of variance. We used repeated measures analysis of variance, with size, connectivity, and their interaction as fixed factors, and patch and date as random effects.

Results

Spatial Characteristics

We identified 634 patches of *Spartina patens* (SP) at the field site in Tuckerton, NJ. Most patches were small, with a median size of 8.07 m^2 (range: 0.014 to 40,032 m^2; Figure 1.1 A). Most patches were also close to other patches, with a median interpatch distance of 3.28 m and a range between 0.13 and 307.5 m. The incidence function measure of connectivity ($\log_{10}$ transformed) ranged from -22.7 to 10.6, with a median of 5.4 (Figure 1.1B). Patch size and connectivity were slightly positively correlated in this full set of patches (Pearson's correlation, r = 0.081, t = 2.033, P = 0.042; Figure 1.1 C).

We randomly selected 65 of these patches that were accessible by foot for repeated surveys of the arthropod community, and patch size and connectivity among this subset were uncorrelated (r = 0.021, t = 0.25, P = 0.80; Figure 1.1C). Sampled patches spanned nearly the entire range of patch sizes and levels of connectivity compared to the entire set of patches (Figure 1.1; Table 1.2). Among sampled patches, connectivity and log-transformed nearest neighbor distance between patches were negatively correlated ($r = -0.488$, $P < 0.0001$). Because of the strong collinearity between these variables and because it is more biologically meaningful to incorporate the potential influence of patches beyond the single nearest patch, we used connectivity in all subsequent analyses.

Patch occupancy as a function of patch size and connectivity

The effect of patch size and connectivity on patch occupancy differed among species, with a significant three-way interaction between species, patch size, and patch connectivity in the repeated measures logistic regression model (Likelihood ratio test, LRT, for interaction: $\chi^2 = 19.48$, df = 9, $P = 0.021$). To better understand these results and to address whether species required critical patch sizes or levels of connectivity, we used multiple logistic regressions for each species, with date and patch as random factors. With the repeated measures analysis, we found a consistent and positive influence of patch size on patch occupancy for 9 of the 10 species (Figure 1.2; Appendix A). The probability of occupancy increased with increasing patch size for all herbivores (Figure 1.2 A). Likewise, for all three patch-restricted natural enemies (*T. alboornatus, Haplogonatopus sp.,* and *T. striatus*), the probability of patch occupancy increased with patch size (Figure 1.2 B), whereas the patch occupancy of the habitat generalist spider *P. littoralis* was unrelated to patch size, as this species was ubiquitous across patches (Figure 1.2 B top line). Patch occupancy was also significantly and positively influenced by patch connectivity for three of the six herbivores (*A. simplex, D. detecta,* and *T. minuta*; Fig. 1.2 C, bold lines) and the patch-restricted spider *T. striatus* (Fig. 1.2 D, bold line).

Using parameter estimates from repeated measures logistic regressions, we found that species differed greatly in the patch sizes required for 90% probability of occupancy (Figure 1.3 A, Appendix A). The parasitoid *Haplogonatopus sp.* ("Ha" in Figure 1.3 A) was predicted to require patches of 86.8 m^2 for 90% probability of patch occupancy. In contrast, patch size requirements for the patch-restricted egg predator, *T. alboornatus* ("Ta"), were far less restrictive; this species is predicted to occur on patches as small as 0.6 m^2. Of the four species for which patch connectivity was a significant predictor of patch occupancy (Figure 1.3 B), the herbivore *A. simplex* ("As") was predicted to require high patch connectivity for 90% probability of patch occupancy, and the spider *T. striatus* also required well-connected patches. Although significant, *D. detecta* ("Dd") and *T. minuta* ("Tm") are predicted to only require minimal connectivity for patch occupancy. Using the more restrictive 'All Dates' dataset, defining as occupied those patches on which we observed a species at any point during our surveys, patch size was a significant predictor of patch occupancy for each of the three patch-restricted predators (*Haplogonatopus sp.*, *T. striatus*, and *T. alboornatus*) and two of the herbivores (*A. simplex* and *Am. simplex*; Figure 1.3 A, open symbols). The herbivore *A. simplex* was the only species for which patch connectivity was a significant predictor of patch occupancy with the more conservative dataset (Figure 1.3 B, open symbol). Additionally, this species was the only one for which there was a significant interaction between patch size and connectivity for patch occupancy (LRT for interaction, $\chi^2 = 5.52$, df = 1, P = 0.019).

Several ecological traits differ among these species (Table 1.1). To investigate which of these traits might explain the variation in patch size – occupancy relationships, we regressed the slope parameter for patch size from the repeated measures analysis on the traits body mass, trophic position, and the proportion of mobile individuals in a population. For this analysis, we excluded data for *P. littoralis* because the regression for this species was not significant and because the remaining species were all patch-restricted species. Through backwards stepwise regression, we found that of these traits, only trophic position was significant. Thus, natural enemies had steeper patch size – occupancy slopes than herbivores (predators: 2.079 ± 0.437 (SE), herbivores: 1.255 ± 0.134; ANOVA: $F_{1,7} = 5.636$, $P = 0.0493$, $R^2 = 0.45$).

The proportion of surveys in which a species was observed on a patch also varied among species and as a function of patch size. For the herbivore *D. detecta,* the proportion of surveys during which a patch was occupied increased with both patch size and connectivity (size: $P < 0.0001$; connectivity: $P = 0.001$), and for *M. lobatus* with patch size ($P < 0.0001$). Although the proportion of surveys occupied increased with patch size for other species, overdispersion led to poor model fit.

Population density as a function of spatial and local factors

Population density varied greatly among patches and species (Figure 1.4 A, B). Density was significantly influenced by patch size, species, connectivity, and the interactions between species and connectivity ($\chi^2 = 29.474$, df = 9, $P < 0.001$) and between species and patch size ($\chi^2 = 110.8$, df = 9, $P < 0.0001$). We subsequently examined, as for occupancy relationships, the simple relationship between density and the factors patch size and connectivity (Table 1.3). The most abundant herbivore, *T. minuta*, exhibited the steepest relationship between density and patch size, while density-patch size relationships were not significant for *M. lobatus* or *D. bisignata* (Table 1.3; Figure 1.4 A, thin lines for individual species). Additionally, although the herbivore *A. simplex* was observed to have the largest patch size requirement among herbivores for patch occupancy, the density of this species was only significantly related to patch connectivity in the analysis for density (Table 1.3). Among predators, each of the patch-restricted species exhibited a strong positive relationship between patch size and density, whereas *P. littoralis* declined slightly with increasing patch size. Connectivity significantly and positively influenced densities of *P. littoralis* and *T. striatus* (Table 1.3). As with the occupancy data, we tested which traits best predicted the slope of the density-area relationship using backwards selection, and found a significant negative relationship between DAR and body size ($F_{1,8} = 6.90$, $P = 0.03$; $R^2 = 0.46$). Unlike the occupancy data, however, we did not find differences in DAR estimated from the repeated measures analysis based on trophic position ($F = 0.13$, $P = 0.73$), regardless of the inclusion of *P. littoralis*.

Species differed greatly in the importance of local factors in a multiple regression using time-averaged densities (Table 1.4). Patch size was an important variable in multiple regressions for 9 of the 10 species (plotted in Figure 4 A, B), and connectivity for 8 species, and density was significantly influenced by a patch size x connectivity interaction for 5 species (Table 1.4). Within the guild of sap-feeding herbivores, we discovered several notable differences in the relationship between explanatory variables and average population density. Patch size, connectivity, the amount of thatch, and the interaction between patch size and connectivity were important for both *T. minuta* and *D. detecta*. The percent nitrogen in SP was positively related to the densities of *A. simplex*, *D. bisignata*, and *Am. simplex*, and culm density was important for the latter species as well. Notably, *D. bisignata* density was negatively influenced by patch connectivity, and patch size was not found to be important for this species in the multiple regression.

The densities of natural enemies were also differentially influenced by the set of explanatory variables (Table 1.4). For each of the three patch-restricted natural enemies, patch size and elevation were significant variables. Density of the spider *T. striatus* was significantly influenced by patch connectivity and the interaction between patch size and connectivity. In contrast, the density of the habitat generalist spider *P. littoralis* was lower on larger patches, higher on well-connected patches, and not influenced by any other measured variable.

Effects of patch size and connectivity on trophic structure

Overall herbivore density increased significantly with patch size (simple linear regression, $F_{1,42} = 16.07$, $P = 0.00024$, $R^2 = 0.28$; Figure 1.4 A bold line), whereas the total density of natural enemies increased slightly with patch connectivity (simple linear regression, $F_{1,42} = 9.03$, $P = 0.0045$, $R^2 = 0.18$; Figure 1.4 B bold line). Considering only the patch-restricted species, total natural enemy density was a strongly increasing function of patch size ($F_{1,42} = 29.98$, $P < 0.0001$, $R^2 = 0.42$). The total density of patch-restricted natural enemies also increased more steeply with patch size than did that of herbivores (trophic level x patch size interaction, $\chi^2 = 16.26$, $P = 0.0001$). Herbivores had a significantly higher intercept (2.28 vs. 1.27) and a significantly shallower slope (0.11 vs. 0.37) than these patch-restricted predators.

The relative abundance of species also differed based on patch size and connectivity both for herbivores and predators (Figure 1.4 C, D). We found that the relative abundance of species differed among categories of patch size and connectivity (log-likelihood ratio test of homogeneity across categories for herbivores: $G = 39.26$, $df = 15$, $P = 0.000587$; predators: $G = 96.87$, $df = 9$, $P < 0.0001$). Most notably, *T. minuta* decreased and *M. lobatus* increased in relative abundance on small compared to large patches. For predators, *P. littoralis* comprised 85% of all predatory individuals on small, isolated patches and only 61% on large, well-connected patches.

Considering the three species for which specific trophic interactions are known (see Methods), we found that the ratios of predator density to prey density varied based on patch size. Single species analysis with categorical classifications of patch size and connectivity corresponded to that of the continuous variables (Table 1.4; Figure 1.5 left panels; A) *T. minuta* effect of size $\chi^2 = 19.57$, $P < 0.0001$; B) *T. alboornatus,* size $\chi^2 = 23.30$, $P < 0.0001$; C) *P. littoralis,* connectivity $\chi^2 = 7.00$, $P = 0.0083$). We found that the ratio of mesopredators to herbivores (*T. alboornatus: T. minuta*) was higher on large patches (Figure 1.5 B; square-root transformed, removing fixed effect of size, $\chi^2 = 15.64$, $P < 0.0001$; connectivity $\chi^2 = 0.72$, $P = 0.39$), but the ratio of generalist spiders to herbivores (*P. littoralis: T. minuta*) *was* not different based on size or connectivity (Figure 1.5 D; size $\chi^2 = 0.61$, $P = 0.43$; connectivity $\chi^2 = 0.88$, $P = 0.35$). In contrast, the mesopredator faced much higher densities of its primary predator (*P. littoralis: T. alboornatus*) on small patches (Figure 1.5 F; size $\chi^2 = 14.86$, $P = 0.00012$), with a non-significant trend towards a higher ratio on patches of low connectivity (connectivity $\chi^2 = 2.13$, $P = 0.14$).

Discussion

In this study, we examined the effects of patch size, connectivity, and local environmental conditions on a guild of sap-feeding herbivores and their natural enemies. We found striking differences among species in the patterns of patch occupancy (Figure 1.2) and density (Figure 1.4) both within and between trophic levels, such that the overall density of individuals among trophic levels (Figure 1.4 A, B), species' relative abundances (Figure 1.4 C, D), and predator-prey ratios (Figure 1.5) were also functions of patch size, connectivity, or the interaction between patch size and connectivity. This study builds upon previous work with several of these species (Raupp and Denno 1979, Denno 1980, Hines et al. 2005) by specifically addressing the role of patch connectivity, by quantifying critical patch size and connectivity thresholds for occupancy, and by characterizing the impact of patch size and connectivity on trophic structure. More generally, we demonstrated that even among taxonomically-similar species feeding on the same resource and on patches relatively well-connected (Table 1.2), density-area and density-connectivity relationships differed greatly and were related to the suite of ecological traits that characterize these species.

Patch occupancy and critical thresholds

Patch occupancy is predicted to increase with patch size for species in fragmented habitats (Hanski 1994). We discovered positive occupancy – patch size relationships among all of the patch-restricted species in this study (Figure 1.2). The strength of these relationships and the importance of patch connectivity for occupancy, however, differed greatly among species. Patch occupancy increased with patch size for each of the six sap-feeding herbivore species (Figure 1.2A), as expected for specialist consumers (Ewers and Didham 2006). For two of these species, *Aphelonema simplex* and *Amplicephalus simplex*, the logistic regression was significant even when we used the 'Any Date' response variable, which captured the occurrence of the species at any time during our seven surveys across three years (Figure 1.3, Appendix A). We estimated that *Aphelonema simplex* required patches of 28.1 m^2 for 90% probability of occurrence, using the repeated measures logistic regression. Considering as well the connectivity requirements estimated for this species and the distribution of patches in this system (Figure 1.1), we estimate that this species is only likely to be found with 90% probability on 19% of all patches on the marsh. In contrast, *Am. simplex*, the herbivore with the second-largest patch size requirements, would be likely to be found on 83% of SP patches based on its area requirements. Of the natural enemies, *Haplogonatopus sp.* was the rarest of the 10 species considered here and required the largest patch sizes for 90% probability of occupancy. This threshold level likely restricts this parasitoid to only the largest 25% of the patches on the marsh. The spider *T. striatus* would also only be predicted to occur with high probability on 49% of all patches.

Density-area and density-connectivity relationships

Our findings for density-area and density-connectivity relationships among these species largely parallel those from the logistic regressions for occupancy data. We found substantial variation among species for the strength of the relationship between patch size and density (Figure 1.4 A, B). Differences among species within a trophic level also led to variation in the relative abundance of different species as a function of patch size and connectivity (Figure 1.4 C, D). For herbivores, the most abundant species overall (*T. minuta*) declined greatly in relative abundance on small and isolated patches, where, instead, the herbivore *M. lobatus* was dominant (Figure 1.4 C). Predator relative abundance was also strongly influenced by patch size and connectivity, with *P. littoralis* comprising 85% of predator individuals on small patches, and both the relative abundance and absolute densities of the other three species strongly depressed on small patches (Figure 1.4 B, D).

In the context of multiple regressions to find the best explanatory model for each species, we found that, again, patch size, connectivity, and their interaction were significant for many of the species investigated here (Table 1.4). The importance of local factors differed among species, however, with at least one local factor (%N, thatch, culm density) important in final models for 5 of 6 herbivores. Local factors were only important for one natural enemy species (Table 1.4). Stoner and Joern (2004, see also Tscharntke and Brandl 2004) noted that herbivores may be more influenced by local habitat condition and natural enemies by spatial factors due to the higher sensitivity of herbivores to variation in resources. Consistent with those studies, local factors were relatively more important for herbivores than for natural enemies in the current study (Table 1.4), and patch occupancy of natural enemies was more sensitive to patch size than that of herbivores (Figure 1.2 B), although notably, spatial structure was important across both trophic levels in our study (Table 1.4).

Among herbivores, only densities of the leafhopper *D. bisignata* were unaffected by patch size (Table 1.4). This species also had one of the smaller patch size requirements for occupancy from the logistic regression analyses (Figure 1.3). For this species, we found evidence that factors such as %N, amount of thatch, and patch elevation were more important than patch size for determining population density. Because of its higher potential dispersal ability (Table 1.1), *D. bisignata* might be able to select the best quality patches and be less constrained by habitat structure than other, less mobile species. In the matrix habitat on the marsh, mobility allowed the planthopper *Prokelisia marginata* to colonize experimentally fertilized plots of *Spartina alterniflora* much faster than did the brachypterous *P. dolus* (Denno et al. 2002). Likewise, the ability of species to sort to their optimal environments in space is predicted only for those species of sufficient dispersal ability (species sorting perspective of metacommunities; Leibold et al. 2004)

The best model for *Pardosa littoralis* also differed from those of other species, with significant but negative effects of patch size and significant positive connectivity effects. This species is nearly ubiquitous on the marsh (Figure 1.2 B; Döbel et al. 1990, Lewis and Denno 2009) and was not expected to respond to patch size and connectivity in the same manner as the other species; however, the negative impact of patch size was unexpected. This species is well-known to feed on prey in

S. alterniflora, and Lewis and Denno (2009) recently demonstrated that seasonality impacts the movement of this species from SP into SA. However, movement through the season is an unlikely explanation of our findings, as patch size was uncorrelated with connectivity among patches in our study. The adjacency of multiple habitats can provide important access to complementary resources for habitat generalists (Ries et al. 2004). Higher densities on small patches might afford *P. littoralis* access to prey in both habitats but protection from cannibalism in the densely-thatched SP patches (Finke and Denno 2002). In a similar system of arthropods on patches of host grass, Cronin et al. (2004) also found higher densities of spiders on small patches, and proposed that access to multiple habitats led to the spider build-up. Such high densities of predators on small patches is also one of the predictions behind the resource concentration hypothesis (Root 1973), and may be an important mechanism structuring the SP community (see below).

Species traits

Theoretical studies of multitrophic interactions in patchy or fragmented systems predict that predators should be more sensitive to declines in patch size or connectivity than their prey, as they depend sequentially on the presence of lower trophic levels for patch occupancy (Holt 1996). Aside from the nearly ubiquitous *P. littoralis*, natural enemies were more sensitive to variation in patch size than herbivores and exhibited steeper occupancy – patch size relationships (Figure 2B). Indeed, from the suite of traits tested, only trophic position was significantly related to the value of these parameters. Thus our results are consistent with predictions from food web models (Holt 1996) and fragmentation theory (Bender et al. 1998, Henle et al. 2004, Ewers and Didham 2006) and with empirical findings from other studies of arthropods in patchy or fragmented habitats (Kruess and Tscharntke 1994, 2000, Komonen et al. 2000, van Nouhuys 2005). Among patch-restricted species, the importance of trophic level in the relationship between patch size and occupancy thus seems to be a widespread phenomenon.

Within trophic levels, we had predicted that the proportion of flight-capable individuals in a population might impact occupancy-patch size relationships and explain variation among species. However, the variation we observed among species did not systematically depend on wing morphology, and the most (*A. simplex*) and the least (*T. minuta*) sensitive herbivores to patch size, in terms of critical patch size predictions and regression parameters, were both brachypterous (< 1% macroptery); the second most sensitive species (by patch size requirements; *Am. simplex*) was the only fully macropterous species in this study (see Table 1.1). In contrast, DAR slopes were significantly and negatively related to body size among these species. Our findings are consistent with those of Roland and Taylor (1999), who found that parasitoids responded to the spatial structure of fragmented forests according to their body size. Likewise, in a study of Lepidoptera in fragmented habitats, Hambäck et al. (2007) found that, although the densities of large species were relatively insensitive to patch size, small species exhibited steep DAR slopes. They suggested that smaller species were dispersal-limited and unable to effectively colonize all patches in the landscape. Other studies of species traits in fragmented habitats, however, have suggested that larger species may be more, not less, sensitive to fragmentation, due to presumed correlations with abundance, trophic level, and habitat use, although this prediction was largely driven by studies of mammals (reviewed in Henle et al. 2004, Ewers and Didham 2006). In our study, body size was not systematically correlated with trophic level, habitat affinity, or abundance, and the smallest species may be strongly movement-limited regardless of wing morphology due to the scale of the patches in which it resides. As we only investigated 10 species, however, the overall importance of body size will have to be tested among a greater range of species.

Trophic changes and the spatial structure of the Spartina patens *arthropod community*

Patch size effects on individual species led to emergent effects on trophic structure, such that the trophic context in which a species resided depended on the spatial structure of the habitat. Large patches were characterized by higher densities of both herbivores and patch-restricted predators compared to small patches, but these predators had both lower intercepts and steeper DAR slopes than did the herbivores (Figure 1.4 A, B). The difference in the response of the generalist predator *P. littoralis* compared to those of patch-restricted natural enemies led to changes in the ratios of predators to prey across patches that may shed light on mechanisms underlying the patterns we observed in this study. First, because of the steep DAR for the mesopredator *T. alboornatus*, the herbivore *T. minuta* faced relatively higher densities of these specialist predators on large patches (Figure 1.5 B). On the other hand, the reduction of mesopredators and the increase in density of *P. littoralis* on small patches resulted in a higher ratio of *P. littoralis* to *T. alboornatus* on small patches (Figure 1.5 F), and we cannot reject the hypothesis that predation may indeed limit prey populations on small patches.

The predation hypothesis of Root (1973) posits that herbivore densities are lower in heterogeneous habitats due to increased predator density or diversity. In our study, however, the effect of predators, if any, is likely to be on mesopredators, not herbivores, as the ratio of predators to herbivores was either higher on large patches (*T. alboornatus: T. minuta*) or not different based on patch size (*P. littoralis: T. minuta*). In other systems, low densities of natural enemies on small patches or in fragmented habitats led to herbivore outbreaks (Kruess and Tscharntke 1994, Roland and Taylor 1997). In light of strong effects of patch connectivity on herbivore densities, we expect that dispersal limitation likely prevents such outbreaks in our system.

Most patches of SP on this landscape are small, although most of the total habitat is found in large patches. Furthermore, because species differ in patch occupancy in relation to patch size and connectivity, we expect that this system can be described as a metacommunity on a mainland-island patch network. Metacommunities are sets of local communities connected at least somewhat by dispersal (Wilson 1992, Leibold et al. 2004, Holyoak et al. 2005). We have documented here that species differ in occupancy and density in relation to both patch size and connectivity. We also found that patch occupancy was more consistent through time on large than small patches for at least two of the species, and that empty but suitable patches therefore exist in the landscape. Small and isolated patches therefore have higher turnover of species and an altered community structure compared to large patches. Such variation in patch occupancy within and between trophic levels and changes in the ratios of predators to prey indicate that not only single species but also their trophic interactions might depend on patch size in this system.

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Tables

Table 1.1. Ecological traits of the 10 focal species. Data are from Denno 1980. Trophic position was assigned as herbivore (plant-feeding) or natural enemy (predators and parasitoids). Habitat affinity: *Spartina patens* (SP) and *S. alterniflora* (SA). Body size is given as dry mass (mg). Prop. Mobile: the proportion of macropterous (long-winged) individuals.

Species	Family	Trophic Position	Habitat affinity	Body size (mg)	Prop. Mobile
Tumidagena minuta	Delphacidae	herbivore	SP	0.15	0.01
Aphelonema simplex	Issidae	herbivore	SP	0.68	0.01
Megamelus lobatus	Delphacidae	herbivore	SP[1]	0.25	0.03
Delphacodes detecta	Delphacidae	herbivore	SP	0.3	0.14
Destria bisignata	Cicadellidae	herbivore	SP	0.34	0.5
Amplicephalus simplex	Cicadellidae	herbivore	SP	0.78	1
Tytthus alboornatus	Miridae	natural enemy	SP	0.15	0.01
Pardosa littoralis	Lycosidae	natural enemy	SP, SA	1.58	1[2]
Thanatus striatus	Philodromidae	natural enemy	SP	0.47	1[2]
Haplogonatopus sp.	Dryinidae	natural enemy	SP	0.2	0

Notes: [1] The habitat affinity of *M. lobatus* is questionable due to the presence of a sister species in *S. alterniflora* indistinguishable from the morph in SP (G. Wimp personal communication). [2] For the purposes of comparison, spiders were considered to be fully mobile.

Table 1.2. Local and spatial variables included in multiple regressions of population densities of arthropods on patches of the salt marsh grass *Spartina patens* (SP). Local factors were measured with quadrat samples of above-ground biomass, and patch size and connectivity were determined with field measurements and GIS. Patch connectivity was calculated with a modified incidence function model (IFM) measure that incorporates the sizes of all patches weighed by their distance from a focal patch. Data presented are for the 65 sampled patches.

Characteristics	Measurements	Mean (min., max.)
Local Factors		
Host plant density	# culms / quadrat	337 (146, 916)
Thatch biomass	dead plant biomass (g)	34.2 (6.5, 99.5)
Percent N of live plants	%N of live culms	1.29 (0.95, 2.15)
Spatial Factors		
Patch size	continuous SP cover	m^2: 285 (0.29, 5679)
		$\log_{10}m^2$: 1.26 (-0.53, 3.75)
Patch connectivity	log IFM measure	4.99 (-3.86, 8.35)
Elevation	% initial plaster remaining	80.73 (48.29, 96.40)

Notes: Patch size descriptive statistics are provided for interpretation; $\log_{10}m^2$ was used for all analyses.

Table 1.3. Repeated measures estimates of the simple effects of patch size ($\log_{10}$ m^2) and connectivity ($\log_{10}$ IFM connectivity measure) on population density across species, with date and patch as random effects. The significance of each term was evaluated with likelihood ratio tests (LRT). Bold font indicates significant models at the $P < 0.05$ level.

	Patch Size				Connectivity			
Species	Estimate	SE	LRT	P-value	Estimate	SE	LRT	P-value
Amplicephalus simplex	1.49	2.32	0.41	0.52	-0.80	0.94	0.71	0.40
Aphelonema simplex	1.95	1.38	1.96	0.16	1.13	0.55	4.03	**0.045**
Delphacodes detecta	13.48	3.20	15.39	**< 0.0001**	1.08	1.50	0.51	0.47
Destria bisignata	6.68	3.35	3.84	0.050	-0.46	1.40	0.11	0.74
Haplogonatopus sp.	1.18	0.32	11.29	**0.00078**	0.067	0.15	0.19	0.66
Megamelus lobatus	-6.16	9.93	0.38	0.55	-0.30	4.07	0.0053	0.94
Pardosa littoralis	-20.77	12.04	2.89	0.089	14.51	4.65	8.96	**0.0028**
Thanatus striatus	5.54	1.34	14.85	**0.00012**	1.78	0.58	8.74	**0.0031**
Tumidagena minuta	44.82	8.84	20.98	**< 0.0001**	6.85	3.72	0.00	1.00
Tytthus alboornatus	36.5	6.40	25.28	**< 0.0001**	1.94	3.31	0.34	0.56

Table 1.4. Multiple regression for time-averaged population density for 10 species. After specifying the full model with each variable included (columns), terms were removed with backwards stepwise selection. Terms were iteratively tested for inclusion in the model, and included terms were retained based on AIC criteria. Presented are parameter estimates (and standard errors) for all retained terms in final models for each species.

Species	Patch size (log$_{10}$m^2)	Connectivity (log$_{10}$IFM)	Elevation (proportion plaster remaining)	%N	Thatch (g)	Culm Density (#/m^2)	Patch Size x Connectivity	R2	F (df)	P-value
T. minuta	88.9 (30.87)	12.87 (5.95)			0.79 (0.51)		-9.41 (5.51)	0.48	9.25 (4, 39)	< 0.0001
Aph. simplex	2.11 (0.99)	0.98 (0.40)		14.55 (4.90)				0.30	5.82 (3,40)	0.0021
M. lobatus	28.66 (17.37)	5.37 (3.49)	-1.18 (0.50)				-5.09 (3.12)	0.15	1.75 (4, 39)	0.16
D. detecta	27.31 (10.62)	4.10 (2.05)			0.29 (0.18)		-3.76 (1.90)	0.34	5.01 (4, 39)	0.0024
D. bisignata		-2.42 (1.25)	1.13 (0.33)	39.23 (15.08)	0.36 (0.17)			0.43	7.48 (4, 39)	0.00014
Am. simplex	12.56 (6.89)	1.88 (1.29)	-0.89 (0.20)	17.34 (10.38)		0.022 (0.012)	-1.71 (1.24)	0.46	5.22 (6, 37)	0.00056
T. alboornatus	36.64 (6.75)		0.99 (0.63)					0.47	18.36 (2, 41)	< 0.0001
Haplogonatopus sp.	0.98 (0.30)		0.068 (0.029)			0.0029 (0.0019)		0.38	9.03 (3, 44)	< 0.0001
T. striatus	-7.36 (4.30)	-0.68 (0.91)	0.21 (0.13)				2.73 (0.79)	.60	16.02 (4, 43)	< 0.0001
P. littoralis	-24.03 (12.52)	14.40 (5.13)						.22	5.67 (2, 41)	0.0067

Figure Legends

Figure 1.1. Distribution of sizes (A) and levels of connectivity (B) of patches of the high marsh grass *Spartina patens* (SP) at the field site in Tuckerton, New Jersey. Sampled patches (dashed lines, black marks on the horizontal axes; n = 65) were a randomly selected subset of all available patches (solid lines, gray marks; n = 634). Patch size (in m^2) was measured via field surveys and from digitized aerial photographs and was $\log_{10}$ transformed for all analyses. Patch connectivity was assessed as a modified incidence function connectivity metric (see Methods), which was also $\log_{10}$ transformed prior to analysis. C) Sampled patches (black symbols) and all patches (gray symbols) with respect to patch size and connectivity.

Figure 1.2. Fitted probabilities of patch occupancy for six herbivorous (A, C) and four predaceous (B, D) species commonly found in SP habitat. Plotted are generalized linear model estimates with binomial error structure for patch occupancy as a function of $\log_{10}$ patch size (A, B) and $\log_{10}$ patch connectivity (C, D). Bold lines indicate significant models. Abbreviations: Tm: *Tumidagena minuta*; As: *Aphelonema simplex*; Ml: *Megamelus lobatus*; Dd: *Delphacodes detecta*; Db: *Destria bisignata*; Ams: *Amplicephalus simplex*; Ta: *Tytthus alboornatus*; Ha: *Haplogonatopus sp.*; Ts: *Thanatus striatus*; Pl: *Pardosa littoralis*.

Figure 1.3. Critical patch size (A) and connectivity (B) requirements across species. Parameter estimates from logistic regressions for each species were used to calculate the size or connectivity of a patch on which species would have 90% probability of

occurrence (refer to text for calculations). These parameters were estimated first with repeated measures logistic regression (black symbols) and second based on the occurrence of a species at any time during the seven surveys (open symbols, ‘Any Date’ model). The absence of a symbol indicates a non-significant model. Species are arranged from highest to lowest patch size or connectivity responses, and only significant relationships are depicted in (B). See abbreviations in Figure 1.2.

Figure 1.4. Density – patch size relationships among herbivores (A) and their predators (B). Data are time-averaged densities ($\log_{10}$ transformed # / m^2) for individual species (thin lines; abbreviations as in Figure 1.3) and the total time-averaged density of individuals within each trophic level (thick line, points). The effect of patch size and connectivity on relative abundance for C) herbivores and D) predators. Time-averaged densities for each species are plotted as the proportion of total density within the trophic level in stacked bar graphs. Patch size and connectivity categories are based on median values such that S = patches smaller than median patch size, L = patches larger than median, Far = patches with lower than median connectivity, Near = patches with higher than median connectivity. Abbreviations are as in Figure 1.2.

Figure 1.5. The effect of patch size and connectivity on densities of the dominant herbivore *T. minuta* (A), the most abundant mesopredator *T. alboornatus* (C), the hunting spider *P. littoralis* (E). The effect of patch size and connectivity on the ratio of predator density to prey density for B) *T. alboornatus: T. minuta*, D) *P. littoralis: T. minuta*, and F) *P. littoralis: T. minuta.* Patch size and connectivity categories as in Figure 1.4.

Figures

Figure 1.1

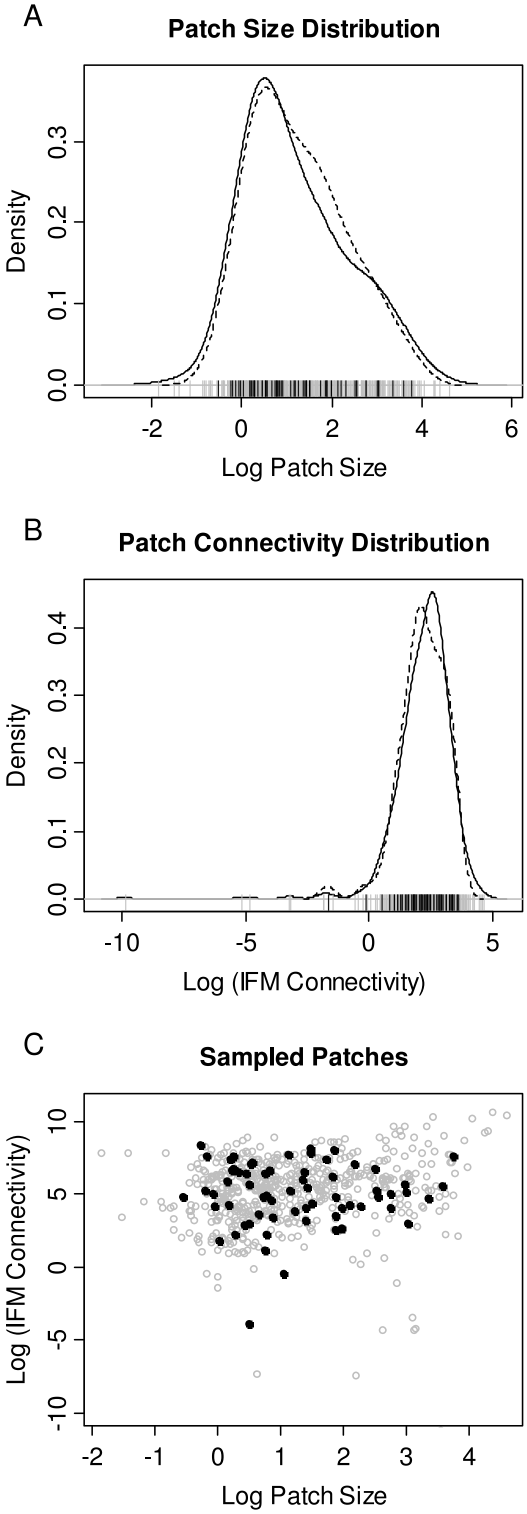


Figure 1.2

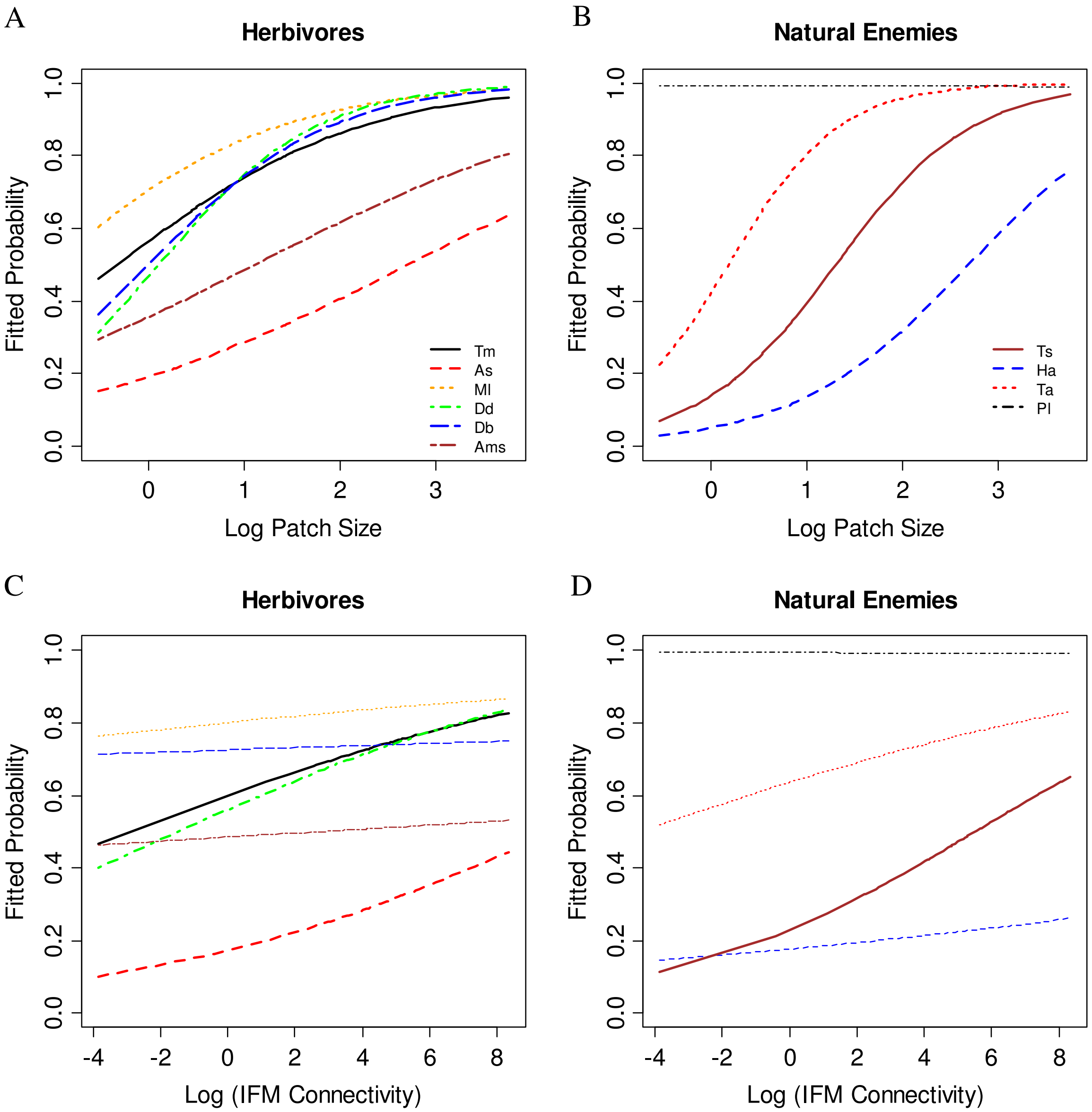

A
Herbivores
Fitted Probability
0.0
0.2
0.4
0.6
0.8
1.0
0
1
2
3
Log Patch Size
Tm
As
Ml
Dd
Db
Ams
B
Natural Enemies
Fitted Probability
0.0
0.2
0.4
0.6
0.8
1.0
0
1
2
3
Log Patch Size
Ts
Ha
Ta
Pl
C
Herbivores
Fitted Probability
0.0
0.2
0.4
0.6
0.8
1.0
-4
-2
0
2
4
6
8
Log (IFM Connectivity)
D
Natural Enemies
Fitted Probability
0.0
0.2
0.4
0.6
0.8
1.0
-4
-2
0
2
4
6
8
Log (IFM Connectivity)

Figure 1.3

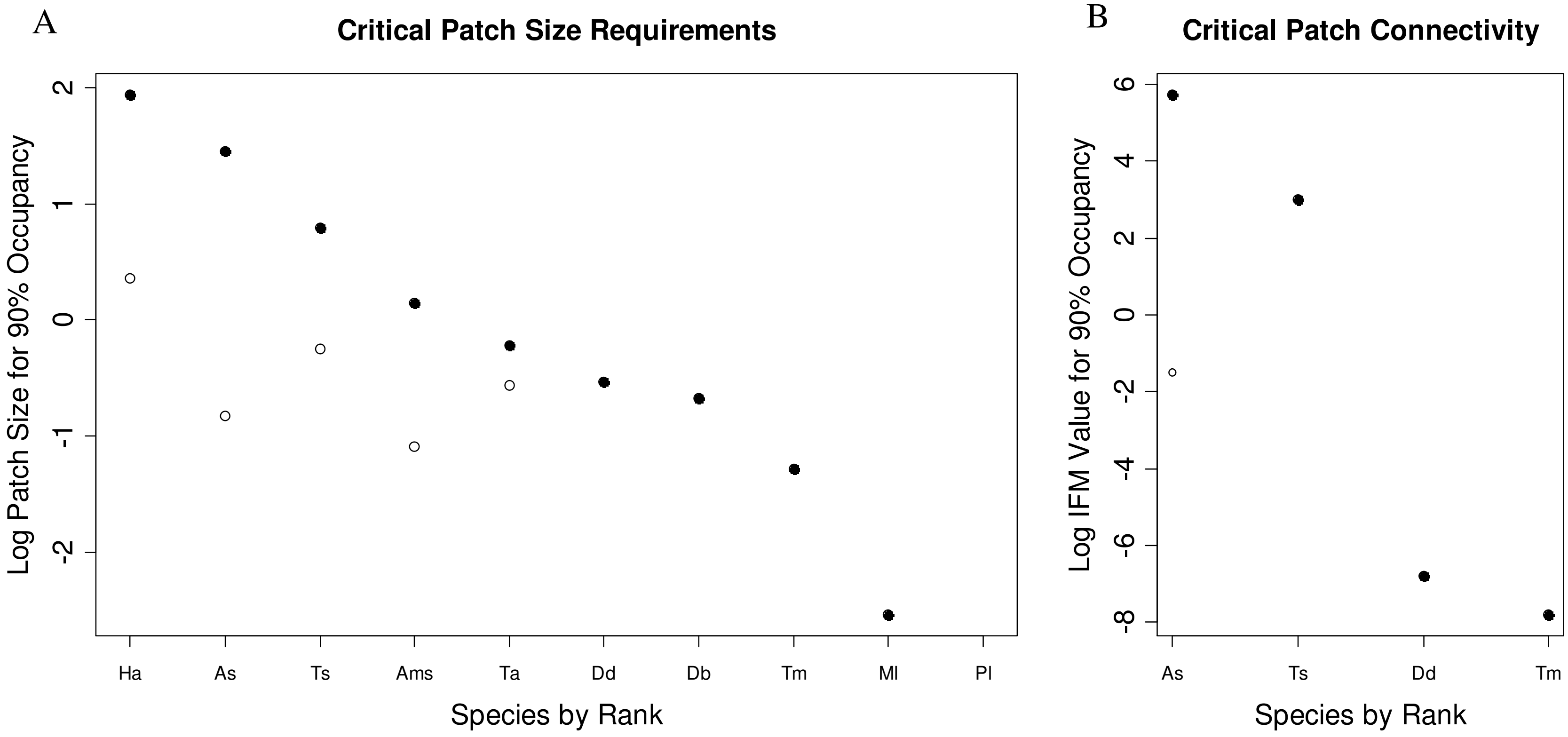

A
Critical Patch Size Requirements
Log Patch Size for 90% Occupancy
2
1
0
-1
-2
Ha
As
Ts
Ams
Ta
Dd
Db
Tm
Ml
Pl
Species by Rank
B
Critical Patch Connectivity
Log IFM Value for 90% Occupancy
6
4
2
0
-2
-4
-6
-8
As
Ts
Dd
Tm
Species by Rank

Figure 1.4

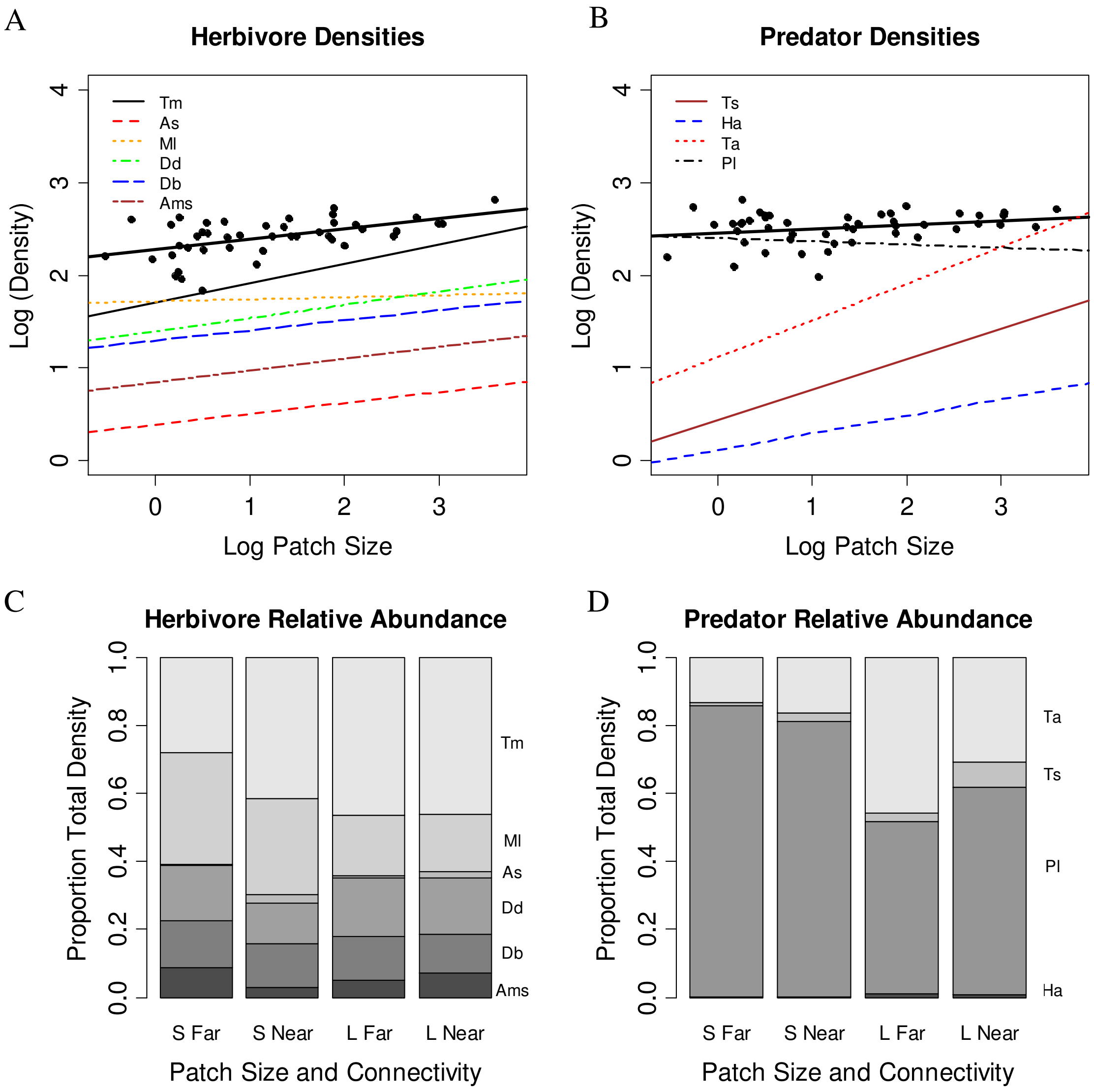
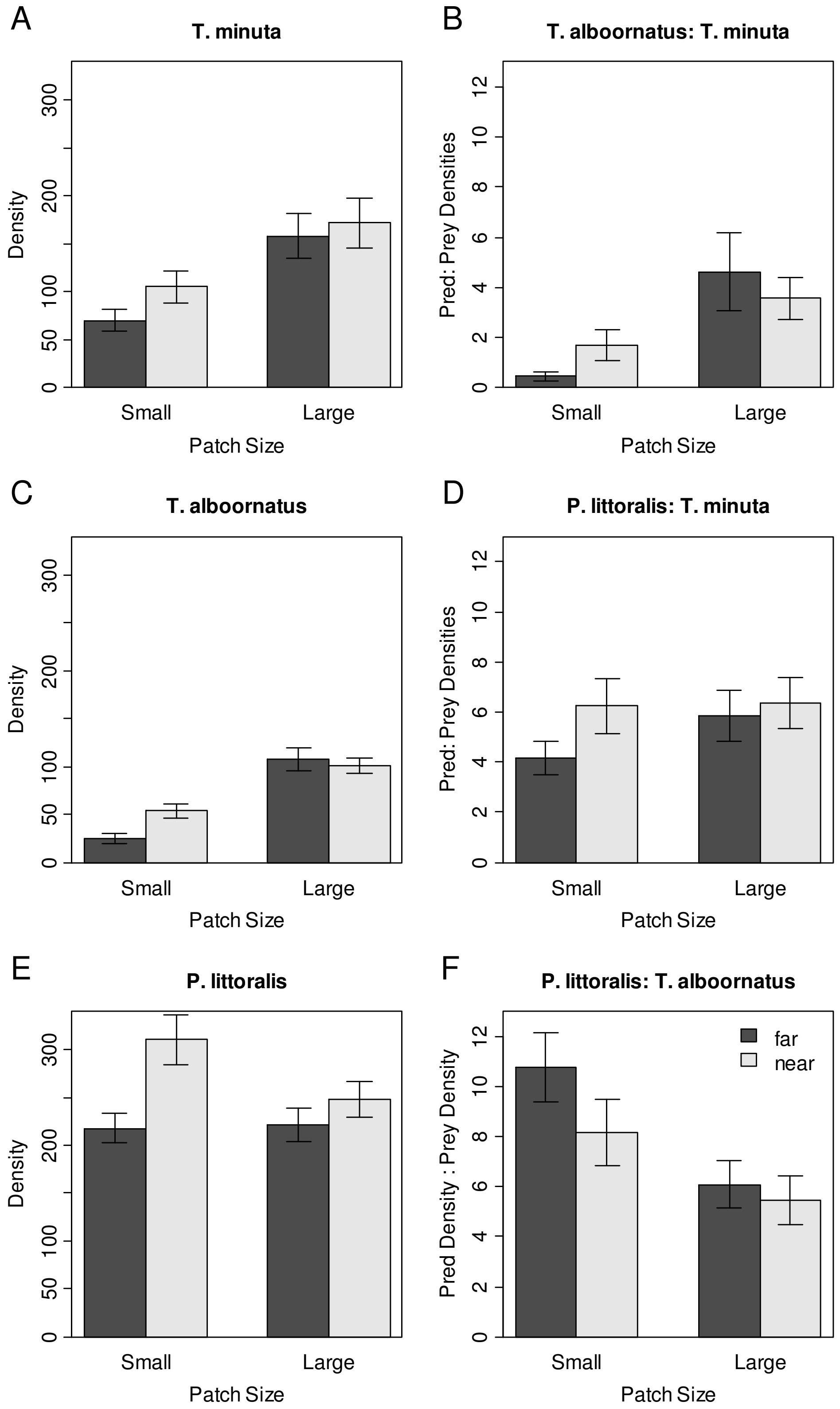

A
Herbivore Densities
Tm
As
Ml
Dd
Db
Ams
Log (Density)
0
1
2
3
4
0
1
2
3
Log Patch Size
B
Predator Densities
Ts
Ha
Ta
Pl
Log (Density)
0
1
2
3
4
0
1
2
3
Log Patch Size
C
Herbivore Relative Abundance
Proportion Total Density
0.0
0.2
0.4
0.6
0.8
1.0
Tm
Ml
As
Dd
Db
Ams
S Far
S Near
L Far
L Near
Patch Size and Connectivity
D
Predator Relative Abundance
Proportion Total Density
0.0
0.2
0.4
0.6
0.8
1.0
Ta
Ts
Pl
Ha
S Far
S Near
L Far
L Near
Patch Size and Connectivity

Figure 1.5


A
T. minuta
Density
0
50
100
200
300
Small
Large
Patch Size
B
T. alboornatus: T. minuta
Pred: Prey Densities
0
2
4
6
8
10
12
Small
Large
Patch Size
C
T. alboornatus
Density
0
50
100
200
300
Small
Large
Patch Size
D
P. littoralis: T. minuta
Pred: Prey Densities
0
2
4
6
8
10
12
Small
Large
Patch Size
E
P. littoralis
Density
0
50
100
200
300
Small
Large
Patch Size
F
P. littoralis: T. alboornatus
Pred Density : Prey Density
0
2
4
6
8
10
12
far
near
Small
Large
Patch Size

Chapter 2: Dispersal limitation mediates the importance of bottom-up and top-down effects in a salt marsh metacommunity

Co-authored with: *W. F. Fagan and R. F. Denno*

Abstract

The mechanisms underlying the spatial structure of populations and communities can include local factors such as abiotic conditions, resource quality, and trophic interactions, as well as spatial factors, such as movement between patches. Seldom are such factors experimentally manipulated in a field system to investigate the relative importance of different mechanisms or how these mechanisms might interact to influence population density across patches. In this study, we address several potential mechanisms underlying the metacommunity structure of salt marsh arthropods on patches of the grass *Spartina patens*. In response to manipulation of host plant quality, the density of most herbivores increased, but this positive response was attenuated on small patches, and most species colonized defaunated mainland plots much faster than they did even high quality small patches. In contrast, the habitat generalist spider *Pardosa littoralis* quickly colonized all vacant plots, and densities were highest on small patches. To examine the influence of the high absolute and relative abundance of this spider on small patches, we manipulated spider densities in field enclosures and found that only the mesopredator was sensitive to this spider addition. Using stable isotope analysis of field-collected spiders on small and large patches, we found that *P. littoralis* fed at a higher trophic

level on smaller patches, a result consistent with our hypothesis that this spider has disproportionate impact on other predators on small compared to large patches. Overall, this study demonstrates that both bottom up and top down effects are important in this system, but their effects are strongly mediated by dispersal limitation among patches.

Introduction

Studies of spatially subdivided populations and communities are receiving increasing attention due to habitat fragmentation and the recognition that many natural habitats are spatially structured (Saunders et al. 1991, Harrison and Bruna 1999, Hanski 1999, Fahrig 2003, Ewers and Didham 2006). Mechanisms leading to different patterns of patch occupancy (Hanski 1994), population density (Connor et al. 2000, Bender et al. 2004), and community composition (Tscharntke and Brandl 2004, Crist et al. 2006) among study systems involve variation in the relative importance of movement (immigration and emigration; Hanski 1994) and patch quality (birth and death rates; Pulliam 1988, Thomas and Kunin 1999). Metacommunity theory investigates this variation explicitly (Leibold et al. 2004), emphasizing different dynamics when communities are structured largely by colonization-extinction dynamics on patches of similar quality (patch dynamic perspective), by a combination of dispersal and local variation in patch quality or species interactions (species-sorting), by the impact of dispersal on local population densities (mass-effects), or by neutral dynamics (Leibold et al. 2004, Holyoak et al. 2005).

In empirical systems, the relative importance of local (resource quality, abiotic conditions, species interactions) and spatial (immigration, emigration) determinants of metacommunity structure have been investigated largely in the framework of multivariate statistics, where the variance in community composition is decomposed into spatial and environmental components (Cottenie et al. 2003, van de Meutter et al. 2007, van der Gacht et al. 2007). In a review of observational studies of community structure, Cottenie (2005) found widespread support for species sorting across environmental gradients as well as widespread dispersal constraints across patches. Within a community, however, different guilds or species may respond differently to variation in patch quality or be differentially sensitive to patch size (Connor et al. 2001, Crist et al. 2006, Hambäck et al. 2007). Although a particular metacommunity perspective may best describe a given system, guilds or species within guilds may also vary in the relative importance of spatial and local factors. For example, Crist et al. (2006) found that species richness, abundance, and within-guild species composition responded differently to the same manipulation of habitat structure and that certain species and guilds were more sensitive to spatial structure, whereas others responded largely to plant composition.

Recently, Gripenberg and Roslin (2007) emphasized the need to investigate how spatial structure might impact bottom-up or top-down forces and how these might in turn impact the distribution of species among patches of habitat. Experimental manipulations of habitat quality in spatially-structured populations, either from the bottom-up perspective of resource quality or from the top-down perspective of predation pressure, are rare (but see Cronin et al. 2004, Haynes et al.

2007), but can provide valuable insight into the mechanisms behind spatial community structure. In this study, we employ two field experiments and the use of stable isotopes to examine alternative mechanisms leading to spatial structure in an arthropod metacommunity. Herbivores and their specialist natural enemies found on patches of the salt marsh grass *Spartina patens* exhibit strong, though varied, responses to gradients in patch size, connectivity, and quality (Raupp and Denno 1979, Denno 1981, Hines et al. 2005, Chapter 1). Total densities of herbivores and specialist natural enemies increase with patch size, but natural enemies exhibit a stronger and steeper density- patch size relationship than do herbivores (Chapter 1). On the other hand, the density of the dominant and voracious habitat generalist spider, *Pardosa littoralis,* can be higher on small compared to large patches, leading to changes in predator: prey ratios that depend on patch size (Chapter 1).

In this study, we first examined overall movement rates of herbivores and natural enemies and their responses to augmented resource quality on small and large patches in a field experiment. Second, we tested whether abundant generalist predators might limit prey populations on small patches due to their high relative abundance, through the use of a spider manipulation experiment in the field. Finally, because of the stronger impact of these spiders on mesopredators rather than herbivores, we examined whether the trophic position of *P. littoralis* was a function of patch size through the use of stable isotopes. Collectively, these results suggest that both bottom up and top down effects are important in this system, but their effects are strongly mediated by dispersal limitation among patches.

Methods

Study System

This study was conducted on an extensive intertidal marsh in Tuckerton, NJ. *Spartina* grasses are spatially segregated on intertidal marshes (Redfield 1972), and, at this site, local elevation changes lead to a naturally patchy distribution of the high marsh grass *S. patens* (hereafter SP) within extensive meadows of the low marsh grass *S. alterniflora* (SA; Denno 1981, Hines et al. 2005). The primary consumers of live SP are sap-feeding herbivores of the families Delphacidae (*Tumidagena minuta, Delphacodes detecta,* and *Megamelus lobatus*), Issidae (*Aphelonema simplex*; abbreviated *A. simplex*), and Cicadellidae (*Destria bisignata* and *Amplicephalus simplex*; abbreviated *Am. simplex*; Raupp and Denno 1979, Denno 1980). These herbivores differ in the proportion of flight-capable individuals in a population (proportion macroptery), with three essentially flightless species (<3% macroptery: *T. minuta, M. lobatus,* and *A. simplex*), and three species with greater than 10% macroptery (14% macroptery: *D. detecta*, 50%: *D. bisignata*, and 100%: *Am. simplex*; see also Chapter 1). Natural enemies of these herbivores include the egg predator *Tytthus alboornatus* (Miridae), the parasitoid *Haplogonatopus sp.*, and several species of spiders (Döbel et al. 1990, Hines et al. 2005), including the patch-restricted philodromid *Thanatus striatus* and the habitat generalist *Pardosa littoralis* (Lycosidae). For the current study, we focus on the mechanisms driving spatial patterns in patch occupancy, density, and relative abundance among these ten species.

All arthropod samples for this study were collected with a D-Vac suction sampler (D-Vac, Ventura, California, USA) with 4 s placements of the 0.031 m^2

opening. Specimens were killed in ethyl acetate immediately. Arthropods for the defaunation and spider manipulation experiments were transferred to 70% ethanol; those collected for stable isotope work were immediately transported back to the lab on ice and stored at -20º C until processing. All arthropod counts were converted to densities to allow comparisons across sites and experiments.

All statistical tests were conducted with R (version 2.8.1; R Development Core Team 2008), with specific packages noted below.

Defaunation Experiment

We examined species' responses to manipulations of host plant quality and colonization ability with a defaunation experiment. We selected 36 small "island" patches (<10 m^2; mean: 2.6, range: 0.4 - 9.4 m^2) and 6 large "mainland" patches (> 100 m^2; mean = 2101 m^2, range: 141-8855 m^2). We selected patches using the following criteria: small island patches were selected to represent the range of distances from large patches that exist at the field site, while remaining distant from other small patches. Large patches nearby those small patches were then selected as mainland sites. We use the language of mainland and island here to represent the great difference in size between these categories and because we selected small patches for which the only predicted source of colonists was the nearby mainland patch. Due to the restriction of SP to high elevations on the marsh, patches are often distributed as archipelagoes of small patches nearby a large patch (Hines et al. 2005). Although not a complete block design, we considered separate archipelagoes as spatial blocks to account for shared local conditions among nearby patches.

This experiment is composed of two parts. First, we manipulated host plant quality with fertilizer and tested species' responses to fertilization and ability to make use of high quality host plants both on mainland and island sites. Second, we examined species colonization abilities by defaunating plots with repeated suctioning with the D-Vac. This allowed us to quantify colonization rates over time and how these rates depended on patch quality, patch size (mainland or island) and species. To these ends, in each large mainland patch, we marked off three 2 x 2 m plots which received a random assignment of treatments: 1) unmanipulated reference, 2) defaunation, or 3) fertilization and defaunation. Small patches received one of two treatments: 1) defaunation or 2) fertilization and defaunation. We collected pre-treatment samples on 5 June 2006 before any experimental treatments were applied. We then applied ammonium nitrate and phosphate fertilizers at 45 g N + 15 g P / m^2 on 10 small patches and on the 6 mainland plots assigned to the fertilization treatment. A second round of the same 3:1 fertilizer was applied 3 weeks later. This amount of fertilizer has been used on many occasions in this system and provides a reliable increase in plant quality compared to unmanipulated grass (Gratton and Denno 2003a, b, Huberty and Denno 2006). On 11 July, six weeks after the first application of fertilizer, we collected a 'pre-defaunation' sample, with which we quantified the response of species to host plant fertilization, prior to defaunation.

To quantify colonization rates among species, we then defaunated all small patches and plots within the mainland, with the exception of mainland reference sites. Defaunation was performed by passing the D-Vac head over all vegetation until no more arthropods were collected, about 15 – 20 minutes. On the same day, a second pass was made, and three days later, a final defaunation pass was made to ensure that as few individuals remained as possible.

After defaunation, we sampled arthropods from all sites at the following times. An immediately post-defaunation sample was collected within 3 hours of the final defaunation pass to correct calculations of colonization by any individuals we did not remove with the defaunation treatment. Although some species may have been able to colonize sites within this 3 h time period, we consider these individuals to be residual on the patch, not colonists. We then sampled one day, ten days, 19 days, and 31 days post-defaunation for each site. We did not collect past one month, as local *in situ* production from embedded eggs would not reliably be distinguishable from adult colonization after this point (Denno 1980).

Analysis of Defaunation Data: Species differences in response to N-addition

For pre-defaunation data, we tested whether treatment (fertilized or unfertilized), patch size (mainland or island), or the interaction between treatment and patch size influenced population densities, and whether this differed among species. For these analyses, we considered all small patches to be "islands," as densities before and after defaunation were very low across these small patches for most species, regardless of distance from large mainland patches. The response variable, density, was square root transformed to improve homogeneity of variance. We used a linear mixed effects model (lme function in nlme package, Pinheiro et al. 2008) to test whether square-root transformed density was a function of the fixed effects of species, patch size (mainland or island), treatment (fertilized or unfertilized), and their interactions, with sample site within block as a random effect. Significance of model terms was determined with likelihood ratio tests with the function dropterm (MASS package, Venables and Ripley 2002). To examine how individual species responded to treatment and patch size, we then used a similar linear mixed effects model for each species, testing whether square root transformed density was a function of treatment, patch size, and their interaction, with sample site within block as a random effect.

Total colonization rates

For each species, we calculated colonization rate as the total number of individuals collected per m^2 between the 1 d and 31 d samples, inclusive, divided by the total number of days available for colonization after defaunation (31). Prior to the 31 d sample, densities of several species were so low as to make comparisons across species difficult. Again, we used linear mixed effects models to test whether the effect of treatment and patch size varied among species, specifying the random effects of immediately-post defaunation density, site, and block. The most parsimonious model was selected by testing the significance of interaction terms with likelihood ratio tests, leaving simple terms if interactions were significant. As above, we then tested how treatment and patch size influenced colonization for each species separately.

Spider Manipulation Experiment

To test the hypothesis that generalist predators might contribute to low densities of herbivores and mesopredators on small patches, we conducted a spider manipulation experiment. In addition, we analyzed the stable isotope content of spiders to assess whether trophic position differed as a function of patch size (see *Stable Isotope Analysis*, below). For the spider manipulation experiment, We set up six blocks of four treatments each on small patches; for this experiment, each block was located on a unique small patch. Pre-treatment arthropod samples were collected on 13 June 2007, and treatments were applied randomly within blocks as follows. Ambient controls were marked with a stake and left unmanipulated. The addition, removal, and cage control treatments made use of 0.46 m^2 arenas constructed from polyvinyl chloride (PVC) sheets (2.4 m long, 0.46 m high, 1.6 mm thick; see Langellotto and Denno 2006). These enclosures were embedded 8 cm into the marsh surface for the addition and removal treatments to prevent spiders from moving underneath them. A cage control was used to allow unrestricted movement of all species and was suspended on stakes 15 cm above the marsh surface. Next to the inside edge of removal plots, we placed four pitfall traps, each consisting of two nested plastic cups (473 mL capacity) filled to one-fifth full with soapy water. Traps were covered loosely with elevated plastic plates to exclude rainwater and were emptied weekly throughout the experiment to prevent overflow from any tidal inundation and to refresh the soapy water. Additionally, to maintain the lowest possible spider densities, we also removed any visible *Pardosa littoralis* by hand. We added a total of 500 *P. littoralis* individuals collected from nearby large SP patches to addition plots on three dates (21 June, 26 June, and 3 July) to ensure treatment application. Additions of similar numbers of spiders in SA habitat have been used effectively in predation studies on the marsh (Denno et al. 2004), and the resulting densities in the current experiment were similar to the highest densities observed in a multi-year survey (Chapter 1). We then sampled enclosures and ambient and cage controls every three weeks for the duration of the growing season, with samples taken on 11 July, 2 August, 28 August, and 16 September. All data are presented as densities.

Analysis of spider manipulation data

We analyzed treatment effects with linear mixed effects models with the fixed effect of spider treatment and random effects of experimental unit, block, and date. First, we investigated whether treatment imposition was successful by testing whether *P. littoralis* densities were significantly influenced by treatment, date, and their interaction. Next, we investigated how treatments impacted the densities of two species of potential prey for *P. littoralis*, the dominant herbivore in SP, *T. minuta*, and its abundant egg predator, *T. alboornatus*. We used total adult and nymph densities for these species, as it is unknown what life stage *P. littoralis* might feed upon. Because *P. littoralis* can feed on both herbivores and other predators (Denno et al. 2004), we tested how the ratio of *T. alboornatus* to *T. minuta* (arcsine square root transformed to improve homogeneity of variance) differed among treatments as an index of spider preference.

Stable Isotope Analysis

Following approaches formalized in Peterson and Fry (1987, see also Post 2002a, Gratton and Denno 2006), we next used stable isotope techniques to test whether the feeding position of *P. littoralis* was a function of patch size. We selected large (> 500 m^2) and small (<20 m^2) patches of SP in seven spatial blocks and collected arthropod and plant samples at several locations: from the center and edge of the large patch, the center of the small patch, and in the SA meadow at least 20 m from any SP. The edge sample was collected in SP within 2 m of the patch edge to determine whether patch size per se or adjacency to an alternative habitat would contribute to any differences in trophic position. Arthropod samples comprised ten non-overlapping 4 s placements of the D-Vac head; live plant material was collected from the same sites as the arthropod samples to provide a local isotopic baseline (Post 2002a). In preparation for analysis, plants were rinsed with dH_20 and arthropods were identified and counted. Specimens (plants and arthropods), were dried at 55° C for 48 h. Dried plant material was ground to a powder using a coffee grinder. Arthropods were weighed and ground to a fine powder with mortar and pestle, or crushed on glass, depending on specimen size. Aliquots of 3 mg plant material, individual *P. littoralis*, and samples of 7 – 10 *T. minuta*, combined due to their small size, were sent for isotopic analysis.

Stable isotopes of C and N were assessed with a continuous flow isotope ratio mass spectrometer (Delta Plus XP, Thermofinnigan, Bremen) coupled to an elemental analyzer (ECS 4010, Costech Analytical, Valencia, CA) at the Washington State University Stable Isotope Core Laboratory (Pullman, WA). Isotope ratios of samples (subscript 'samp' below) are reported in relation to known standards ('std') in per mil notation, such that $\delta^{15}N = [({}^{15}N/{}^{14}N_{samp}) \,/\, ({}^{15}N/{}^{14}N_{std}) - 1] \times 1000$; $\delta^{13}C$ is calculated similarly for ${}^{13}C/{}^{12}C$ ratios (Peterson and Fry 1987). Standards were atmospheric nitrogen and Vienna Pee Dee Belemnite (VPDB) for N and C analyses, respectively, and delta values were calculated using a multi-point normalization; internal standards were interspersed for calibration.

The trophic position of an individual can be assessed by accounting for the well-documented step-wise fractionation of $\delta^{15}N$ with trophic transfers (Peterson and Fry 1987, Post 2002a) and the isotopic values at the base of the food web, with the equation $trophic = \lambda + (\delta^{15}N_{consum} - \delta^{15}N_{base})/\Delta_n$, where λ is the trophic level of the base used for calibration (i.e. 1 for plants), $\delta^{15}N$ values are measured directly, and Δ_n is the trophic fractionation. In a previous study of this system, Gratton and Denno (2006) found a fractionation of 1.5 to be appropriate for estimating the trophic position of spiders, and we adopt this value here, noting that relative differences in trophic position among patches are robust to the exact value of fractionation applied (results not shown). Initial findings show a slight difference in $\delta^{15}N_{base}$ between SA and SP habitats. To test the robustness of our findings, we also calculated an alternative, more conservative value for the trophic position of *P. littoralis*. Considering the possibility that a spider in a sample from a small patch had only just arrived on the patch from the adjoining SA habitat, we calculated this alternative trophic position based on SA plant material as $\delta^{15}N_{base}$. We also calculated the trophic position of *T. minuta*, an herbivore whose trophic position should not differ among samples.

Results

Defaunation Experiment

Species differed greatly in response to fertilization, as a function of patch size (mainland vs. island), and the interaction between fertilization and patch size (Table 2.1, Figure 2.1). For the pre-defaunation effects of fertilization and patch size, density (square root-transformed) was significantly affected by treatment, species, patch size, a treatment x species interaction (Likelihood Ratio Test (LRT) for treatment x species, $\chi^2 = 20.87$, df = 9, $P = 0.01323$) and a patch size x species interaction (LRT for patch size x species, $\chi^2 = 152.94$, df = 9, $P < 0.0001$; Figure 2.1, see also Appendix B). Analyzing each species separately, fertilization and patch size were important predictors of pre-defaunation density for the majority of species (Table 2.1). Considering the three brachypterous species (Figure 2.1 A-C), *T. minuta* exhibited a strong response to treatment, patch size, and their interaction, with highest densities on fertilized mainland sites, and lowest on unfertilized island sites (Figure 2.1 A). Densities of *A. simplex* were very low during this sample but were positively influenced by fertilization treatment (Figure 2.1 B). The herbivore *M. lobatus* (Figure 2.1 C) did not exhibit a response to either fertilization or patch size. Fertilization treatment positively influenced densities of the three macropterous species (Figure 2.1 D-F; Table 2.1); notably, both *D. detecta* (Figure 2.1 D) and *D. bisignata* (Figure 2.1 F) responded positively to fertilization regardless of patch size (non-significant treatment x patch size interaction; Table 2.1). For predators (Figure 2.1 G-I), the specialist egg predator *T. alboornatus* was significantly affected by both treatment and patch size (Figure 2.1 G). Densities of the parasitoid *Haplogonatopus sp.* were low during this study and were not significantly affected by treatment or patch size in this pre-defaunation sample (Table 2.1; graph not shown). Regardless of fertilization, each species of spider responded significantly to patch size, but in different manners (Figure 2.1 H, I). Densities of the habitat specialist *T. striatus* were strongly depressed on island patches (Figure 2.1 H), whereas *P. littoralis* densities were significantly higher on these small patches (Figure 2.1 I).

After defaunation, species colonized vacant plots at different rates (Figure 2.2). Colonization rates (mean number of colonists per day, square root transformed) differed among treatments, patch sizes, species, and all two-way interactions (treatment x patch size, $\chi^2 = 5.42$, df = 9, $P < 0.02$; treatment x species, $\chi^2 = 19.77$, df = 9, $P = 0.019$; patch size x species, $\chi^2 = 100.95$, df = 9, $P < 0.0001$). Investigating each species separately, the colonization rate of nearly every species was significantly influenced by patch size (Figure 2.2; Table 2.2). With one exception, each species colonized defaunated plots on mainlands faster than islands; colonization rates of the habitat generalist *P. littoralis*, on the other hand, were higher on islands. Four of six herbivores and two of four predators colonized fertilized plots faster than unfertilized plots (Table 2.2). Although prior to defaunation, *D. bisignata* densities were not different between mainlands and islands, colonization rates were significantly lower on islands than mainlands for this species (Figure 2.2 E). Colonization rates for the fully macropterous herbivore, *Am. simplex*, were also depressed on islands, although this species exhibited a robust recovery on fertilized mainland plots after defaunation (Figure 2.2 E). Patch-restricted predators colonized islands slower than mainlands (Figure 2.2 G, H, Table 2.2), but only the spider *T. striatus* colonized fertilized patches faster than unfertilized (Figure 2.2 H; Table 2.2). *Pardosa littoralis* colonized island patches faster than mainlands (Figure 2.2 I), mirroring the same patterns as the pre-defaunation response to patch size (Figure 2.1 I).

Spider Manipulation Experiment

Prior to treatment imposition, densities of the three focal species did not differ systematically across sites (test of pretreatment density with respect to treatment: *P. littoralis*: $F_{3,15} = 0.056$, $P = 0.98$; *T. alboornatus*: $F_{3,15} = 0.15$, $P = 0.93$; *T. minuta*: $F_{3,15} = 0.24$, $P = 0.86$). The addition and removal treatments were successfully imposed in this experiment, with high densities of *P. littoralis* achieved in addition plots and low densities achieved in removal plots (Figure 2.3 A). There was a significant effect of time and a treatment x time interaction, such that *P. littoralis* densities declined over time, especially in addition treatments (Likelihood ratio test, dropping treatment x time interaction, $\chi^2 = 69.70$, $P < 0.001$).

Treatment, but not time or a treatment x time interaction, significantly influenced the densities of *T. alboornatus* and *T. minuta*, such that spider treatments had consistent effects on these two potential prey species throughout the experiment (*T. alboornatus*: LRT, dropping treatment x time interaction, $\chi^2 = 0.32$, $P = 0.96$; test of treatment effect: $\chi^2 = 11.82$, $P = 0.008$; *T. minuta*: LRT, dropping treatment x time interaction, $\chi^2 = 0.25$, $P = 0.97$; test of treatment effect: $\chi^2 = 13.63$, $P = 0.0034$). Densities of the egg predator *T. alboornatus* were strongly depressed in addition treatments throughout this experiment (Figure 2.3 B), whereas densities of *T. minuta* were not significantly lower in addition treatments (Figure 2.3 C). To investigate the relative sensitively to predation, we assessed how the ratio of *T. alboornatus* and *T. minuta* varied among treatments. The ratio of *T. alboornatus* to *T. minuta* (arcsine square root transformed to improve homogeneity of variance) was strongly affected by treatment and was much lower in spider addition plots than other treatments (treatment effect: LRT = 25.00, $P < 0.0001$; Figure 2.4). As a result, both the absolute density (Figure 2.3 B) and the relative abundance of *T. alboornatus* (Figure 2.4) were strongly depressed in spider addition treatments.

Stable Isotope Analysis

Among samples collected quantitatively on small and large patches for stable isotope analysis, *P. littoralis* densities did not differ significantly as a function of location (large patch centers and edges, small patch centers, and SA meadows; Figure 2.5 A; Table 2.3). Densities of *T. alboornatus* and *T. minuta* in these samples were, however, significantly lower on small patches than large (Figure 2.5 B; Table 2.3), a finding consistent with the pre-defaunation results (Figure 2.2).

The estimated trophic position of *P. littoralis* differed among sites and was highest on small patches (Table 2.3; Figure 2.5 C); this pattern held even when trophic position was calculated conservatively using SA material as the base of the food web (Table 2.3, ‘alternative trophic position’). *Pardosa littoralis* individuals on small patches had an estimated trophic position of 4.39 (± 0.12 SE), whereas those found on large patches had an estimated trophic position of 3.56 (± 0.08 SE). Importantly, the estimated trophic position of *T. minuta* did not differ between small and large patches (Table 2.3). The density of non-*P. littoralis* spiders was significantly influenced by patch size ($\text{mean}_{\text{Large}} = 28.14$, $\text{mean}_{\text{Small}} = 84.86$, $F_{1,6} =$

12.14, P = 0.013), and the estimated trophic position of *P. littoralis* was significantly positively related to the density ($\log_{10}$ transformed) of other spiders in these samples (Figure 2.5 D; Table 2.3).

Discussion

Understanding the relative importance of local and spatial mechanisms in driving patterns of relative abundance across patches is a major aim of modern ecology (Holyoak et al. 2005). This focus on relative importance of structuring forces represents a shift from studies of purely local or purely spatial determinants of species richness, coexistence, and abundances. At the level of the metacommunity, recent studies have investigated the relative influence of dispersal and local quality for whole community data (Bocard 1992, Cottenie 2005, Thompson and Townsend 2006, van de Meutter et al. 2007, van der Gacht et al. 2007) and for competition among species at a given trophic level (Amarasekare et al. 2004, Kneitel and Chase 2004). Studies at the species level have also begun to include measures of patch quality (Moilanen and Hanski 1998, Thomas et al. 2001). Regardless of the level of organization investigated (species, guild, metacommunity), these recent developments towards understanding the relative roles of local and spatial mechanism highlight that, although local processes can influence the relative abundance or performance of a species, spatial processes may mediate species' responses to local conditions (Haynes et al. 2004, Matter et al. 2009).

Movement and responses to augmented resource quality among herbivores

In our experimental manipulation of host plant quality, we found that five of the six herbivores exhibited strong positive responses to grass fertilization in pre-defaunation samples (Table 2.1). This result is consistent with other fertilization studies in the marsh (Gratton and Denno 2003a, b) and indicates either better performance or higher colonization rates on fertilized plots. Fertilized plots on large "mainland" sites may be easily colonized by individuals in adjacent, unfertilized regions of the patch, leading to rapid increases in arthropod densities, whereas immigration to small "island" patches may be severely limited among these species. For the herbivores *T. minuta* and *Am. simplex*, the positive effect of fertilization on pre-defaunation densities was attenuated on small patches (significant treatment × patch size interaction; Tables 2.1, 2.2). Although responses to the pre-defaunation fertilization treatment may have been due to immigration, growth, or reproduction, recovery after defaunation could only be due to immigration due to the short duration of this experiment. On mainland plots, the same five herbivores colonized fertilized mainland plots with a greater number of colonists per day compared to unfertilized mainland plots (Figure 2.1, 2.2; see note in Table 2.1 with regard to the sixth herbivore, *M. lobatus*). On island patches, however, colonization rates were very low, even on patches receiving fertilization treatment (Table 2.2, Figure 2.1, 2.2).

Although we predicted differences in colonization rates based on variation in wing morphology among these species (Denno 1981), we did not observe a systematic pattern among species either in pre-defaunation samples or in colonization rates after defaunation (Figure 2.1, 2.2, compare top (brachypterous) and middle (macropterous) rows). Instead, we found mixed responses across the herbivore guild. For pre-defaunation densities and post defaunation colonization rates, a significant interaction between fertilization and patch size indicated that two species, *T. minuta* and *Am. simplex*, did not effectively make use of fertilized island plots (Table 2.1, 2.2). However, these species differ greatly in wing morphology and were not predicted to respond similarly, as *T. minuta* is largely brachypterous (< 1% macroptery) and *Am. simplex* was the only fully macropterous species in this study (100% macroptery). Likewise, colonization rates over the one month post-defaunation period were lower for *D. bisignata* and *A. simplex* on islands than on mainland plots, despite the lack of a detectable difference in pre-defaunation densities between mainlands and islands for these two species (Table 2.1). Consistent with predictions based on wing morphology, however, the macropterous *Am. simplex* was the only species to make use of fertilized mainland plots within one day of defaunation (Figure 2.1 F).

Experimental studies in aquatic bacteria-based systems (Cadotte et al. 2006) and rock-pool metacommunities (Cottenie et al. 2003) indicate that the relative importance of quality, movement, and species interactions can vary among systems. Far fewer studies have experimentally tested the relative roles of local (patch quality and species interactions) and spatial (dispersal) mechanisms for population density and spatial distribution in the field for terrestrial species. In a notable exception, Haynes et al. (2007) found that movement of planthoppers among patches of *Spartina pectinata* in a prairie ecosystem was relatively more influenced by the type of matrix than experimentally manipulated patch quality, due to differential movement rates at edges of brome than mudflats for *Prokelisia crocea*. In our similar system of sap-feeding herbivores on patches of *S. patens* in the marsh, movement rates may be much lower, and patch size may be a dominant factor determining patch occupancy and density. Colonization rates were consistently lower on islands than mainland plots, even for the two species without a significant effect of patch size prior to defaunation (*A. simplex* and *D. bisignata*), indicating that even one month may not be enough time to colonize a patch. Although local quality can enhance population density (Figure 2.1, 2.2) and was found to be an important factor in a multiple regression for a multi-year observational study (Chapter 1), results from these experimental manipulations suggest that colonization of even high-quality small patches may be a slow process. As tidal influences can be very important in intertidal marshes, the colonization of patches extirpated by storm-mediated inundation may be very slow and leave many small patches unoccupied. Our experimental results finding low colonization rates on small patches and a significant patch size x quality interaction are also consistent with findings from an observational study by Matter et al. (2009), who found that movement rates of the butterfly *Parnassius smintheus* were only increased to high quality patches that were well-connected. Thus, movement rates may in general mediate the effects of patch quality across many herbivore-plant systems.

Predation as a structuring mechanism

Among natural enemies, differences in pre-defaunation density (Table 2.1) and colonization rates (Table 2.2, Figures 2.1, 2.2) depended more strongly on patch size than patch quality. Each of the three patch-restricted natural enemies (*T. alboornatus*, *Haplogonatopus sp.*, and *T. striatus*) colonized small patches slower than mainland sites (Figure 2.1), and only *T. alboornatus* had higher densities on fertilized patches prior to defaunation. On the other hand, the habitat generalist *P. littoralis* was more abundant on small patches prior to defaunation and colonized small patches faster than mainland sites (Figure 2.1 I, Figure 2.2 I). This spider is well-known to be a habitat generalist (Döbel et al. 1990, Lewis and Denno 2009), and likely only had to travel very short distances to colonize either mainland plots or island patches. We also observed this elevated density on small patches in a multi-year survey (see Chapter 1) and thus investigated whether such high predator densities on small patches might contribute to the low prey densities on small patches (i.e. Figure 2.1).

Few studies of patchy habitats have investigated how generalist predators might impact the spatial distribution of prey populations. Cronin et al. (2004), in a largely analogous system of the prairie cordgrass *Spartina pectinata* found that high densities of spiders on small patches induced density-dependent herbivore emigration from small patches. In our study, several lines of evidence suggest that high densities of the generalist spider *P. littoralis* on small patches may contribute to the observed low densities of the mesopredator *T. alboornatus*, but not of the abundant herbivore *T. minuta*. First, we found that high densities of *P. littoralis* strongly depressed mesopredator (*T. alboornatus*) populations in spider addition enclosures (Figure 2.3). This was most likely a direct consumptive effect, as these brachypterous mesopredators were unlikely to escape the field enclosures, and the depression of mesopredator densities lasted throughout the experiment. Increased spider densities did not, however, reduce herbivore densities in this experiment (Figure 2.3 C). Second, the ratio of mesopredators to herbivores in spider addition treatments indicates a relative preference for mesopredators by *P. littoralis* (Figure 2.4). Feeding experiments in SA found that *P. littoralis* had a higher catch rate of *Tytthus vagus*, a congener of the mesopredator in the current study, than *Prokelisia* herbivores in laboratory experiments (Matsumura et al. 2004). Third, previous work found that the ratio of *P. littoralis* to *T. alboornatus* was higher on small compared to large patches, whereas patch size did not influence the ratio of *P. littoralis* to *T. minuta*. (Figure 1.5). Thus, unlike in Cronin et al. (2004), spatial structure in the marsh may influence spider predation rates on mesopredators far more that spider predation rates on herbivores.

Because of high spider densities and the finding that predation may limit the density of the mesopredator *T. alboornatus* but not of the herbivore *T. minuta* on small patches, we investigated whether the trophic position of *P. littoralis* was a function of location. With quantitative samples of the centers and edges of large patches, the centers of small patches, and in the matrix, we found no significant difference in spider density among locations in this single-date sample (Figure 5 A), but consistent with results from the defaunation experiment (Figure 2.1 A, G) we found strongly reduced densities of both *T. minuta* and *T. alboornatus* on small patches (Figure 2.5 B). Evidence from the stable isotope analysis indicates that *P. littoralis* on small patches occupied a higher trophic position that those at the centers or edges of large patches or in SA habitat (Figure 2.5 C).

This finding is contrary to expectations of longer food chain length on large patches (Holt 1996), as well as findings from other empirical systems (Post et al. 2000, Post 2002b, Takimoto et al. 2008). We suggest that the trophic position of *P. littoralis* may be a complex function of patch size, prey availability, and the structure of the local environment. *Pardosa littoralis* readily consumes other predators (Matsumura et al. 2004), and the higher density of non-*P. littoralis* spiders on small patches may contribute to its observed higher trophic position (Figure 5 D). The density of spiders in several guilds was also elevated in the study of Cronin et al. (2004), and this elevation in generalist predator densities at habitat edges may be quite general due to increased access to multiple habitats (Ries et al. 2004) and increased structural heterogeneity near habitat boundaries. Additionally, *P. littoralis* can more easily capture other predators in simple compared to complex habitats (Finke and Denno 2002). A positive correlation between the amount of dead grass buildup and patch size in the observational study indicates that predators on small patches may also be more easily captured, although actual tests of capture rates in SP habitat have not been performed. Thus, we expect that on small patches, the adjacency of alternative habitats and the relative structural simplicity of the small compared to large patches may contribute to higher densities of alternative prey and a higher relative ease of capture, leading to changes in *P. littoralis* feeding ecology. These predictions suggest fruitful avenues for future research in this system.

Conclusion: The relative importance of quality, predation, and movement

Gripenberg and Roslin (2007) called for the investigation of top down and bottom up interactions in space, noting that variation in patch quality or species interactions over a network of patches may be of great importance in understanding how real heterogeneous systems function. Here, we provide evidence that the bottom-up force of patch quality may only influence herbivore densities on large patches, as small patches, regardless of quality and regardless of distance, failed to be colonized by several species. Top-down forces, however, may be stronger on small patches in this system and may contribute to the consistently low densities of mesopredators on small patches. By taking an experimental approach towards investigating alternative mechanisms, we confirmed many of the patterns seen in observational studies of this system and provided insight into the importance of movement, resource quality, and species interactions structuring this arthropod assemblage.

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Tables

Table 2.1. The effects of fertilization treatment (fertilized or unfertilized), patch size (mainland or island), and their interaction on densities of ten *Spartina patens* arthropods prior to defaunation of patches. Random effects of site within block were included for each model. Significant effects (P < 0.05) are highlighted in bold font.

	Treatment			Patch size			Treatment x Patch size		
	F	df	P	F	df	p	F		p
T. minuta	8.20	1, 46	**0.0063**	51.24	1, 46	**<.0001**	7.23	1, 46	**0.01**
A. simplex	4.08	1, 46	**0.049**	1.16	1, 46	0.29	0.03	1, 46	0.86
M. lobatus	0.25	1, 46	0.62	0.36	1, 46	0.55	0.91	1, 46	0.34
D. detecta	15.31	1, 46	**0.0003**	7.69	1, 46	**0.008**	3.57	1, 46	0.065
D. bisignata	7.40	1, 46	**0.0092**	2.00	1, 46	0.16	0.00	1, 46	0.98
Am. simplex	6.39	1, 46	**0.015**	5.95	1, 46	**0.0187**	6.36	1, 46	**0.015**
T. alboornatus	5.41	1, 46	**0.025**	74.83	1, 46	**<.0001**	1.52	1, 46	0.22
Haplogonatopus sp.	2.80	1, 46	0.10	0.73	1, 46	0.40	0.12	1, 46	0.74
T. striatus	0.41	1, 46	0.52	44.46	1, 46	**<.0001**	0.11	1, 46	0.74
P. littoralis	2.02	1, 46	0.16	8.78	1, 46	**0.0048**	0.00	1, 46	0.99

Note: The herbivore *M. lobatus* was collected on SP, but may represent individuals from a sister species *M. nr lobatus*; these species are distinguishable largely by host plant affinity but may mix on small patches (G. Wimp pers. comm.).

Table 2.2. The effects of fertilization treatment (fertilized or unfertilized), patch size (mainland or island), and their interaction on colonization rates of ten *S. patens* arthropods. Colonization rates were calculated as the summed density of individuals collected over the one month post-defaunation period, divided by the time since defaunation (31 days). Density immediately post defaunation was included with site and block as random effects. Significant effects (P < 0.05) are highlighted in bold font.

	Treatment			Patch size			Treatment x Patch size		
	F	df	P	F	df	P	F	df	P
T. minuta	32.51	1,38	**<.0001**	93.93	1,38	**<.0001**	5.06	1,38	**0.030**
A. simplex	26.62	1,38	**<.0001**	59.29	1,38	**<.0001**	0.07	1,38	0.79
M. lobatus	1.16	1,38	0.29	2.29	1,38	0.14	3.99	1,38	0.053
D. detecta	2.16	1,38	0.15	25.61	1,38	**<.0001**	1.57	1,38	0.22
D. bisignata	17.10	1,38	**0.0002**	11.55	1,38	**0.0016**	0.03	1,38	0.85
Am. simplex	19.94	1,38	**0.0001**	59.86	1,38	**<.0001**	5.40	1,38	**0.026**
T. alboornatus	2.83	1,38	0.10	28.59	1,38	**<.0001**	1.31	1,38	0.26
Haplogonatopus sp.	2.84	1,38	0.10	4.63	1,38	**0.038**	1.26	1,38	0.27
T. striatus	9.77	1,38	**0.0034**	22.86	1,38	**<.0001**	0.80	1,38	0.38
P. littoralis	0.57	1,38	0.45	15.72	1,38	**0.0003**	0.82	1,38	0.37

Table 2.3. Effects of location on the density and trophic levels of arthropods. Samples were collected from four locations: the centers and edges of large *S. patens* (SP) patches, the centers of small SP patches, and the surrounding *S. alterniflora* (SA) matrix habitat. Each table entry shows results of a test of either density or trophic position for the hunting spider *P. littoralis*, the mesopredator *T. alboornatus*, or the herbivore *T. minuta*. Trophic position was calculated based on stable nitrogen isotopes of consumers, standardized by the isotope values of the basal resource at the site on which they were collected. An alternative trophic position for *P. littoralis* was calculated based on the isotope values of the basal resources from adjacent SA meadow habitat for small patches, under the conservative assumption that individuals had just moved into patches from SA. See text for details on calculations.

Test	Focal species	df	F	p
Density among locations	*P. littoralis*	3, 24	1.2032	0.3299
	T. alboornatus	2, 16	7.77	0.0044
	T. minuta	2, 16	14.35	0.0003
Trophic position among locations	*P. littoralis*	3, 30	15.71	<0.0001
	T. minuta	1, 6	1.26	0.31
Alternative trophic position among locations	*P. littoralis*	3, 30	6.26	0.002
Trophic position in relation to density of other spiders	*P. littoralis*	1, 20	7.24	0.0141

Figure Legends

Figure 2.1. Recovery of nine arthropod species on defaunated plots of *Spartina patens* in response to fertilization treatment (unfertilized or fertilized) and as a function of patch size (large "mainland" or small "island" patches). A-C brachypterous herbivores (<1% macropterous, or long-winged individuals); D-F, herbivores with higher levels of macroptery (D, *D. detecta*: 14%, E, *D. bisignata*: 50%; F, *Am. simplex*: 100%); G-I, predatory species. Pre-defaunation samples were collected on 11 July 2006 (Ordinal Date 192), after which multiple passes of the D-Vac suction sampler were used to defaunate plots. Means of cumulative densities for each treatment-patch size combination are plotted following defaunation (Ordinal Dates 196 – 227). Fertilized plots are represented with filled symbols, unfertilized plots are represented with open symbols. Mainland sites (> 100 m^2) are plotted with solid lines and islands (< 10 m^2) with dashed lines. Unmanipulated mainland reference sites are indicated with thick solid lines. Note differences in the y-axes in panels G-I due to large differences in relative abundance of predators. Legend abbreviations: ML: mainland, Isl: island, Ref: unmanipulated reference, Fert.: fertilized and defaunated, Defaun.: unfertilized and defaunated.

Figure 2.2. Colonization rates of nine species on defaunated plots in response to fertilization treatment (unfertilized or fertilized) and as a function of patch size (mainland or island). Rates are calculated as the total number of individuals collected from a site after defaunation, divided by the total number of days since defaunation

(31 d). Species are arranged as in Fig. 1. Open bars are unfertilized, filled bars are fertilized plots. Error bars are ± 1 SE.

Figure 2.3. Effects of the manipulation of densities of *P. littoralis* in field enclosures over time. Treatments were the addition of *P. littoralis*, an elevated cage control, open unmanipulated control, and the removal of *P. littoralis*. A) Densities of *P. littoralis*. B) Densities of the mesopredator *T. alboornatus*. C) Densities of the herbivore *T. minuta*. Note differences in the y-axes due to differences in relative abundance.

Figure 2.4. The effect of spider manipulation on the ratio of *T. alboornatus* to *T. minuta* among spider addition, cage control, open control, and spider removal treatments. Error bars are ± 1 SE.

Figure 2.5. The effect of location on the density of A) *P. littoralis* and B) $\log_{10}$ transformed densities of *T. minuta* (dark bars) and *T. alboornatus* (pale bars) for samples collected for stable isotope analysis. Locations are as follows: centers of large SP patches (L Center), edges of large SP patches (L Edge), centers of small SP patches (S Center), and meadows of *S. alterniflora* (SA); note that neither of the habitat specialist species in (B) occurs in SA, and this location was not plotted. C) The effect of location on the trophic position of *P. littoralis*. Trophic position was estimated from $\delta^{15}N$ values of *P. littoralis* after accounting for local differences at the base of the food web and trophic fractionation of ^{15}N; see text for more details. Error

bars are ± 1 SE. D) The relationship between the trophic position of *P. littoralis* estimated from stable N isotopes and the $\log_{10}$ transformed density of other spiders.

Figures

Figure 2.1

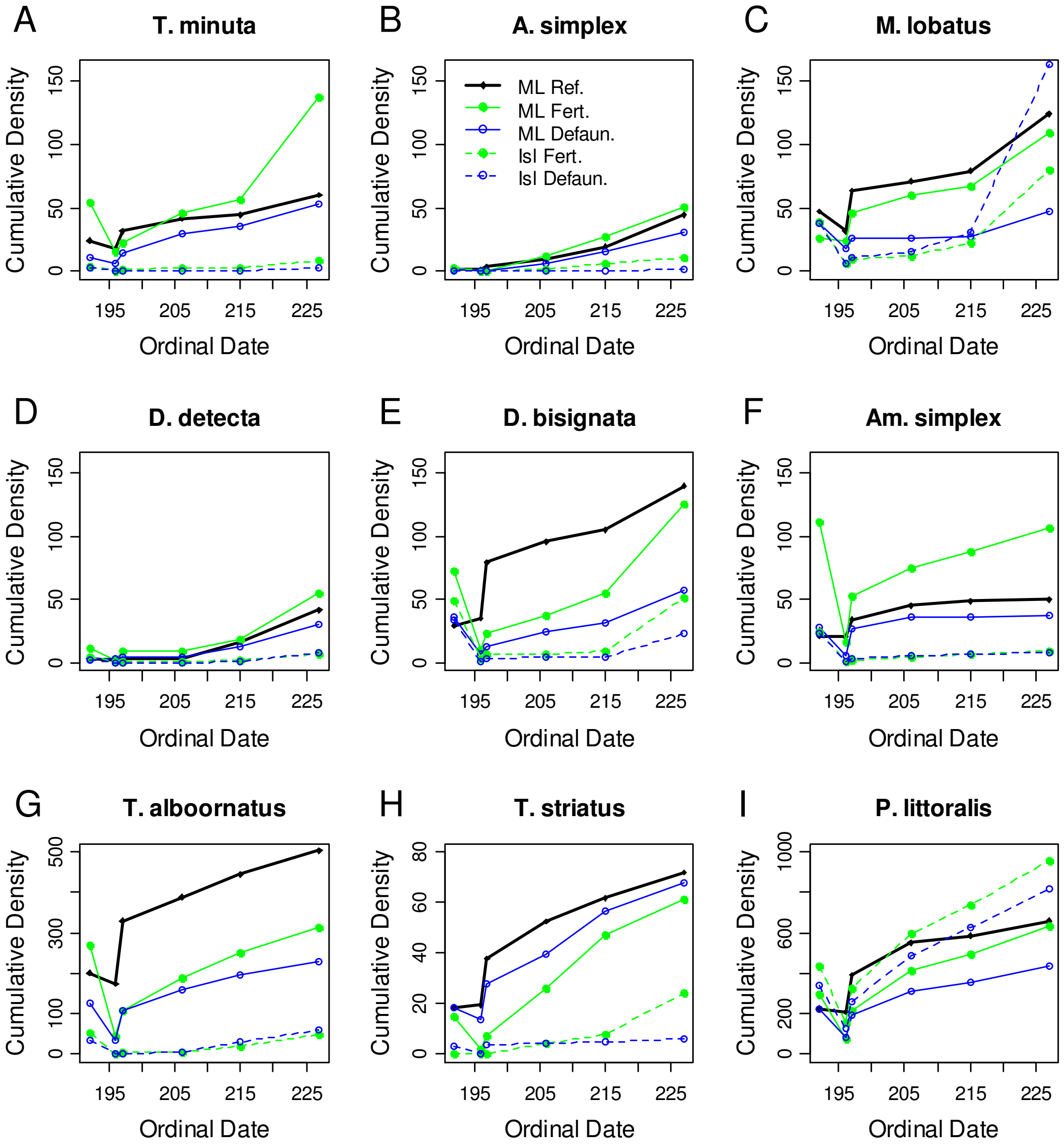


Figure 2.2

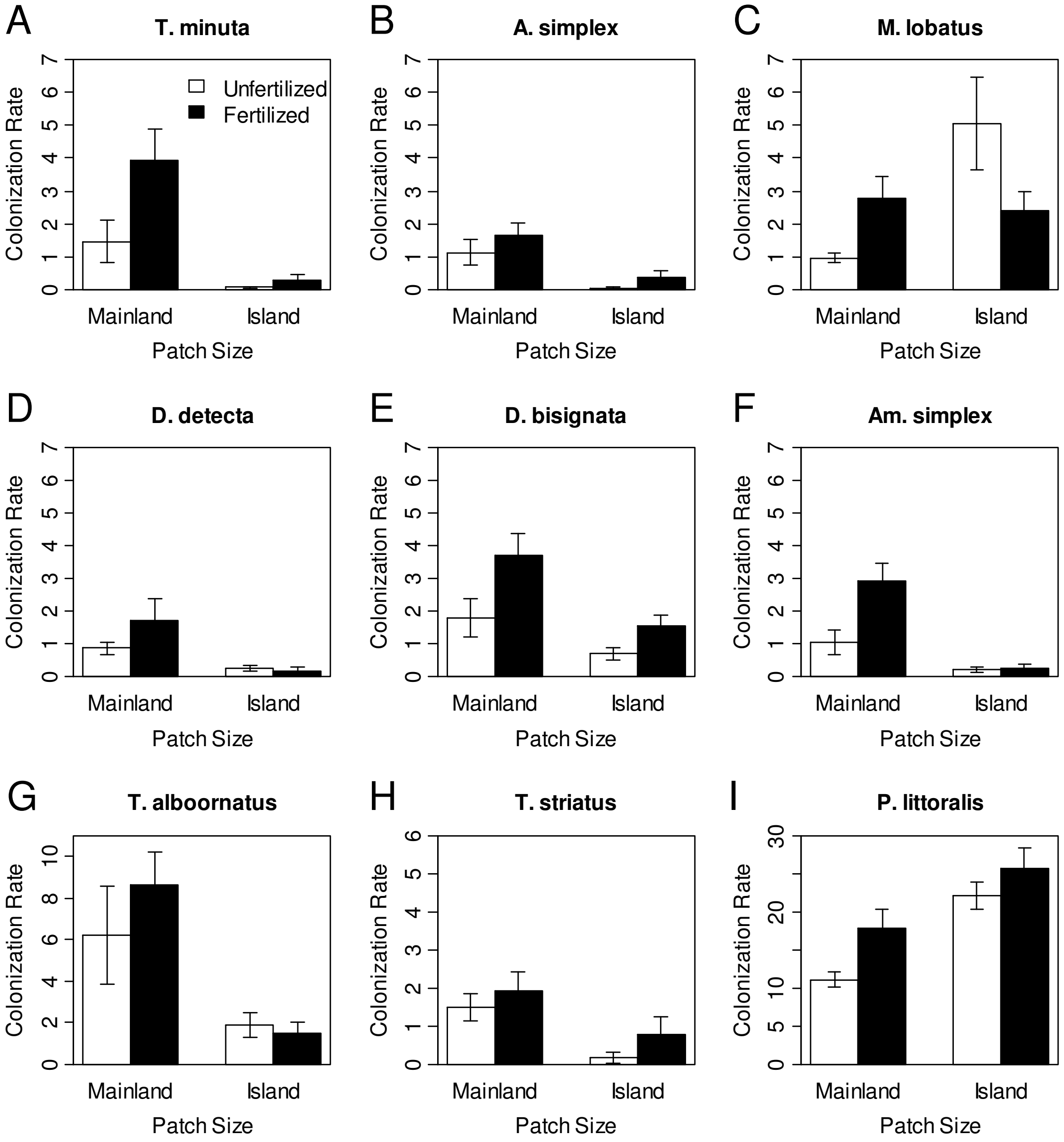

A
T. minuta
☐ Unfertilized
■ Fertilized
B
A. simplex
C
M. lobatus
D
D. detecta
E
D. bisignata
F
Am. simplex
G
T. alboornatus
H
T. striatus
I
P. littoralis
Colonization Rate
0
1
2
3
4
5
6
7
8
10
20
30
Mainland
Island
Patch Size

Figure 2.3

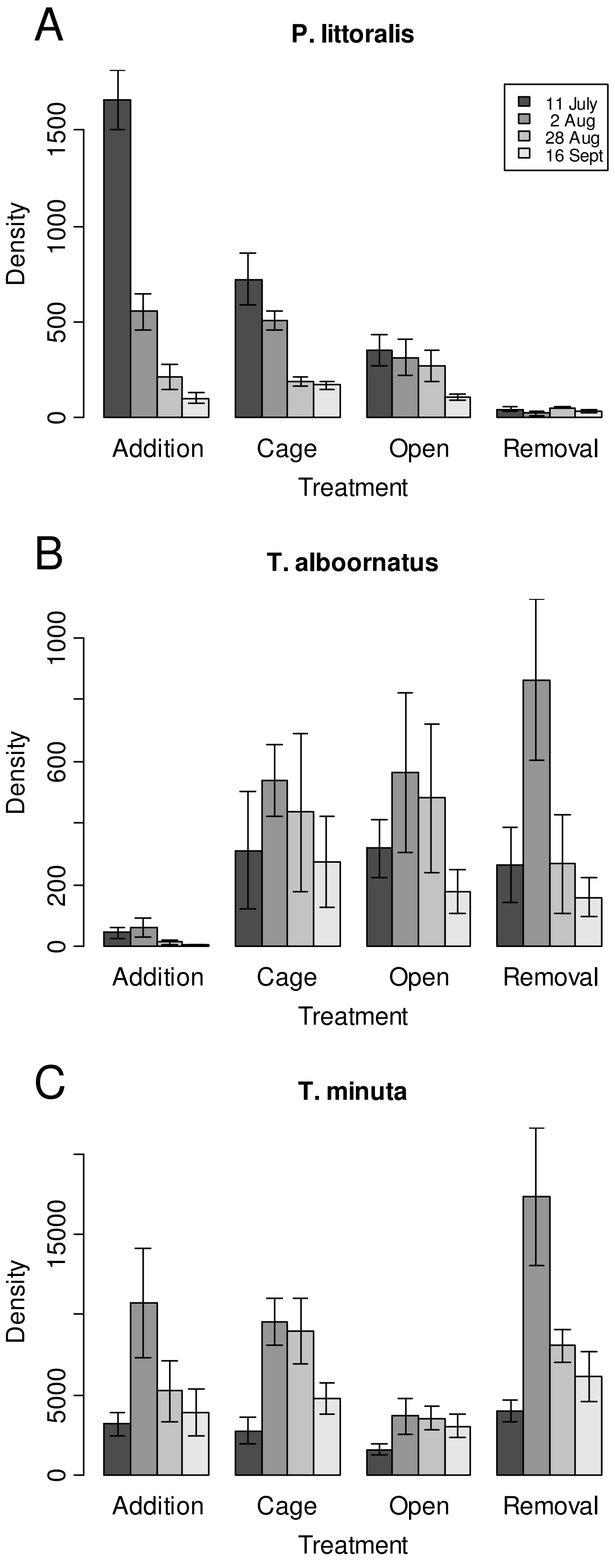

A
P. littoralis
Density
0
500
1000
1500
11 July
2 Aug
28 Aug
16 Sept
Addition
Cage
Open
Removal
Treatment
B
T. alboornatus
Density
0
200
600
1000
Addition
Cage
Open
Removal
Treatment
C
T. minuta
Density
0
5000
15000
Addition
Cage
Open
Removal
Treatment

Figure 2.4

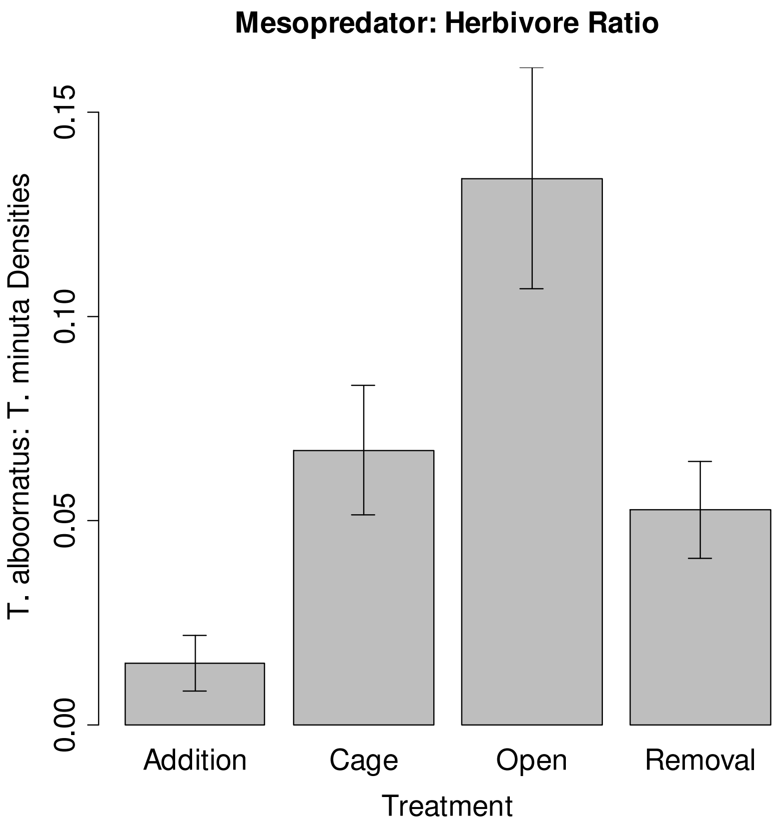
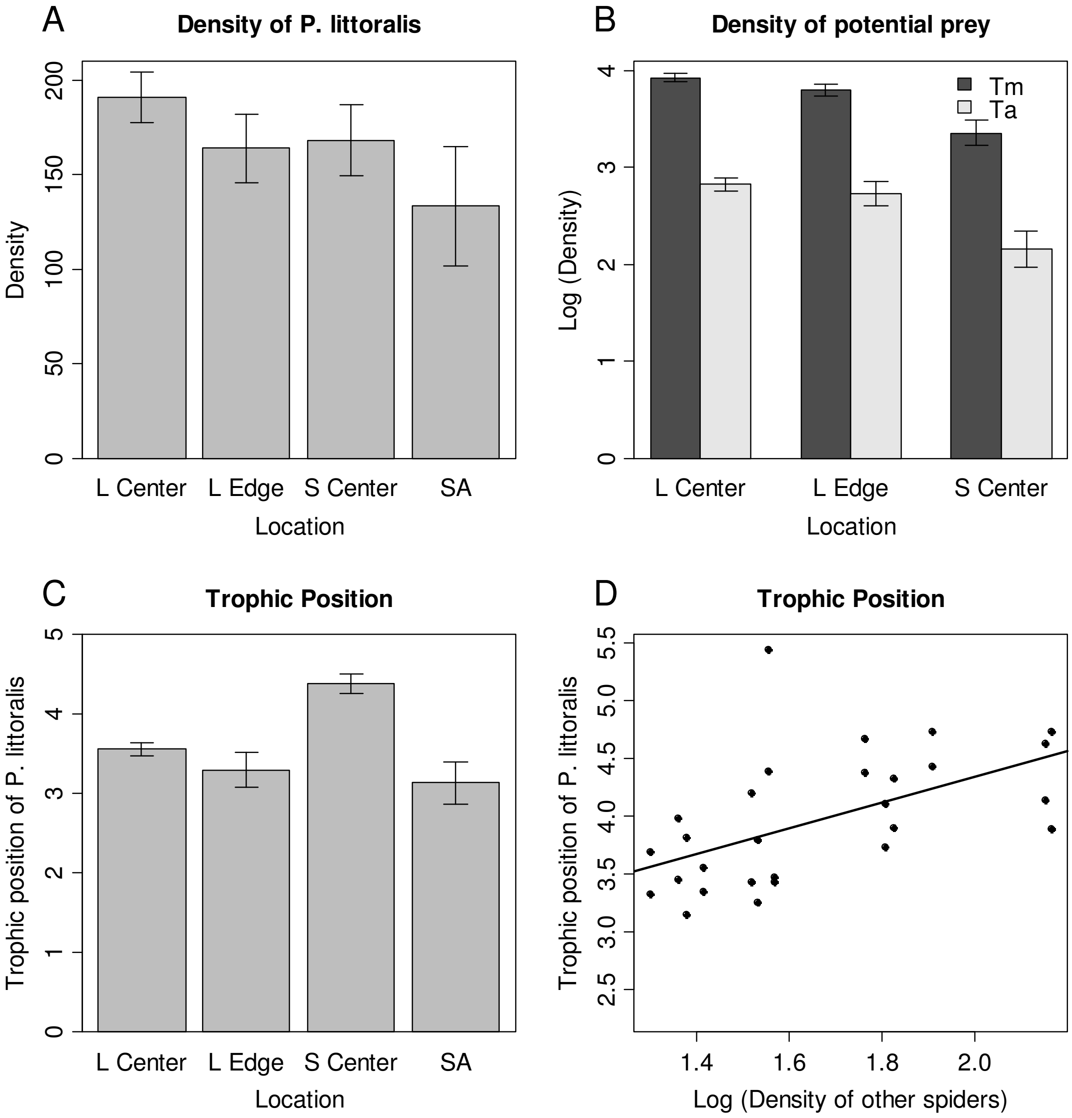

Mesopredator: Herbivore Ratio
T. alboornatus: T. minuta Densities
0.00
0.05
0.10
0.15
Addition
Cage
Open
Removal
Treatment

Figure 2.5


A
Density of P. littoralis
Density
0
50
100
150
200
L Center
L Edge
S Center
SA
Location
B
Density of potential prey
Log (Density)
0
1
2
3
4
Tm
Ta
L Center
L Edge
S Center
Location
C
Trophic Position
Trophic position of P. littoralis
0
1
2
3
4
5
L Center
L Edge
S Center
SA
Location
D
Trophic Position
Trophic position of P. littoralis
2.5
3.0
3.5
4.0
4.5
5.0
5.5
1.4
1.6
1.8
2.0
Log (Density of other spiders)

Chapter 3: Interactions lost and gained: A review of how trophic interactions are impacted by the fragmentation of habitats

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Abstract

The fragmentation of habitats can have profound effects on species persistence, population density, and species richness. Many recent studies have also documented how habitat fragmentation and related variables can influence trophic structure and species interactions, yet this diverse literature has not been brought together and examined for commonalities in mechanism and outcome. In this study, we investigate how fragmentation in the broad sense has been shown to impact species interactions and test the prediction that, as for single species, the habitat affinity of interacting species is a major determinant of whether a trophic interaction will be lost or gained in fragmented habitats. Through a literature review, we identified 171 studies of how patch-level (patch size, distance to edge, patch connectivity) or landscape level (fragmentation per se, proportion habitat, matrix composition, patch arrangement) factors impact trophic interactions. The majority (54%) of these studies focused on just a few specific trophic interactions: seed predation, insect parasitoid-host interactions, and bird nest predation and parasitism. More complex food web modules, such as food chains, apparent competition, or those involving indirect interactions, were infrequent in the literature (4% of studies). Overall, the habitat specificity of the interacting species was a key trait influencing whether the trophic interaction occurred more or less frequently in relation to

fragmentation variables. Across systems, trophic interactions in which the top species was a habitat specialist were more likely to occur on large patches, whereas those involving habitat generalists were more likely to occur on small patches. Similar differences between interactions involving generalists versus specialists were found for other variables as well, including connectivity, distance from edge, and proportion habitat in the landscape. Although other ecological traits may mediate the strength of these responses, the habitat specificity of interacting species was a consistent predictor of whether diverse trophic interactions were lost or gained in fragmented habitats.

Introduction

Habitat fragmentation is a pervasive global problem, leading to declines in species abundance and richness due to the breaking up of habitat, overall habitat loss, and the isolation of remaining fragments (Saunders et al. 1991, Fahrig 2003, Tscharntke and Brandl 2004). Several ecological and life history traits are predicted to influence species' relative extinction risks in fragmented habitats. Rare species and those with highly variable population sizes generally have an increased risk of extinction (Pimm 1988, Gaston 1994, Fagan et al. 2001) and may undergo local extinction via demographic stochasticity on small patches. Taxa with feeding and habitat specialization face a decreased likelihood that their required resources will be found on a patch (Lawton 1995, With and Crist 1995, Tscharntke et al. 2002), while feeding or habitat generalists may even increase in density on smaller patches due to edge effects (Debinski and Holt 2000, Ries et al. 2004, Fletcher et al. 2007). Zabel and Tscharntke (1998), for example, found monophagous species were less likely to occur on small rather than large nettle patches, while polyphagous species showed no effect of patch size. Likewise, species with high dispersal ability relative to the scale of patchiness may show less of a response to habitat heterogeneity compared to poor dispersers (Hambäck et al. 2007, Zaller et al. 2008), as has been seen in diverse taxa in fragmented forests (Roland and Taylor 1997, Laurance et al. 2002, Driscoll and Weir 2005).

Species at higher trophic levels may be more sensitive to habitat fragmentation, as those species depend on the availability of resources at each lower trophic level in order to persist on a patch, and an extinction in lower rank species leads necessarily to loss of their specialist predators (Lawton 1995, Holt 1996). Such species may additionally have inherently lower population density and higher variability, making them even more at risk of extinction on small patches (Lawton 1995). These predictions are supported by empirical studies documenting reduced density and diversity of parasitoids in several systems (van Nouhuys 2005) and the loss of top predators on forest islands (Terborgh et al. 2001). Other authors, however, have found variation among taxa that may better reflect changes in resource distribution than trophic position *per se* (Laurance et al. 2002).

From this suite of species' life history and ecological traits, whether a species is a habitat specialist and uses only patch habitat or is a habitat generalist and makes use of both patch and matrix habitats is a fundamental trait in the context of fragmented habitats (Bender et al. 1998, Henle et al. 2004, Ewers and Didham 2006). In a meta-analysis, Connor and colleagues (2000) found that this distinction explained much of the variation in density-area relationships across diverse taxa. Likewise, in a review of fragmentation experiments, Debinski and Holt (2000) found that, although habitat specialists declined in density on small patches, generalists were often more abundant (see also Bowers and Matter 1997).

Habitat specificity can also influence the potential for threshold dynamics in fragmented habitats. At the patch scale, habitat specialists may exhibit critical patch sizes, or thresholds below which they are unlikely to persist, due to low population growth rates or high rates of diffusion into a hostile matrix (Skellam 1951, Kierstead and Slobodkin 1953). In a comparison of the relative extinction risks of Costa Rican birds and mammals, Pereira et al. (2004, Pereira and Daily 2006, see also Holmes et al. 1994) found that the relative rates of population growth within a patch and in the surrounding matrix was a key parameter influencing species' densities, relative extinction risk, and the occurrence of critical patch sizes. At a larger spatial scale, metapopulations (Hanski and Ovaskainen 2000) and landscapes (Andrén 1994) may also exhibit threshold dynamics, with a threshold number of patches or proportion of habitat in the landscape required for persistence of certain species.

Because species may respond differently to habitat fragmentation and related variables according to their suite of ecological traits, their trophic interactions are also likely to be disrupted. We expect that the occurrence or strength of food web interactions may be a function of patch size, fragmentation, and related variables and may depend on species' traits. In this paper, we review the literature to investigate how trophic interactions are influenced in fragmented habitats. This literature is large, diverse, and broadly scattered across taxa. While certain pair-wise species interactions, especially pollination (Aguilar et al. 2006, Ricketts et al. 2008) and avian nest predation (Chalfoun et al. 2002), have received separate attention recently, this literature has not been brought together and examined for commonalities in mechanism or outcome. To these ends, we have the following goals for this paper: 1) to identify the types of trophic interactions that have been studied in the context of variation in patch size, habitat fragmentation, and related variables, 2) to determine whether the occurrence, frequency, or strength of trophic interactions is a function of fragmentation variables and whether the outcome is predictable based on the habitat affinity of the component species, and 3) to investigate the conditions under which different types of trophic interactions in empirical systems may exhibit critical thresholds for occurrence.

Predictions for trophic interactions based on habitat affinity

Just as for single species, the habitat specificity of interacting species may be a key determinant of how the trophic interactions in which they are engaged will be altered in fragmented habitats. Much of the theory on how patch size impacts trophic interactions focuses on habitat specialists and predicts a lower probability of occurrence of a trophic interaction on smaller patches. The occurrence of outbreaks of spruce budworm in forests (Ludwig et al. 1979) and the maintenance of parasitoids on patches of herbivorous hosts (Cobbold et al. 2005) have been investigated with reaction-diffusion equations, which have identified critical patch sizes for the occurrence of these interactions. Likewise, food chain length is predicted to be longer on larger patches (Holt 1996, Cantrell and Cosner 2001), due to the sequential dependence of the higher trophic level on lower levels in the food chain. Few studies have investigated other more complex trophic interactions, with the exception of Melián and Bascompte (2002), who predicted the loss of intraguild predation (IGP), apparent competition (APC), omnivory, and the shortening of FCL as the amount of habitat declined. This body of work makes the explicit assumption that all species in the interaction are habitat specialists.

Some of the most well-known examples of changes in trophic interactions in fragmented habitats, however, involve habitat generalists. The nest predation of forest birds by matrix-inhabiting cowbirds is a famous example of changes in trophic interactions in fragmented habitats (Gates and Gysel 1972, Chalfoun et al. 2002). Theory predicts that with species that use matrix habitat and forage at least somewhat into patch habitat can have profound effects on the dynamics of species residing in habitat patches (Fagan et al. 1999, Cantrell et al. 2001).

We expect that trophic interactions in which the top species is a habitat patch specialists may be lost in fragmented habitats (Figure 3.1 A), whereas trophic interactions involving habitat generalists may be gained in fragmented compared to continuous habitats (Figure 3.1 B). We use the term habitat specialist to refer to species known to reside in or utilize only patch and not matrix habitat, whereas habitat generalists reside in or utilize both patch and matrix habitat to at least some extent. Here, we consider how such trophic interactions may be influenced by the suite of variables often impacted by habitat fragmentation (see Fahrig 2003) or that vary in naturally-patchy habitats (Figure 3.1). For a habitat specialist engaged in trophic interactions in patch habitat, increases in patch size are predicted to increase the likelihood that the trophic interaction occurs (↑ arrow in Figure 3.1). Increases in patch size are predicted to have a negative impact (↓ arrow) on the occurrence of an interaction when the upper species is a habitat generalist, such that the interaction occurs less frequently on large compared to small patches. Likewise, trophic interactions involving habitat specialists may occur more frequently with increasing distance from a patch edge, with increasing connectivity, and with increasing proportion habitat in the landscape and may occur less frequently with increasing patch isolation and increasing fragmentation (↓ arrows, Figure 3.1).

Literature Review

Identification of Studies

To examine the types of trophic interactions studied in the context of habitat fragmentation, identify whether habitat affinity influences whether the interaction occurs more or less frequently in fragmented habitats, and identify whether, as predicted by theory, trophic interactions may exhibit thresholds for occurrence, we conducted a literature review. We included studies conducted at the level of the patch (patch size, distance to patch edge, and patch connectivity or isolation) and at the level of the landscape (proportion habitat cover, fragmentation per se, matrix type, and patch number and arrangement; Figure 3.1). We searched the online database Web of Science and supplemented these results with papers cited in reference sections. For the years 1945 – 2008, we used the following combinations of search terms: habitat, patch, fragment*, landscape, connectivity, isolation, matrix, interaction, food web, herbivory, parasit*, and predation, where * indicates a wildcard that allows for variable word endings. We then narrowed down search results to only those studies investigating the occurrence, rate, or strength of a food web interaction as a function of variables related to fragmentation, excluding those studies solely on the effects of habitat quality, type, or disturbance. Specifically excluded, however, were studies of pollination, which has been well-reviewed elsewhere (Aguilar et al. 2006, Ricketts et al. 2008); this review therefore focused on *trophic* interactions only. While the literature of organism abundance and richness in fragmented habitats is extensive, we focus here only on the occurrence and strength of trophic interactions as direct measures of the impacts of fragmentation and patch size on food webs.

We then examined each paper to populate a database of results. To do this, we identified the number of trophic levels, the explanatory variable(s), and type of food web interaction(s) studied. Trophic interactions were categorized as 1) herbivore-plant, 2) predator-prey, 3) parasite-host, 4) other two species interactions, or 5) interactions involving three or more species. Specific sub-categories were also enumerated (e.g., florivory, frugivory, leaf mining, etc. within the category herbivory). Each combination of species engaged in a trophic interaction was considered a unique *entry* in the database with respect to each measured explanatory variable. Trophic interactions at each measured spatial scale (i.e. increasing radii from a focal site) were included as well, as there was often no *a priori* expectation that one particular scale would be most appropriate (Thies et al. 2003). As an example, four unique entries were possible for the study of Elzinga and colleagues (2005), who studied the effects of patch size *and* connectivity on plant-herbivore *and* herbivore-parasitoid interactions in a 2-link food web module.

To characterize the breadth of food web studies in fragmented habitats and identify biases in the literature, we recorded several details of study design. We noted whether studies were observational or experimental, the latter requiring manipulation of a spatial variable or the presence of an interacting species. We distinguished between agricultural and natural settings due to the intensively managed nature of agriculture and the often different goals of agricultural studies compared to those of natural systems (i.e. pest suppression vs. conservation). The types of focal and matrix habitats were also recorded, as were the taxa studied and whether the study was conducted at single or multiple spatial scales.

Predicting trophic interactions in fragmented habitats

For each entry in the database, we recorded whether the occurrence or frequency of the trophic interaction was significantly influenced by the fragmentation variable. For increases in the fragmentation variable (i.e. increasing patch size, increasing fragmentation, etc.), we recorded whether the interaction occurred more frequently (+ response), less frequently (- response), or was unchanged (non-significant). Other responses were more complex and non-monotonic; these we classified as "different" for the purposes of comparing responses across studies.
To test whether these responses were predictable across studies, we focused on a subset of the studies for which predictions were clear and sample sizes were large enough. For this analysis, we focused on three well-studied types of trophic interactions (see *Results*): 1) herbivory, 2) parasitoid-host interactions, and 3) predator-prey interactions in relation to variation in patch size, distance from edge,

connectivity or isolation, the proportion habitat in the landscape, and the amount of fragmentation. We did not have consistent *a priori* expectations for the effects of matrix type and patch arrangement and, as sample sizes for these studies were also low, exclude them from the current analysis. For each of these trophic interactions, we identified the habitat specificity of the interacting species. In all studies identified here, the lower species in the trophic interaction (the plant, host, or prey) was a habitat specialist. The habitat affinity of the upper species in the interaction (the herbivore, parasitoid, or predator), however, varied across studies. For each entry, we evaluated whether study results were 1) consistent with predictions, 2) inconsistent with predictions, or 3) non-significant (see Figure 3.1 for predictions). We tested whether the outcome (consistent, inconsistent, or non-significant) was independent of species' habitat affinity (habitat specialist or generalist) with Chi-squared tests.

In order to investigate the conditions under which trophic interactions may exhibit threshold habitat requirements in fragmented habitats, we also recorded any findings of non-linear or threshold dynamics. While meta-analytic approaches are powerful, quantitative tools to summarize literature, studies included in meta-analyses must use comparable methods to perform an analysis for a narrowly-focused research question (Gurevitch et al. 2001). In contrast, the goals of the current study were to 1) summarize the diversity of interactions and means by which they have been studied and 2) identify commonalities in patch size and fragmentation dependence across different types of interactions. In this context, a meta-analysis would unnecessarily restrict the scope of the review, and we instead report a vote count of studies with various outcomes as a first step towards understanding and summarizing this diverse literature.

Results

Types of Studies

A wide range of trophic interactions have been studied as a function of patch size, landscape fragmentation, and related variables (Table 3.1, Figure 3.2). Overall, we identified 171 studies that met the requirements for inclusion in this review (Appendix C). This set of studies yielded a total of 735 entries in our database, where each entry represented a trophic interaction studied with respect to a fragmentation variable. Studies were classified as herbivory (31.3% of entries), parasite-host (12.0%), parasitoid-host (28.8%), predator-prey (19.3%), other two species interactions (4.5%), and those involving three or more species (4.1%; Table 3.1).

The bulk (96%) of the entries were of two-species trophic interactions, and only 30 (4%) involved three or more species (Table 3.1). Studies of food chain length, apparent competition, two consumers on one resource, and omnivory or intraguild predation were very rare in our database (Figure 3.2). Studies covered a diverse set of taxa, including nematodes, protists, arthropods, birds, and mammals at both the basal and upper levels of the trophic interaction, although patch (Figure 3.3A) and landscape (Figure 3.3B) studies differed somewhat in the distribution of focal taxa, with fewer studies of plants and more studies of birds at the landscape scale compared to the patch scale (Figure 3.3). The most frequently studied specific trophic interactions were the egg predation and parasitism of bird nests (118 entries, 16.1%), parasitoid-host interactions involving insects (212 entries, 28.8%), and insect or mammalian seed predation (71 entries, 9.7%; Table 3.1, Figure 3.3). Together, this narrow set covered 54.6% of the literature examined (Table 3.1).

More studies were conducted in natural (87.8% of entries) than agricultural (12.2%) habitats, but experiments were more commonly used in agricultural habitats (71.1% experimental for agriculture, 41.4% for natural; Chi-square test for non-independence of system and method; $\chi^2 = 26.99$, df = 1, P < 0.0001). Patch studies were more common that landscape studies (Figure 3.3; 57.4% and 42.6%, respectively), but both scales of investigation relied upon experimental methods to a similar degree (44.8% experimental for patch studies, 45.4% for landscape; $\chi^2 = 0.0066$, df = 1, P = 0.94). Landscape studies were conducted either at single (51.8%) or multiple (48.2%) spatial scales. All major patch- and landscape- level variables were studied, although patch size and the proportion of habitat in the landscape were the most common explanatory variables (Table 3.1).

Predicting trophic interactions in fragmented habitats

The literature search provided strong evidence that the occurrence or strength of many different trophic interactions can be a function of patch size and other variables related to habitat fragmentation. Of all entries and at all scales investigated, nearly half of the entries (338 of the 702 with necessary statistical details) reported significant relationships between the occurrence or strength of a trophic interaction and a fragmentation-related variable (Appendix D). Across the commonly studied interactions of herbivory, parasitoid-host, and predator-prey interactions, impacts of habitat fragmentation on the occurrence or strength of trophic interactions were largely consistent with our predictions (Table 3.2; Figure 3.4; Chi-square test of independence of habitat affinity and consistency of results with predictions: χ^2 = 40.12, df = 2, $P < 0.0001$). Likewise, for each type of trophic interaction separately, we found the predicted relationships between habitat use and study outcome (Figure 3.4), although many interactions were non-significant and we identified several studies of herbivory with results contrary to our expectations (Figure 3.4 A).

Critical Thresholds

Nearly half the entries in our database (310 / 735) were conducted with categorical explanatory variables, making it difficult to detect any patch size thresholds that may have existed in those systems. Of the 425 entries for which the explanatory variable was continuous, only 11 reported a critical threshold in response. Of these, 6 were related to patch size, 3 to edge, and 2 to isolation (Table 3.3); we did not find any studies of landscape-level threshold effects in our database. Despite the small number of studies, the types of interactions exhibiting thresholds were diverse and included herbivory, food chain length, predation, and parasitoid-host interactions (Table 3.3).

Discussion

Predicting trophic interactions in fragmented habitats

We found that trophic interactions were profoundly impacted by the structure of the patch or landscape, indicating that fragmentation processes can have broad impacts on ecological communities by strengthening or weakening trophic interactions. Of the entries in our database presenting the necessary statistics, approximately half (338/702) were significantly affected by a variable related to fragmentation (Appendix D, see also Table 3.2). At first glance, that these significant findings were nearly as often positive as negative may underscore the great difficulties in reaching conclusions about the impacts of fragmentation on species and food webs (van Nouhuys 2005, Chust 2007). However, we argue that the relationship between the occurrence of trophic interactions and variation in patch size, fragmentation, and related variables is quite predictable across the dataset, based on the key ecological trait of the whether the higher-level species in the relationship was a habitat specialist (found only in the patch) or generalist (found in patch and matrix).

Both metapopulation (Hanski 1994) and CPS (Cantrell and Cosner 2001) theories predict that species at higher trophic levels will be more sensitive to habitat loss, patch size, and patch isolation than those of lower trophic levels, and that certain patches may therefore lack top predators. We found that trophic interactions, measured by the frequency of plant damage, the percent of hosts parasitized, the number of prey taken, the length of food chains, and other related measures of trophic interactions (Table 3.1), were indeed strongly impacted by these fragmentation-related variables. In certain cases of highly specialized trophic interactions, critical thresholds for the occurrence of these interactions were observed, in which small or isolated patches were devoid of certain food web interactions (Table 3.3).

In light of these findings, it is instructive to note that the type of trophic interaction (herbivory, parasitoid-host, or predator-prey) did not exhibit a consistent response to fragmentation variables (Table 3.2). Although the trophic hypothesis for extinction risk derived from various theoretical backgrounds (Holt 1996, Cantrell and Cosner 2001) is highly intuitive and has a great deal of empirical support (Table 3.2, "+" entries for habitat specialists; Kruess and Tscharntke 1994, Komonen et al. 2000, Post 2000), knowing *only* the trophic position of a species was not enough information to predict the direction of the response of the trophic interaction to fragmentation: parasitoid-host interactions did not differ substantially from herbivory in the proportion of responses that were positive (Table 3.2), despite the high overlap in the taxonomic representation of these studies (Figure 3.2).

Taking the case of parasitoid-host interactions, which are often highly specific and were thus expected to show strong positive responses to patch size (van Nouhuys 2005), we found unexpectedly mixed study outcomes (Table 3.2). Despite the high specificity in host use for reproduction, parasitoids often use nectar or other alternative resources as adults (Landis et al. 2000). Consistent with this apparent habitat generality, agricultural landscapes in which flowering or overwintering resources were available for adult parasitoids often had higher rates of parasitism (Thies et al. 2003). Likewise, the proximity of flowering matrix habitat increased parasitism in the cabbage herbivore, *Trichoplusia ni* (Lee 2005). These results support the expectations laid out by Tscharntke and Brandl (2004) and van Nouhuys (2005) for how diet breadth and mobility can influence parasitoid abundance and diversity. These conclusions also coincide well with a review of theory by Ryall and Fahrig (2006), who predicted that unrecognized differences in the diet breadth and habitat use of predators in fragmented habitats may underlie some of the idiosyncratic results in empirical papers.

Across studies of herbivore-plant, parasitoid-host, and predator-prey interactions, we found results consistent with predictions based on habitat affinity (Figure 3.4). Trophic interactions involving habitat generalists were negatively impacted by increasing patch size, distance from the patch edge, and the proportion of habitat in the landscape (Table 3.2), and with very few exceptions, study results were either consistent with predictions or non-significant (Figure 3.4 B). These results confirm the predictions of theory (Cantrell et al. 2001) and the consistent findings of studies of bird nest predation and nest parasitism (Patten et al. 2006 and references therein) that such interactions are strongly influenced by edges and fragmentation. Aside from this burgeoning literature of bird reproductive success, several other studies confirm that this negative impact of patch size and distance from edge on interactions involving habitat generalists is a general finding, not specific to nest success of birds in forested habitats. Trophic interactions involving seed predators known to forage both in forest patches and open fields, predominantly small mammals, were often negatively impacted by increasing patch size, distance from edge, and related variables (Jules and Rathcke 1999, Garcia 2007). Large herbivores foraging on patches of grass and heather often used patch habitat more in fragmented landscapes or small patches (Clarke 1995, Hester 1999), likely due to the availability of complementary resources in these landscapes (see Ries et al. 2004).

Although the responses of different trophic interactions to fragmentation-related variables were largely consistent with species' habitat use (Figure 3.4), not every response was correctly predicted. In some cases, trophic interactions involving an assemblage of species were studied, and the identity and importance of individual species was unknown. This was the case for most studies of bird nest predation (for example Manolis 2002), and the overall outcome of these assemblage-level studies may depend on the relative impact of different taxa that respond differently to the landscape. In other cases, factors such as behavior, dispersal ability, or interactions with other species may be important. For example, Cronin (2003) found that the occurrence of parasitism increased but per capita rates of interaction decreased with increasing patch size and attributed this difference to the searching behavior of the parasitoid. Likewise, certain insect herbivores are known to respond positively to the perimeter-to-area ratio of host plant patches, leading to negative patch size – density relationships based on searching behaviors, despite habitat specificity (Hambäck and Englund 2005, Hambäck et al. 2007). These movement and behavioral influences may modify predictions based on habitat use alone, though this information is rarely available. Such influences may be responsible for some of the results for herbivory that were contrary to predictions based solely on habitat specificity (Figure 3.3A).

Critical thresholds

Critical patch sizes for the occurrence of trophic interactions were observed for herbivory and parasitoid-host interactions, as well as FCL (Table 3.3). Likewise, in experimentally-created patches of host plants, Watts and Didham (2006) found that herbivory did not occur farther than 800 m from a source, indicating a critical level of connectivity for this interaction. Similarly, Kruess and Tscharntke (2000) found that parasitism rates dropped precipitously beyond 100 m on small host plant patches. In accordance with theoretical predictions for habitat specialists (Holt 1996, Pereira et al. 2004), only those systems in which the species of higher trophic level was a patch-specialist had demonstrable critical patch sizes or levels of connectivity for occurrence, such that certain patches were devoid not only of the top species, but also of the food web interaction in which it participated.

On the other hand, several authors found strong and non-linear impacts of edges, where trophic interactions were quite strong at the edge and attenuated quickly towards the interior (Table 3.3). Such a strong edge response may mean that certain small patches are all edge. One study also found a strong patch size threshold for matrix-derived predation. In this study, small colonies of nesting shorebirds were strongly susceptible to predation compared to larger colonies, and a critical threshold of 640 nests was required for protection from predation (Cuthburt 2002), as predicted for matrix-derived predators by Cantrell et al. (2001). While more data on fitness for organisms on these small or isolated patches may be necessary to determine if these patches can support viable populations, it is clear that food web interactions, not just single species, can have threshold patch size and connectivity requirements.

Can the patch size requirements for the occurrence of trophic interactions be predicted? While more studies investigating threshold requirements for trophic interactions clearly are needed, our results suggest that the relative patch size requirements of different trophic interactions may depend at least in part on body size or dispersal ability. In insects, body size and wing morphology can be predictors of relative dispersal ability among taxa and are often positively correlated (Roland and Taylor 1996, Tscharntke and Brandl 2004). At a coarse level, those studies in which larger insects were the upper species, small patches of just 21 plants (butterfly herbivory, Kéry et al. 2001) or 11 plants (moths, Munzbergova 2006) were required for the occurrence of the trophic interaction. Trophic interactions involving the substantially smaller gall wasps (Ouborg et al. 2006) or anthomyiid flies (Colling and Matthies 2004) required larger patches of 300 or 495 plants, respectively. Likewise for patch isolation, herbivorous moths colonized patches up to 800 m away from a source (Watts and Didham 2006), whereas smaller wasps were only able to parasitize herbivorous beetles up to a distance of 100 m from a source (Kruess and Tscharntke 2000).

Biases in studies of trophic interactions

With regard to the habitat use of species in well-studied trophic interactions (Table 3.2), some noticeable biases are apparent. For example, of all the studies of predator-prey interactions at habitat edges, the great majority (28 of 29 entries) were of habitat generalist predators (Table 3.2). As predicted, this resulted in strongly negative effects of habitat edges on predator-prey relationships. Predators are indeed often predicted to have large home ranges, mobility, and diet breadth (Holt 1996). However, certain predators may be largely restricted to patch habitat (Döbel et al. 1990), and the impact of habitat edges on such interactions is largely unexplored. We also expect that the consistently positive influence of connectivity across studies (Table 3.2) was due to the strong patch affinity of species chosen for those studies. With respect to increasing proportion of habitat, negative outcomes were most common, and most species studied for this variable were habitat generalists. We suggest that a more complete understanding of the effects of fragmentation, connectivity, and the proportion habitat in a landscape may require the study of species with a more diverse suite of ecological traits.

We found only a handful of studies of parasite-host interactions aside from nest parasitism. These studies reported negative relationships more often than positive, but there are not yet enough data to know how general these trends are. Other poorly-studied trophic interactions included detritivory, fungivory, and decomposition, all of which may be key drivers of ecosystem function (Didham et al. 1999).

Although theoretical studies suggest that FCL increases with patch size (Holt 1996, Brose 2004), few empirical studies have actually tested this prediction. Post and colleagues (2000) found that smaller lakes supported shorter aquatic food chains. In terrestrial forest fragments, an insect food chain was shortened from three to two levels on continuous compared to fragmented habitats (Komonen et al. 2000). Interestingly, although the bulk of the literature in our review was dominated by terrestrial studies, aquatic mesocosms (Spencer and Warren 1996a, b) and natural lakes (Post 2000 et al.) have provided many of the studies of FCL, one of the few three-species interactions found by this review.

Other, more complex three-species interactions were seldom studied. Apparent competition (Figure 3.2, APC) in fragmented habitats has received limited empirical attention but may occur naturally in diverse systems (Bascompte and Melián 2005). For example, associational susceptibility, whereby a focal plant is more likely to suffer from herbivory due to its proximity to palatable plants, can be classified as a specific case of APC. Although a meta-analysis by Barbosa et al.

(2009) did not find that associational susceptibility depended on crop field size, these interactions are also likely to be influenced by edge proximity and other landscape elements. Several studies show that this form of APC can occur in fragmented habitats when the interaction spans a habitat edge. For example, the proximity of landscape elements with complementary resources for herbivores can lead to increased damage on crops (Rand and Tscharntke 2007).

Intraguild predation has also been understudied in fragmented empirical systems. In a study of centipedes, Hickerson (2005) suggested that predation by a native intraguild predator may have kept the invasive intraguild prey at lower densities in patch interiors, but the strength of this interaction was not studied explicitly as a function of spatial position. Few other studies have investigated how habitat fragmentation impacts intraguild predation (IGP; Table 3.1, Figure 3.2). In one example, Amarasekare (2000) found that two parasitoids sharing a harlequin bug host (*Murgantia histrionica*) were more likely to co-occur on large patches and that spatial co-existence was likely mediated through intraguild interactions within their shared host. Based on the frequency of these interactions in real food webs (Bascompte and Melián 2005), the importance of IGP in arthropod food webs (Langellotto and Denno 2004), and the global importance of habitat fragmentation (Saunders et al. 1991, Fahrig 2003), we expect that fragmentation could commonly impact APC, IGP, and other complex food web interactions.

How might these more complex trophic interactions be studied? It is intuitively much easier to demonstrate that a two-species interaction such as herbivory or parasitoid-host interactions has occurred, as the evidence of these is often visible in the form of leaf tissue lost and mummified or parasitized larvae, respectively. In addition to direct observation, new techniques may make the study of food webs in fragmented habitats much easier. Stable isotopes were instrumental in demonstrating the reduction in FCL in temperate lakes (Post et al. 2000) and have been used reliably to assess trophic position and basal resource use (Post 2002a,b). Layman et al. (2007) used isotopes to quantify the functional effects of habitat connectivity on stream fish communities, finding a reduction in trophic diversity and the number of carbon sources used by the fish assemblage in disconnected streams. Another promising approach to quantifying food web interactions is the use of DNA samples taken from consumers' gut contents (Symondson 2002), a technique that has promise to identify how the degree of omnivory and the numbers of prey species might be impacted by fragmentation.

Conclusions

From our study, it is clear that several variables related to habitat fragmentation can significantly impact the occurrence or strength of many different types of trophic interactions. That the study outcomes were significantly related to the habitat use of the interacting species indicates that fragmentation variables do indeed have consistent and predictable impacts on food webs. Trophic interactions involving habitat specialists were often lost with decreases in patch size, whereas those with generalists were often gained. Deviations from these overall trends leave room for the impact of behavior, dispersal, and other traits to be considered, after accounting for habitat affinity.

Key questions moving forward include how fragmentation influences more complex trophic interactions, including food web modules of three or more species, as well as whole-web properties. In one of the few studies to investigate how human modification of landscapes may impact properties of complete food webs, Tylianakis et al. (2007) found that species richness of parasitoids and hosts did not change along a gradient of human impact, but the structure of the interaction webs did. Thus, trophic interactions may be more susceptible than other measures of community structure to alteration by human disturbance, habitat fragmentation, and other landscape changes. Additionally, how changes in guild structure, species richness, and population density may translate into altered rates of trophic interactions remains a major challenge in predicting the multifaceted impacts of habitat fragmentation.

Acknowledgements

We thank members of the Fagan Lab Group for guidance on this project, especially Leslie Ries for helpful comments on an earlier version of this manuscript. HM was supported by the Ann G. Wylie Dissertation Fellowship, the BEES program, and an NSF-DIG (DEB-07100004).

Tables

Table 3.1. Food web interactions studied with respect to patch and landscape scale fragmentation variables. Rows list major categories and subcategories of trophic interactions. Columns list well-studied fragmentation variables, at either patch or landscape scales. Each unique combination of interacting species was considered for all relevant spatial variables, leading to a total of 735 entries from 171 studies.

	Patch Scale			Landscape Scale					
	Patch Connectivity	Distance from Edge	Patch Size	Fragmentation	Diversity	Matrix	Proportion	Other	Total
Herbivory	47	33	86	13	3	17	31		230
florivory	4	1	6			10			21
folivory	3	3	7	4					17
frugivory	1	1	2	1			3		8
galling		1	1	1					3
herbivory	6	1	15	4			5		31
leaf mining	1	4	2						7
oviposition	7	3	13			3	6		32
root herbivory		1	2	2					5
seed predation	16	14	29	1		4	7		71
seedling herbivory		4	2						6
stem-boring	9		7		3		10		29
Parasite-Host	2	15	31	23		2	12	5	90

bacterial infection			1					4	5
cestode infection			1	1					2
ectoparasitism		3	2						5
fungal infection	1		7						8
nematode infection			13	12					25
nest parasitism		12	2	4		2	12	1	33
protist infection			5	6					11
viral infection	1								1
Parasitoid-Host	32	20	41	2	17	38	62		212
Predator-Prey	5	29	28	14	13	10	16	25	140
nest predation		18	9	3	10	8	13	21	82
predation	5	11	19	11	3	2	3	4	58
Other Two-Species	3	4	24	2					33
ant-tending	1		10						11
decomposition				1					1
detritivory			6						6
fungivory				1					1
seed dispersal	2	4	8						14
Three-Plus Species	4		18	6				2	30
indirect	1		3						4
apparent competition				1				2	3
food chain length	2		5	1					8
omnivory	1		3	1					5
two consumers			7	3					10
Grand Total	93	101	228	60	33	67	121	32	735

Notes: The sub-category ‘omnivory’ also includes studies of intraguild predation (Figure 3.2: IGP). The sub-category ‘two consumers’ refers to two consumers sharing one resource (Figure 3.2: 2C1R). The column “other” comprises studies of patch arrangement, edge density, and mean patch size in a landscape.

Table 3.2. The responses of trophic interactions to patch size, connectivity, distance from a patch edge, the fragmentation of habitat, and the proportion habitat in the landscape for A) herbivory, B), Parasitoid-host, and C) Predator-prey interactions. Responses were considered negative (-) if the trophic interaction occurred less frequently with increasing values of the explanatory variable, positive (+) if it occurred more frequently, and non-significant (n.s.) if the study found no difference. Number of studies involving habitat generalists and specialists are given (Studies columns).

	Habitat Generalists				Habitat Specialists				*Grand*
Trophic Interaction	-	+	n.s.	Studies	-	+	n.s.	Studies	*Total*
A *Herbivory*	*26*	*6*	*27*	*59*	*26*	*46*	*58*	*130*	*189*
patch size	7	2	9	18	14	19	24	57	*75*
connectivity		1	9	10	2	13	20	35	*45*
edge	13		6	19	5	6	1	12	*31*
fragmentation	1	1	1	3		4	1	5	*8*
proportion habitat	5	2	2	9	5	4	12	21	*30*
B *Parasitoid-Host*	*13*	*2*	*18*	*33*	*7*	*30*	*61*	*98*	*131*
patch size	4	1	2	7		10	14	24	*31*
connectivity			4	4	4	9	10	23	*27*
edge	4	1	3	8	2	3	5	10	*18*
fragmentation						1	1	2	*2*
proportion habitat	5		9	14	1	7	31	39	*53*
C *Predator-Prey*	*27*	*4*	*38*	*69*		*14*	*5*	*19*	*88*
patch size	9		10	19		5	1	6	*25*
connectivity	1	1	1	3		2		2	*5*
edge	10	2	16	28		1		1	*29*
fragmentation	1		4	5		6	2	8	*13*
proportion habitat	6	1	7	14			2	2	*16*
Grand Total	*66*	*12*	*83*	*161*	*33*	*90*	*124*	*247*	*408*

Table 3.3. Critical thresholds for the occurrence of trophic interactions. Thresholds were identified for several fragmentation-related variables (*Variable*) and for herbivory, seed predation, food chain length, predation, and parasitoid-host interactions (*Type*). For each study, the lower and upper species are given, as well as the threshold identified by the authors of the study.

Study	Variable	Type	Lower Species	Upper Species	Threshold
Ouborg et al. 2006	patch size	herbivory	*Salvia pratensis*	*Aylax salviae*	herbivory unlikely below 300 plants
Kéry et al. 2001	patch size	herbivory	*Gentiana cruciata*	*Maculinea rebeli*	21 genets required for 95% probability of occurrence
Munzbergova 2006	patch size	seed predation	*Aster amellus*	*Coleophora obscenella*	seed predation unlikely below 11 ramets
Colling and Matthies 2004	patch size	seed predation	*Scorzonera humilis*	*Heterostylodes macrurus*	495 genets required for 95% probability of occurrence
Post et al. 2000	patch size	food chain length	seston, zooplankton	*Micropterus salmoides, Salvelinus namaycush*	increase from 3.5 to 5 trophic levels with increasing lake size
Cuthbert 2002	patch size	predation	*Puffinus huttoni, P. griseus*	*Sus scrofa, Mustela erminea*	sharp decline in mortality due to predation in patches with more than 620 burrows
Nickel et al 2003	edge	seed predation	*Desmanthus illinoensis, Dalea purpurea*	*Microtus pennsylvanicus*	seed predation leveled off past 2 m from an edge in mice in an old field
Manolis et al. 2002	edge	predation	ground-nesting birds	predator assemblage	high mortality at edge levels off after 100 m
Tylianakis et al. 2004	edge	parasitoid-host	*Metopolophium dirhodum*	*Aphidius rhopalosiphi*	negative exponential decline in parasitism with distance from edge
Watts and Didham 2006	isolation	herbivory	*Sporadanthus ferrugineus*	*Batrachedra sp.*	no herbivory observed on experimental patches greater than 800 m from source
Kruess and Tscharntke 2000	isolation	parasitoid-host	*Oxystoma ochropus*	Pteromalids, Braconids, Eupelmids	no parasitism observed farther than 100 m from a source

Figure Legends

Figure 3.1. Predictions for how habitat fragmentation influences trophic interactions involving A) habitat specialists and B) habitat generalists. Patch habitat is represented by large gray ovals and is utilized by a lower species (white ovals) and upper species (black ovals) engaged in trophic interactions. Arrows denote the flow of resources, such that habitat specialists (A) utilize only patch habitat and generalists (B) utilize both patch and matrix, although the relative use of patch and matrix for generalists may vary among species. Below: definitions and predictions for how variables associated with fragmentation may influence the occurrence, frequency, or strength of trophic interactions. A trophic interaction may occur more (↑) or less (↓) frequently with increasing values of the fragmentation variable, or may depend upon the exact nature of the matrix surrounding the habitat (↕).

Figure 3.2. The frequency of two- and three-species food web interactions, or modules (see Holt 1996), that have been studied with respect to fragmentation variables, with the percent of total entries and the number of entries in each category in parentheses. i) Two-species, ii) linear food chain (FCL), iii) shared consumer or apparent competition (APC), iv) two consumers on one resource (2C1R), and v) intraguild predation (IGP) or omnivory modules.

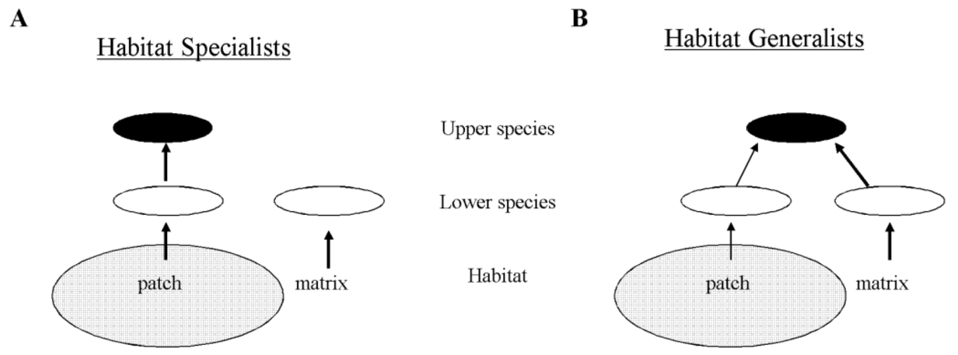
Figure 3.3. Studies have investigated trophic interactions in fragmented habitats at the patch (A) and landscape (B) scales among diverse taxa. Basal taxa are arranged in rank order in the full dataset along the abscissa. For each basal taxon, the upper

taxon with which it interacted in a given study is indicated by various shades of gray. For clarity, only the most frequent taxa at the lower and upper levels in the trophic interaction are presented.

Figure 3.4. The relationship between habitat affinity and the outcome of trophic interactions in fragmented habitats. A) Habitat specialists as the upper species in the trophic interaction. B) Habitat generalists as the upper species. Each study result was considered to be consistent with predictions based on habitat affinity (white bars), inconsistent with predictions (black bars), or non-significant (gray bars; based on data in Table 3.2). Results are presented for herbivory, parasitoid-host, and predator-prey interactions. For each type of trophic interaction, the relationship between habitat affinity and the consistency of findings with our predictions was significant. Herbivory: $\chi2 = 17.93$, $df = 2$, $P = 0.00013$. Parasitoid-host: $\chi2 = 23.15$, $df = 2$, $P < 0.0001$. Predator-prey: Fisher's exact test (used due to low expected frequencies), $P < 0.0001$.

Figures

Figure 3.1



Habitat Specialists	**Fragmentation-related variables** Definitions and Examples	**Habitat Generalists**
↑	**Patch size** Area of habitat patch, volume of a discrete body of water, or number of hosts in a patch.	↓
↑	**Edge distance** Distance into a patch from the boundary between patch and matrix.	↓
↑	**Patch connectivity** Ease of movement between patches.	↓
↓	**Patch isolation** Distance between patches.	↑
↓	**Fragmentation** Breaking up of habitat, fragments vs. continuous habitat.	↑
↑	**Proportion habitat** Proportion of focal habitat in landscape.	↓
↕	**Matrix** Type of habitat surrounding a patch. Predictions depend on type of matrix.	↕

Figure 3.2

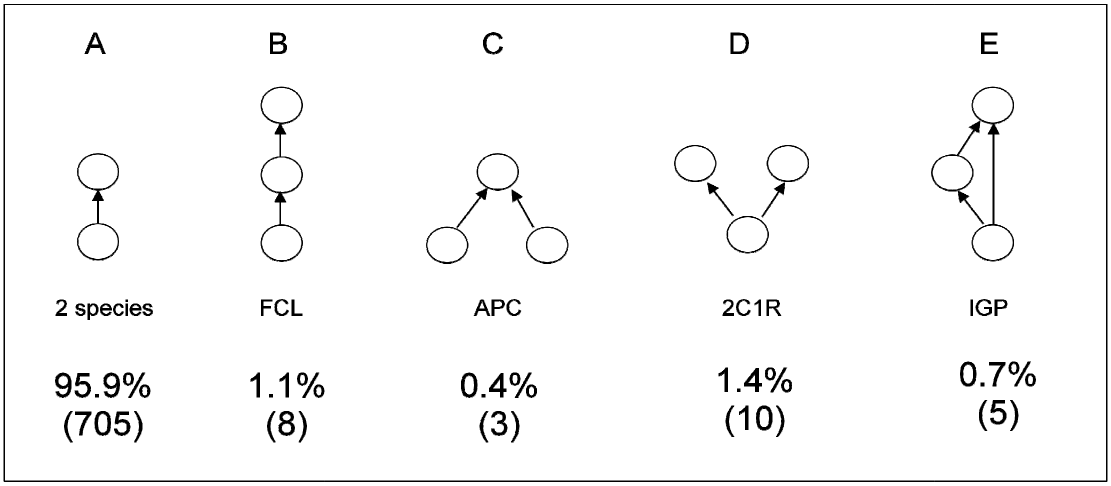


Figure 3.3

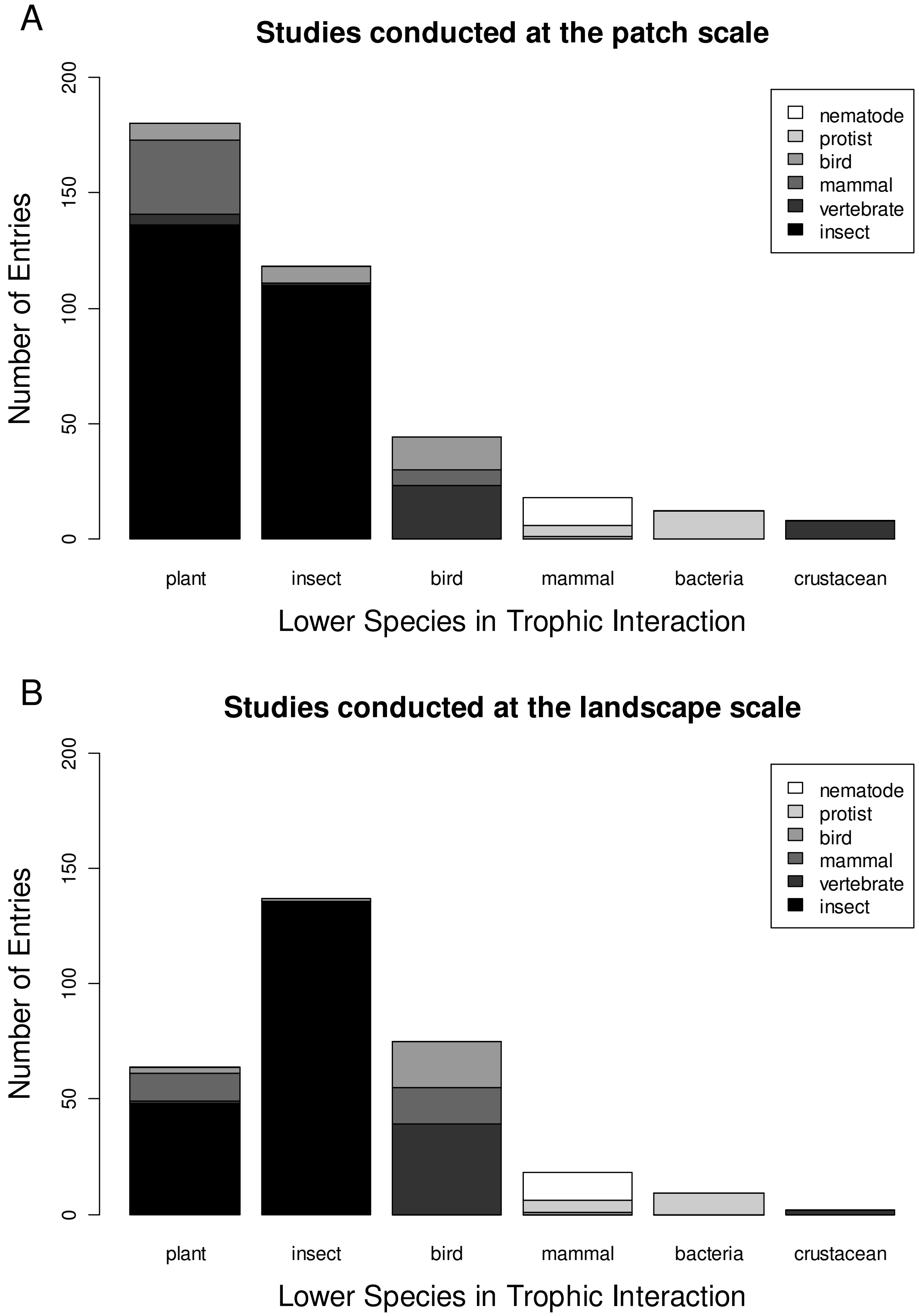
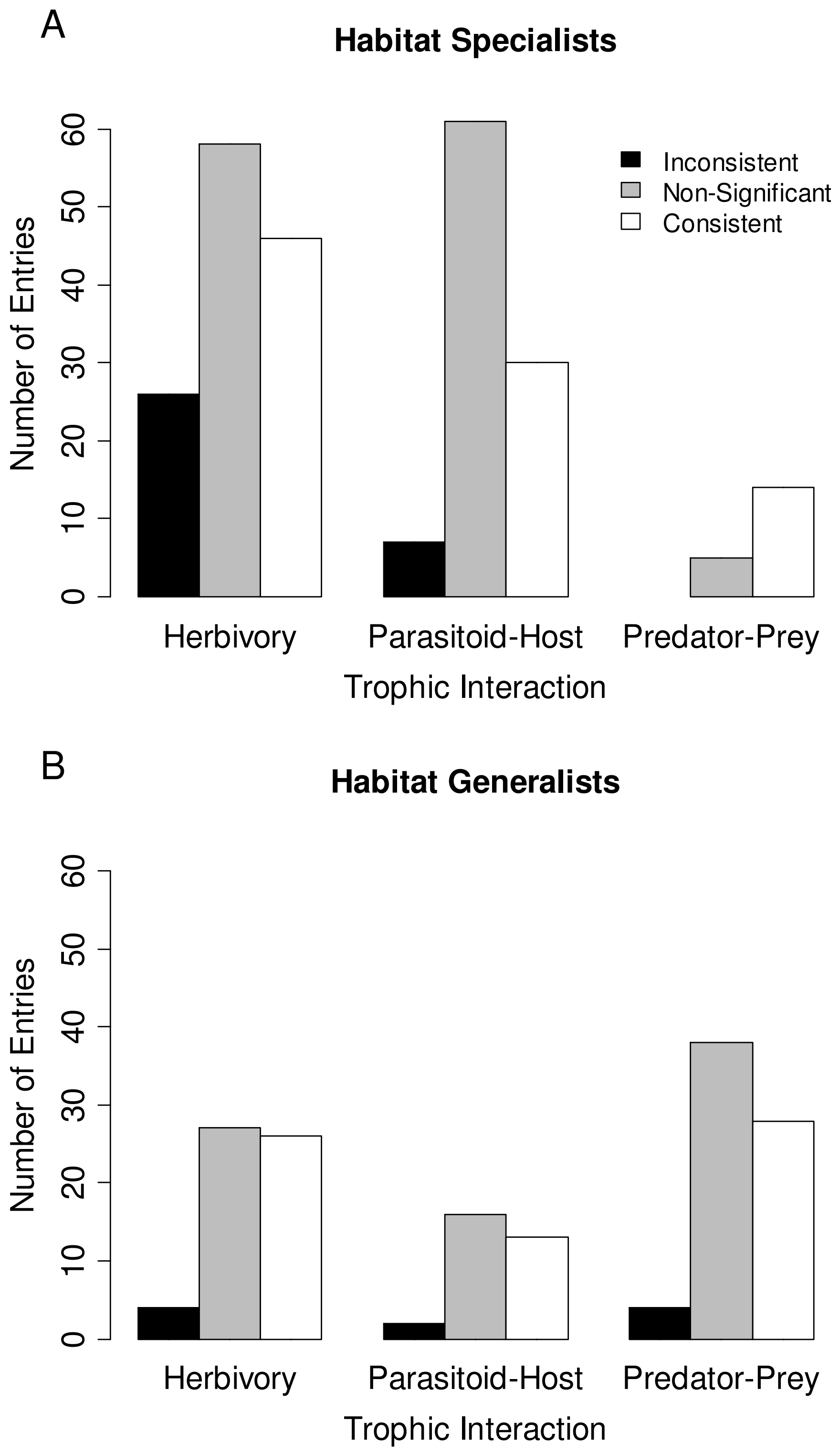

A
Studies conducted at the patch scale
Number of Entries
0
50
100
150
200
nematode
protist
bird
mammal
vertebrate
insect
plant
insect
bird
mammal
bacteria
crustacean
Lower Species in Trophic Interaction
B
Studies conducted at the landscape scale
Number of Entries
0
50
100
150
200
nematode
protist
bird
mammal
vertebrate
insect
plant
insect
bird
mammal
bacteria
crustacean
Lower Species in Trophic Interaction

Figure 3.4


A
Habitat Specialists
Number of Entries
0
10
20
30
40
50
60
■ Inconsistent
▨ Non-Significant
☐ Consistent
Herbivory
Parasitoid-Host
Predator-Prey
Trophic Interaction
B
Habitat Generalists
Number of Entries
0
10
20
30
40
50
60
Herbivory
Parasitoid-Host
Predator-Prey
Trophic Interaction

Chapter 4: Critical Patch Sizes for Food Web Modules

Co-authored with: *W. F. Fagan and R. F. Denno*

Abstract

A key concept in spatial ecology is that of the critical patch size, the minimum habitat patch size below which a species is not predicted to persist. As a step towards understanding the complex ways in which spatial structure and habitat fragmentation may influence biological systems, we examined how the critical patch size concept might be applied not only to individual species but to entire food web modules in patchy habitats. In a well-studied arthropod assemblage, food web modules (sets of interacting species within a larger food web) exhibited patch size thresholds. The potential for parasitism, egg predation, and intraguild predation all increased as functions of patch size, indicating that food web structure and dynamics may vary systematically among patches in a network, and providing concrete empirical support for a key prediction from spatial food web theory.

Introduction

Spatial ecology has often focused on the primacy of patch size and connectivity (or its inverse, isolation) in determining species richness (MacArthur and Wilson 1967) and occupancy patterns (Levins 1969, Hanski 1994). While the number of species generally increases with patch size and decreases with patch isolation (MacArthur and Wilson 1967, Connor and McCoy 1979), classic island biogeographic approaches do not address which species are likely to be found on a given patch, nor how interspecific interactions are likely to differ on large, well-connected patches compared to smaller, more isolated patches.

A key concept in spatial ecology is that of critical patch size (CPS), which is the minimum habitat size below which a species is not predicted to persist (Skellam 1951, Kierstead and Slobodkin 1953, Ludwig et al. 1979). Critical patch size theory predicts that thresholds for species persistence exist where loss from a patch via death and dispersal is greater than gain through birth and immigration. CPS theory has been used to predict the relative extinction risk of Costa Rican vertebrates (Pereira et al. 2004, Pereira and Daily 2006), the size of species' geographic ranges in fragmented landscapes (Fagan et al. 2009), the spatial spread and outbreak dynamics of forest pests (Ludwig et al. 1979, Cobbold et al. 2005), and the persistence of herbivores in the face of predator incursions (Cantrell et al. 2001).

In other contexts, CPS theory has been extended to focus on sets of interacting species. For example, theory predicts that food chain length may be constrained by patch size, at least for chains of stacked specialists (Holt 1996, Cantrell and Cosner 2001, Holt 2002). A key theoretical paper by Melián and Bascompte (2002) also demonstrated that the persistence of a particular species can be determined not only by the amount of habitat available, but also by the types of trophic interactions in which that species is engaged. For a given patch size, species engaged in intraguild predation (see Polis et al. 1989) and strict linear food chain interactions were more susceptible to extinction as a function of habitat loss than omnivores feeding on both producer and consumer species (Melián and Bascompte 2002). These findings lead directly to the prediction that food web modules will themselves exhibit critical patch size dynamics depending on the types of interactions involved and the traits of the species in the modules (Melián and Bascompte 2002). This prediction has not previously been tested.

To examine empirically whether species and their interactions exhibit critical patch sizes, we studied the arthropod community found on patches of the salt marsh grass, *Spartina patens* (Ait.) Muhl. From previous research in this well-studied system, it is known that many patch-specialist species have strong density-area relationships (Raupp and Denno 1979, Hines et al. 2005, Chapter 1) and that species interactions can be important drivers of population dynamics and community structure (Denno et al. 2000, Finke and Denno 2002, Denno et al. 2005, Chapter 2). For this paper, we identified species engaged in different types of food web interactions and tested the hypothesis that individual species have critical patch size thresholds that depend on ecological traits such as habitat specificity and trophic position. Second, we asked whether the incidence of food web modules involving these species exhibited threshold patch sizes for occurrence and how such thresholds might vary among module types (Melián and Bascompte 2002).

Overall, we found that small patches not only predictably lacked certain patch specialist and predaceous species but also lacked the species interactions and food web modules (parasitism, egg predation, and intraguild predation) characteristic of large habitat patches.

Methods

Delineation of habitat patches

This study was conducted on a spatially extensive intertidal salt marsh found in the Great Bay – Mullica River estuarine system in Tuckerton, New Jersey. The high marsh grass *Spartina patens* (hereafter SP) is generally found in pure stands above mean high water level and has a characteristic dense thatch layer of previous years' growth through which its narrow live culms protrude (Blum 1968, Bertness and Ellison 1987). In contrast, the low marsh grass *Spartina alterniflora* Lois. (hereafter SA) found near mean high water level and adjacent to SP has flat, broader leaves, lower culm density, and little thatch accumulation (Blum 1968, Denno 1977). The differences between the two species lead to sharp and visually distinct patch boundaries. The marsh at Tuckerton, NJ, is characterized by extensive meadows of SA punctuated by discrete patches of SP at higher elevations (Raupp and Denno 1979, Hines et al. 2005), presenting a relatively simple, nearly binary landscape with patch (SP) and matrix (SA) habitats.

Perimeters of accessible SP patches were mapped with a handheld global positioning device (Garmin GPS 72; Olathe, Kansas, USA). Patch size and orientation were recorded in the field, and all data were imported into a Geographic Information System (ArcView GIS 3.3; ESRI, Redlands, California, USA). Very large patches and those that were inaccessible due to the presence of tidal creeks were identified on a 1 m^2 resolution aerial photograph (USGS digital orthophoto quadrangle) and manually digitized, leading to 634 SP patches at this field site.

Sixty-two accessible patches, spanning four orders of magnitude of patch size (from 0.3 to 5679 m^2), were selected for repeated arthropod surveys in 2005.

Arthropod communities in habitat patches and matrix are largely complementary

Decades of study have revealed *Spartina patens* and *S. alterniflora* to have distinct but largely analogous food webs (Denno 1977, Döbel et al. 1990, Finke and Denno 2002, Hines et al. 2005). Insect herbivores and their specialist predators show high levels of host specificity and are found exclusively on either SP or SA (Denno 1977). On SP, the most common herbivores are *Tumidagena minuta* McDermott and *Delphacodes detecta* (Van Duzee; Delphacidae; Raupp and Denno 1979, Hines et al. 2005), whereas *Prokelisia marginata* (Van Duzee) and *P. dolus* Wilson dominate on SA (Denno 1977). Specialist parasitoids of the genus *Haplogonatopus* (Dryinidae) attack these herbivores, and parasitized individuals can be assessed visually (Hines et al. 2005). Research on the SA community has found that another specialist predator, the mirid bug *Tytthus vagus* Knight (Hemiptera), is an important egg predator of *Prokelisia* planthoppers in SA (Finke and Denno 2002). In parallel, the congener *T. alboornatus* is common in SP (Hines et al. 2005).

The top arthropod predators on the marsh are hunting spiders (Döbel et al. 1990, Denno et al. 2003). Like the herbivores, parasitoids, and egg predators discussed above, some spiders exhibit strong habitat specificity. For example, *Thanatus striatus* Koch (Philodromidae) is a relatively abundant spider in SP but is largely absent from SA habitats (Döbel et al. 1990). This spider has a generalized diet and has been observed to feed spontaneously on both *T. minuta* and *T. alboornatus* (from SP; H.M., pers. obs.). In contrast, *Pardosa littoralis* Banks

(Lycosidae), which is the most abundant spider in both SP and SA (Döbel et al. 1990), is a habitat generalist. *Pardosa littoralis* has a generalized diet and is a known intraguild predator, feeding both on herbivores and other predators (Finke and Denno 2002, Denno et al. 2004). Thus, intraguild predation (IGP) is possible for both spiders, and a comparison can be made for how the incidence of each IGP module varies with patch size.

Assessment of diet composition of Tytthus alboornatus *in laboratory mesocosms*

In contrast to all the other species interactions discussed here, each of which was already well-documented, diet composition of *T. alboornatus* had not previously been investigated but was established as part of this study. To test whether *T. alboornatus* feeds on either of the two most common planthoppers in SP, we set up a laboratory mesocosm experiment. SP was purchased from Environmental Concern (St. Michaels, Maryland, USA) as 5 cm plugs originally grown from seed and was grown in the greenhouse at the University of Maryland for one month before use. Mesocosms were constructed with one plug of SP in a 9.5 cm wide pot, with a 30 cm high x 7.5 cm diameter cellulose butyrate cage topped with organdy mesh (as in Denno et al. 2000, Finke and Denno 2002). *Tumidagena minuta*, *D. detecta*, and *T. alboornatus* were collected in Tuckerton using a D-Vac suction device with a 0.093 m^2 sampling nozzle (D-Vac Company, Ventura, California, USA) and transported back to Maryland separately in spare mesocosms. Twenty adult *T. minuta* or *D. detecta* were added to 14 SP mesocosms each and allowed to oviposit for eight days. Two female and two male *Tytthus alboornatus* were added to half the cages and allowed to feed for two weeks. The number of herbivore nymphs per mesocosm was then assessed, and t-tests were used to compare predator-free and predator-addition treatments for each of the two herbivore species.

Arthropod Sampling

Samples of the arthropod community on 62 SP patches were taken in the early and peak growing season of 2005 (July 4 and July 29, respectively; see Hines et al. (2005) for further discussion of seasonality in this system). Community sampling was conducted with the D-Vac suction sampler fitted with a 0.031 m^2 sampling head (the smaller opening providing effective sampling of spiders) for 4 second placements, or "plunks". Sampling effort was scaled with patch size to avoid over-sampling small patches and under-sampling large ones and ranged from 2 plunks on the smallest patches to 10 plunks on the largest patches. These methods yielded a higher proportion of total patch area sampled for the smallest patches, meaning that our tests of patch size effects should be conservative. Samples were transferred to 70% ethanol and counted in the lab.

Identification of food web modules and determination of critical patch sizes

Based on life history and inference from the SA food web (Denno 1977, Finke and Denno 2002, Denno et al. 2004, Hines et al. 2005), we identified the following potential food web modules in SP: 1) egg predation of the herbivore *Tumidagena minuta* by *Tytthus alboornatus*, 2) parasitism of *T. minuta* by *Haplogonatopus sp*., 3) intraguild predation involving *Pardosa littoralis*, *T. alboornatus*, and *T. minuta*, and

4) intraguild predation involving *Thanatus striatus*, *T. alboornatus*, and *T. minuta*. We also considered the full set of all five species to investigate how critical patch size may scale with the number of species in a module. We first examined the single species' responses of each of these five species to gauge whether critical patch sizes existed for individual species according to their trophic level and habitat specificity. Assessments of critical patch size used species incidence (presence) as the response variable and $\log_{10}$ transformed patch size (m^2) as the predictor variable. Based on logistic regression parameter estimates, we then calculated the patch size at which the probability of occurrence of each species would be 0.1, 0.5, and 0.9.

We then tested whether the incidence of these food web modules varied with patch size, scoring the module as present on a patch only if all the component species were present. It was possible to assess the incidence of parasitism in two different ways, first as the co-occurrence of *T. minuta* herbivores and adult *Haplogonatopus* parasitoids and second as the occurrence of parasitized *T. minuta* individuals. We present both calculations, which we term the 'occupancy' parasitism module and the 'evidence' parasitism module, respectively, when considering the parasitism and five-species modules. As with the single species analysis, we used logistic regression for each sample date and calculated the patch size requirements for the occurrence of these modules according to 0.1, 0.5, or 0.9 probability of patch occupancy by the complete module. Finally, we assessed how the intensity of these food web interactions varied with patch size, for both the egg predation and the parasitism modules. For egg predation, we calculated intensity as the ratio of egg predators (*T. alboornatus*) to herbivorous prey (*T. minuta*), which was then $\log_{10}$ transformed to better meet model assumptions. We assessed whether this ratio was a function of patch size with linear regression. For parasitism, we calculated intensity using a generalized linear model with binomially distributed error terms to assess whether the proportion of herbivores parasitized was a function of $\log_{10}$ transformed patch size.

Results

Assessment of diet composition of Tytthus alboornatus *in laboratory mesocosms*

Fewer nymphs of the most common *Spartina patens* herbivore, *Tumidagena minuta*, were produced in the laboratory mesocosms also containing the egg predator *Tytthus alboornatus* than in predator-free mesocosms (t = 3.38, df = 10.04, P = 0.007). In contrast, *Tytthus* had no significant effect on nymphal production for the second most common herbivore, *Delphacodes detecta* (t = 1.48, df = 11.34, P = 0.167). We thus focus on *T. minuta* for the remainder of our analyses.

Critical patch sizes for individual species

Tumidagena minuta incidence increased as a function of patch size in the early season sample; however, by peak season, this herbivore was found on nearly every SP patch, and we found no evidence for incidence depending on patch size. (Figure 4.1a, Table 4.1). Incidence of the egg predator, *T. alboornatus*, increased strongly with patch size both in the early and peak season samples (Figure 4.1b). Adults of the dryinid parasitoid, *Haplogonatopus sp.,* also exhibited strong increases in patch occupancy with increasing patch size, and this pattern was strongest in the early season (Figure 4.1c). *Pardosa littoralis*, a top predator that exhibited both feeding and habitat generalization, was found on every patch regardless of size in both early and peak samples. The incidence of the largely patch-based spider, *Thanatus striatus*, increased significantly as a function of patch size (Figure 4.1d).

The patch sizes required for 50% probability of occurrence also varied greatly among species: the herbivore and egg predator required only small patches (< 2 m^2) for 50% occupancy, especially in the peak season. In contrast, the SP spider, *T. striatus*, had larger patch size requirements for 50% occurrence (13.5 m^2 early and 8.8 m^2 peak season), and the parasitoid, *Haplogonatopus*, was only predicted to occur with 50% probability on patches at least 643 m^2 (early) or 78 m^2 (peak season) in size (Table 4.1).

Critical patch sizes for food web modules

The incidence of particular food web modules increased with patch size. Egg predation of *T. minuta* by *T. alboornatus* was more likely to occur on large compared to small patches (Figure 4.2a, Table 4.1) and required larger patches to be observed with 50% probability than when considering *T. alboornatus* occupancy alone (module occupancy: 3.3 m^2 early and 1.4 m^2 peak season; single species: 0.8 m^2 (early) and 0.9 m^2 (peak); Table 4.1). The intensity of this interaction, measured as the log-transformed ratio of egg predators to herbivorous prey, also increased with patch size in the early season sample (Figure 4.2b; early: $\log(y) = 0.287 + 0.164 \log(x)$, $F = 9.79$, $R^2 = 0.185$, $P = 0.003$; late: $\log(y) = 0.231 + 0.031 \log(x)$, $F = 0.643$, $R^2 = 0.011$, $P = 0.426$). Parasitism of *T. minuta* also increased with patch size: the co-occurrence of this herbivore and adult *Haplogonatopus* parasitoids matched exactly the single-species incidence of *Haplogonatopus* (Table 4.1), and the incidence of parasitized herbivores also increased strongly with patch size (Figure 4.2c; Table 4.1). The patch size required for 50% probability of occurrence of parasitism was even higher than for egg predation (parasitism ‘occurrence’: 643 m^2 early and 78 m^2 peak; ‘evidence’: 53.3 m^2 early and 11.8 m^2 peak season). Likewise, the intensity of parasitism, measured as the proportion of individuals parasitized, was an increasing function of patch size, especially in the peak season sample (Figure 4.2d; early: $y = -5.515 + 0.255 \log(x)$, $P = 0.006$; peak: $y = -5.475 + 0.780 \log(x)$, $P < 0.001$).

The potential for intraguild predation involving *P. littoralis*, the mesopredator *T. alboornatus*, and the herbivore *T. minuta* increased with patch size on both sample dates (Fig 3a, Table 4.1). Incidence of intraguild predation with *Thanatus striatus* as the top predator exhibited even stronger patch size effects, requiring patches that were five to ten times larger in size to occur with 50% probability (*Pardosa* module: 3.3 m^2 and 1.4 m^2 for early and peak season, respectively; *Thanatus* module: 17.4 m^2 and 13.9 m^2; Fig 3b, Table 4.1). Considering the full module of all five species, incidence likewise increased with patch size and required larger patches for 50% probability of occurrence than any of the other modules (Table 4.1; calculated with parasitoid occurrence data: 697.2 m^2 (early) and 105.6 m^2 (peak); with ‘evidence’ data: 215 m^2 (early) and 31.4 m^2 (peak)).

Discussion

A pressing concern in ecology and conservation biology is the disruption of species interactions in the face of habitat fragmentation and spatial structure (Kremen et al. 2007, Tylianakis et al. 2007). While whole food web studies can provide insight as to how the number and types of links are disrupted by fragmentation, most food webs are not fully defined. Food web modules, as discrete entities of intermediate complexity between single species and full food webs, may be appropriate units of study to discover the multi-species effects of habitat loss or fragmentation (Holt 1996, 2002).

Food chains, which are simple linear food web modules, increase in length as a function of forest (Komonen et al. 2000), lake (Post et al. 2000), and island size (Takimoto et al. 2008). Looking beyond strictly linear food chains, Melián and Bascompte (2002) found that the type of trophic interaction in which a predator is engaged is a key determinant of that predator's survival in the face of habitat destruction. In that study, species engaged in intraguild predation had lower occupancy and a higher probability of extinction compared to those involved in apparent competition, linear food chains, or omnivorous interaction modules. The occupancy patterns of the basal and intermediate species also differed with module type (Melián and Bascompte 2002), leading to the hypothesis that the occurrence of food web modules themselves might depend both on module topology and the amount of habitat available. Here, we have demonstrated empirically that food web modules, in addition to single species, are indeed strongly impacted by habitat patch size. This was true for two-species predation and parasitism interactions as well as for more complex modules involving intraguild predation.

In this study, the incidence of all patch specialists increased as a function of patch size (Figure 4.1), and, with the exception of the herbivore, *Tumidagena minuta*, this trend persisted across sampling dates. Two patch specialist consumers, the parasitoid *Haplogonatopus sp*. and the spider *Thanatus striatus*, exhibited critical patch size thresholds and were unlikely to occur on small SP patches in this system (Table 4.1). These data demonstrate that habitat specificity and trophic position are important traits in predicting species' sensitivity to spatial structure (Ewers and Didham 2006).

The potential for two-species modules also increased with patch size (Figure 4.2). The incidence of the *Tytthus alboornatus – T. minuta* egg predation module was an increasing function of patch size, and the ratio of egg predators to herbivorous prey also increased with patch size. Likewise, the incidence of parasitism by *Haplogonatopus sp.* and the proportion of *T. minuta* herbivores parasitized increased sharply with patch size. Together, these findings suggest that herbivores in this system may face substantially reduced pressure from specialist natural enemies on small patches. Our findings are consistent with other studies that have found parasitism to depend on patch size and other spatial variables (Kruess and Tscharntke 1994, Roland and Taylor 1997, Cronin 2003), contributing to herbivore outbreaks. The marsh food web appears to have similar spatial and life history characteristics as some of these other studies, with a relatively common herbivore parasitized less often on small patches. However, herbivore outbreaks seem unlikely in the marsh system for two reasons. First and most importantly, parasitism rates in this study were all below 10%, even in large patches, and thus suppression of herbivores by parasitoids is unlikely (Hawkins and Cornell 1994). Second, other studies in the marsh have shown that generalist predators can strongly impact herbivore and mesopredator populations (Finke and Denno 2002, Chapter 2). Initial tests of grass quality found no co-variation between patch size and the nutrient quality of the SP host plants (Chapter 1), so resource quality is not likely to explain the dependence of occupancy on patch size.

Comparing between these two-species modules, the occurrence of parasitism required much larger patches than did egg predation (Table 4.1), a pattern which may be due to the relative rarity of the parasitoid *Haplogonatopus sp.* compared to *T. alboornatus* (see also Hines et al. 2005). These modules also differed with respect to the occupancy patterns of their component species. The occurrence of egg predation required larger patches than did either the herbivore *T. minuta* or the egg predator *T. alboornatus* in the early season, indicating the presence of the egg predator on patches apparently devoid of its prey. As our sampling methods only captured active life stages, it is likely that herbivores were present only as eggs during this sample, and indeed, *T. alboornatus* was only found on patches occupied by its prey in the peak season. While the occurrence of parasitism also increased with patch size, results from the two methods of quantifying this module differed. No *Haplogonatopus* adults were observed on patches devoid of herbivores, so the co-occurrence of parasitoid adults and *T. minuta* herbivores matched exactly the single species parasitoid patterns (Table 4.1). In contrast, parasitized herbivores were present on smaller patches than were adult parasitoids (Table 4.1), likely due to a combination of poor detection of adult parasitoids via suction sampling and potential interpatch movement by parasitoids. Parasitized herbivores provide evidence of parasitism that persists long after *Haplogonatopus* actually interacts with *T. minuta* and provide the more functional measure of the incidence and intensity of this module.

The potential for hunting spiders to engage in intraguild predation (IGP) was also an increasing function of patch size (Figure 4.3), especially when considering modules comprising species restricted to SP patch habitat. The full, five-species module represented the assemblage of natural enemies of the herbivore *T. minuta* (Hines et al. 2005; see van Nouhuys and Hanski (2005) for a similar approach) and included not only the egg predation, parasitism, and two IGP modules, but also the potential for the intraguild predation of *T. striatus* by *P. littoralis*. Although techniques such as stable isotope analysis may be necessary to determine the exact trophic position of generalist predators such as *P. littoralis* (Post et al. 2000), it is likely that this predator consumes other spiders in SP habitat (see Denno et al. 2004), and this additional IGP module may only be possible on large patches (Table 4.1). While the number of trophic links in a food chain has long been hypothesized to influence community dynamics (Pace et al. 1999), recent studies have demonstrated that IGP is both widespread and important, with the potential to influence species coexistence, alter habitat use, and create alternative stable states (Polis et al. 1989, Arim and Marquet 2004). A recent analysis of empirical food webs by Bascompte and Melián (2005) found that modules involving intraguild predation and apparent competition are more common than expected by chance, while the frequency of other modules, such as those involving omnivores, appears to be context-dependent. Thus, these more complex food web modules are major components of real food webs and, like linear food chains, can be influenced by spatial structure.

The incidence of these food web modules closely matched the incidence of some of their component species. For example, the *Pardosa littoralis* IGP module was strongly influenced by the occupancy patterns of the mesopredator, *T. alboornatus*, whereas the occurrence of the *Thanatus striatus* IGP module was largely determined instead by the occupancy patterns of the top predator itself. The full, five-species module likewise followed closely the occupancy patterns of one species, the parasitoid *Haplogonatopus sp.* Just as colonization and extinction rates of species can lead to the dependence of food chain length on patch size (Holt and Hoopes 2005), so might these rates influence other, more complex modules. Constraining the patch size requirements for *P. littoralis* IGP, the spatial occupancy patterns of the largely flightless mesopredator *T. alboornatus* may be due to low colonization rates or strong predation pressure from *P. littoralis* (Chapter 2). As a consequence, the incidence of IGP depends mostly on *T. alboornatus* incidence, and the type of predation pressure on the herbivore *T. minuta* is likely determined by the patch size requirements of *T. alboornatus*. On the other hand, the incidence of the *T. striatus* IGP module followed that of *T. striatus* itself, possibly due to the strong SP habitat affinity of this spider compared to *P. littoralis* (Döbel et al. 1990). Thus, the ecological traits of the top predators and the mesopredator together determined how the incidence of these three-species modules depended on patch size. These findings are similar to those of van Nouhuys and Hanski (2005), who found that food chain length in a butterfly-parasitoid system was a function both of the metapopulation capacity of the landscape and the mobility and host range of the natural enemies. Finally, the incidence of the five-species module mirrored that of the parasitoid, whether data on co-occurrence or direct parasitism of herbivores were used. Overall, our data suggest that as food web modules became more complex, the associated critical patch sizes tracked the CPS of the rarest species, here specialist consumers.

Occupancy patterns for different types of consumers (egg predators, parasitoids, patch specialist predators, patch generalist predators) exhibited dissimilar dependence on patch size in this study. Consequently, the collective impacts of these consumers on herbivores are also likely to vary with patch size in ways that have important consequences for food web dynamics. On large patches, egg predation, parasitism, and the potential for predation by patch-restricted spiders were all higher than on small patches, which were characterized instead by the presence of the habitat generalist spider, *P. littoralis*. Thomas (1989) proposed that different spatial patterns of herbivores and plants may depend on whether predators in a system are generalists or specialists, as well as the relative dispersal abilities of herbivores and predators. In the marsh system, the relatively small SP patches required for the occurrence of *P. littoralis* intraguild predation modules and the ubiquitous presence of this spider species indicate that herbivores may still face relatively high predation pressure, even on small patches. That this spider can maintain high density in the matrix habitat (Denno et al. 2005), feeding on other predators and herbivores in the SA food web, may prevent herbivore outbreaks on these small SP patches.

We have documented empirically for the first time that the occurrence of complex food web modules depends on habitat patch size. Not only may patch size constrain food chain length, but it may also impact the likelihood of intraguild predation and other complex food web interactions. As a complement to studying the similarities and differences in food web structure across multiple systems, we suggest that the study of food web structure as it relates to factors that vary within systems (such as patch size, isolation, quality) may provide novel insights into the higher-order effects of habitat loss and spatial structure on natural communities.

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Tables

Table 4.1. Estimates of logistic regression parameters (mean ± standard errors) for the incidence of *Spartina patens* salt marsh arthropods, A, and their interactions, B, with respect to $\log_{10}$ transformed patch size. Regression parameter estimates were used to calculate the patch size at which the odds of patch occupancy (θ) were 0.1, 0.5, or 0.9, according to the formula, $\ln(\theta/(1-\theta)) = \beta_0 + \beta_1 x$. Results presented are back-transformed from the log-transformed patch sizes used in the regression models.

		Logistic Regression Parameters		Patch size for occupancy (m^2)		
Species	Timing	β_0	β_1	0.1	0.5	0.9
A. Species						
Tumidagena minuta (herbivore)	early	-0.34 ± 0.47	1.35 ± 0.45 **	0.0	1.8	77.1
	peak	1.93 ± 0.70 **	0.79 ± 0.67	0.0	0.0	2.2
Tytthus alboornatus (egg predator)	early	0.22 ± 0.53	2.19 ± 0.82 **	0.1	0.8	8.1
	peak	0.09 ± 0.54	2.51 ± 0.93 **	0.1	0.9	6.9
Haplogonatopus sp. (parasitoid)	early	-3.34 ± 0.80 **	1.19 ± 0.38 **	9.2	642.7	45041
	peak	-1.87 ± 0.53 **	0.99 ± 0.31 **	0.5	78.3	13195
Thanatus striatus (spider)	early	-2.16 ± 0.61 **	1.91 ± 0.48 **	1.0	13.5	191.5
	peak	-1.21 ± 0.49 *	1.28 ± 0.37 **	0.2	8.8	458.8
B. Species Interactions						
Egg Predation	early	-0.78 ± 0.48	1.53 ± 0.46 **	0.1	3.3	89.8
	peak	-0.30 ± 0.51	2.01 ± 0.66 **	0.1	1.4	17.5
Parasitism†: occurrence	early	-3.34 ± 0.80 **	1.19 ± 0.38 **	9.2	642.7	45041
	peak	-1.87 ± 0.53 **	0.99 ± 0.31 **	0.5	78.3	13195

Parasitism: evidence	early	-1.72 ± 0.53 **	0.99 ± 0.32 **	0.3	53.3	8707.6
	peak	-2.05 ± 0.60 **	1.91 ± 0.48 **	0.8	11.8	167.2
IGP *Pardosa*	early	-0.78 ± 0.48	1.53 ± 0.46 **	0.1	3.3	89.8
	peak	-0.30 ± 0.51	2.01 ± 0.66 **	0.1	1.4	17.5
IGP *Thanatus*	early	-2.49 ± 0.66 **	2.01 ± 0.50 **	1.4	17.4	216.3
	peak	-1.76 ± 0.55 **	1.54 ± 0.41 **	0.5	13.9	369.3
Five species: occurrence	early	-3.69 ± 0.89 **	1.30 ± 0.41 **	14.1	697.2	34574
	peak	-2.36 ± 0.60 **	1.01 ± 0.33 **	1.5	215.3	31928
Five species: evidence	early	-2.74 ± 0.69 **	1.36 ± 0.38 **	2.5	105.6	4405.3
	peak	-2.61 ± 0.66 **	1.74 ± 0.44 **	1.7	31.4	572.1

Significance: *0.01 < P < 0.05; **P<0.01

†Parasitism was calculated alternatively as the co-occurrence of *Haplogonatopus* adults and *T. minuta* (‘occurrence’) or as the evidence of parasitized *T. minuta* (‘evidence’).

Figure Legends

Figure 4.1. Logistic regressions for the incidence (species present, 1, or absent, 0) of single species with respect to $\log_{10}$ transformed *Spartina patens* patch size (m^2): (a) the specialist herbivore *Tumidagena minuta* (Hemiptera: Delphacidae), (b) the specialist egg predator *Tytthus alboornatus* (Hemiptera: Miridae), (c) *Haplogonatopus sp.* (Hymenoptera: Dryinidae), a specialist parasitoid of delphacid planthoppers, and d) *Thanatus striatus* (Philodromidae), a hunting spider found only in *S. patens*. Gray symbols are for early season samples, and black for peak season.

Figure 4.2. Logistic regression for the incidence of (a) egg predation and (c) parasitism with respect to $\log_{10}$ transformed patch size. Food web module structure is depicted in the inset, with genus abbreviations in circles (Ty: *Tytthus alboornatus*; Tm: *Tumidagena minuta*; Ha: *Haplogonatopus sp.*) and feeding interactions as arrows. (b) The potential intensity of egg predation is shown as $\log_{10}$ transformed predator-prey ratio as a function of patch size, with linear regression lines shown for each date. (d) The proportion of *T. minuta* parasitized as a function of patch size, using generalized linear models with binomially-distributed error terms. Symbols as in Fig. 1.

Figure 4.3. The incidence of intraguild predation modules as function of patch size for (a) the *Pardosa littoralis* (Pa), *Tytthus alboornatus*, and *Tumidagena minuta* module and (b) the *Thanatus striatus* (Th), *T. alboornatus*, and *T. minuta* module (b). Other abbreviations and symbols as in Fig. 2.

Figures

Figure 4.1

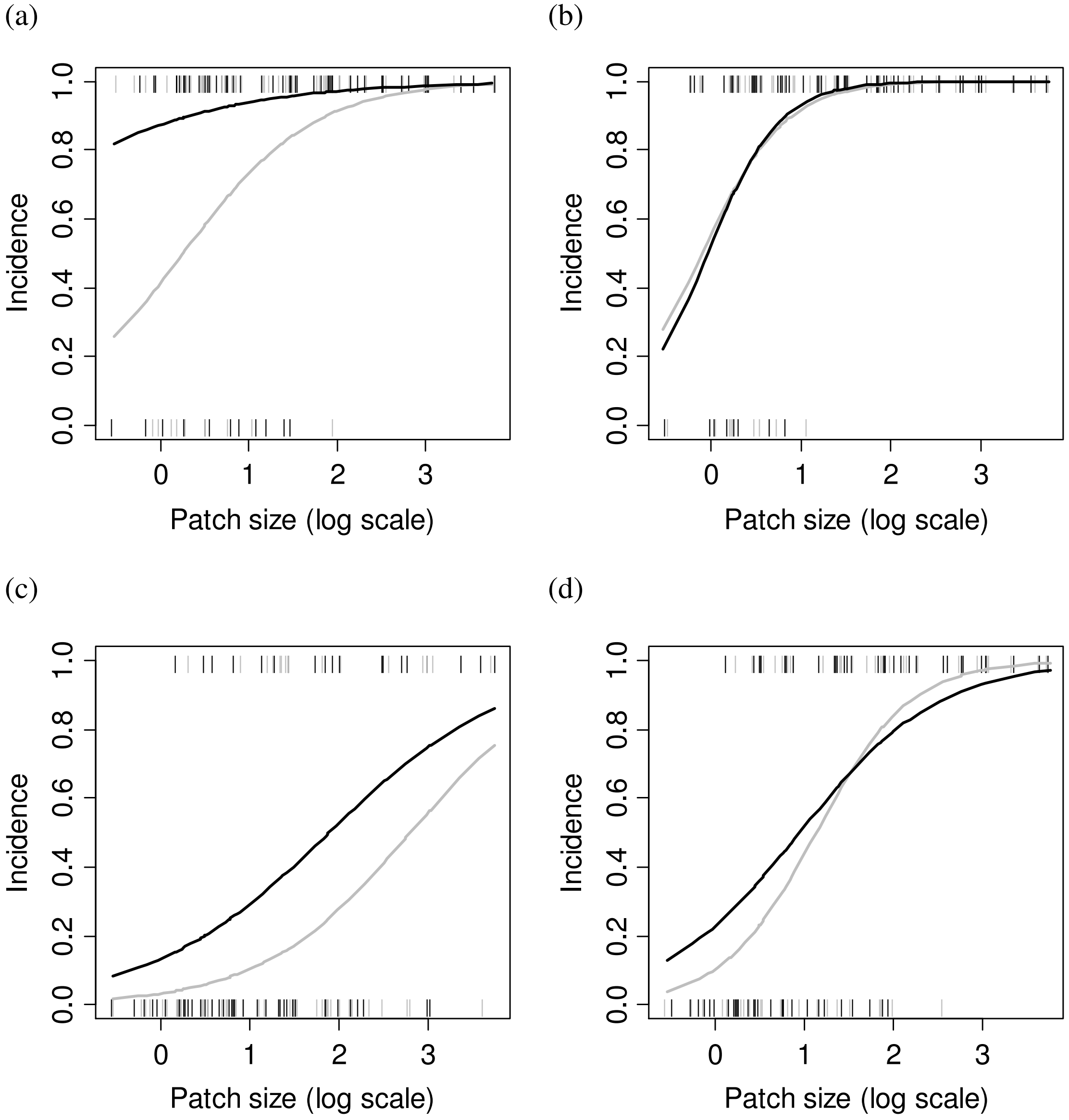
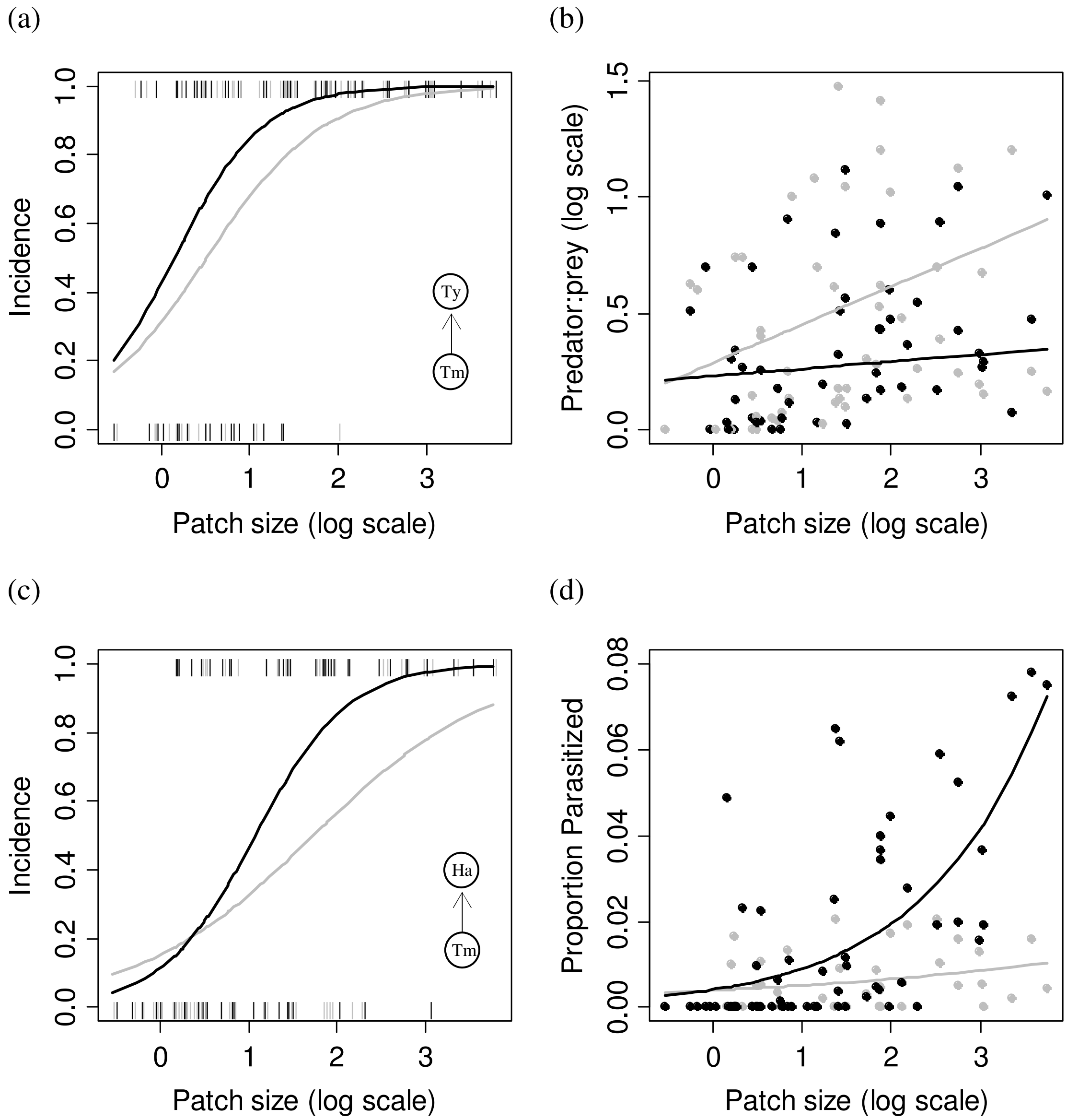


Figure 4.2


(a)
Incidence
1.0
0.8
0.6
0.4
0.2
0.0
Ty
Tm
0
1
2
3
Patch size (log scale)
(b)
Predator:prey (log scale)
1.5
1.0
0.5
0.0
0
1
2
3
Patch size (log scale)
(c)
Incidence
1.0
0.8
0.6
0.4
0.2
0.0
Ha
Tm
0
1
2
3
Patch size (log scale)
(d)
Proportion Parasitized
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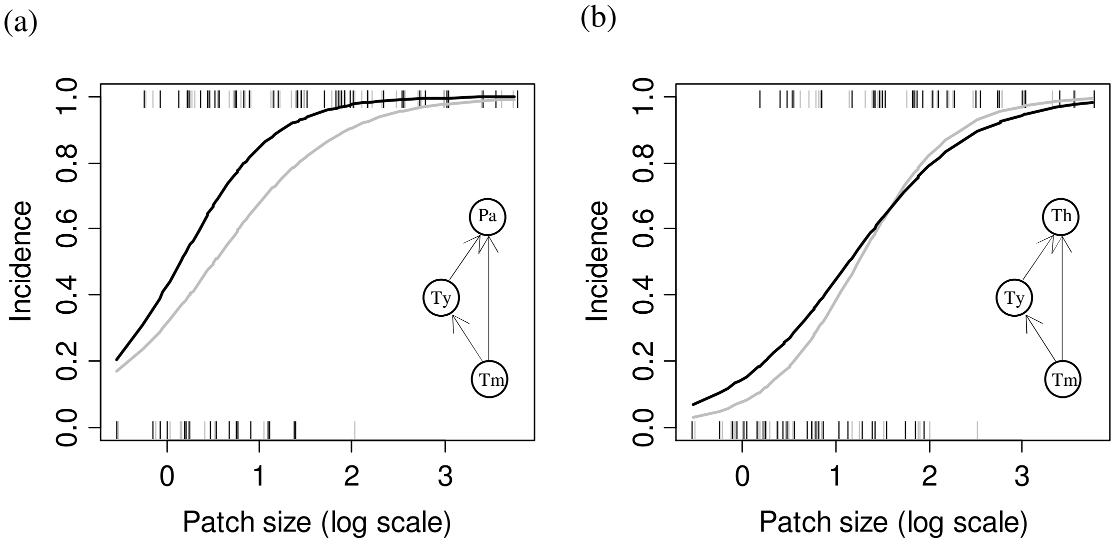
0.06
0.04
0.02
0.00
0
1
2
3
Patch size (log scale)

Figure 4.3


(a)
(b)
Incidence
1.0
0.8
0.6
0.4
0.2
0.0
0
1
2
3
Patch size (log scale)
Pa
Ty
Tm
Th

Appendices

Appendix A: Logistic regression parameters for multi-year survey

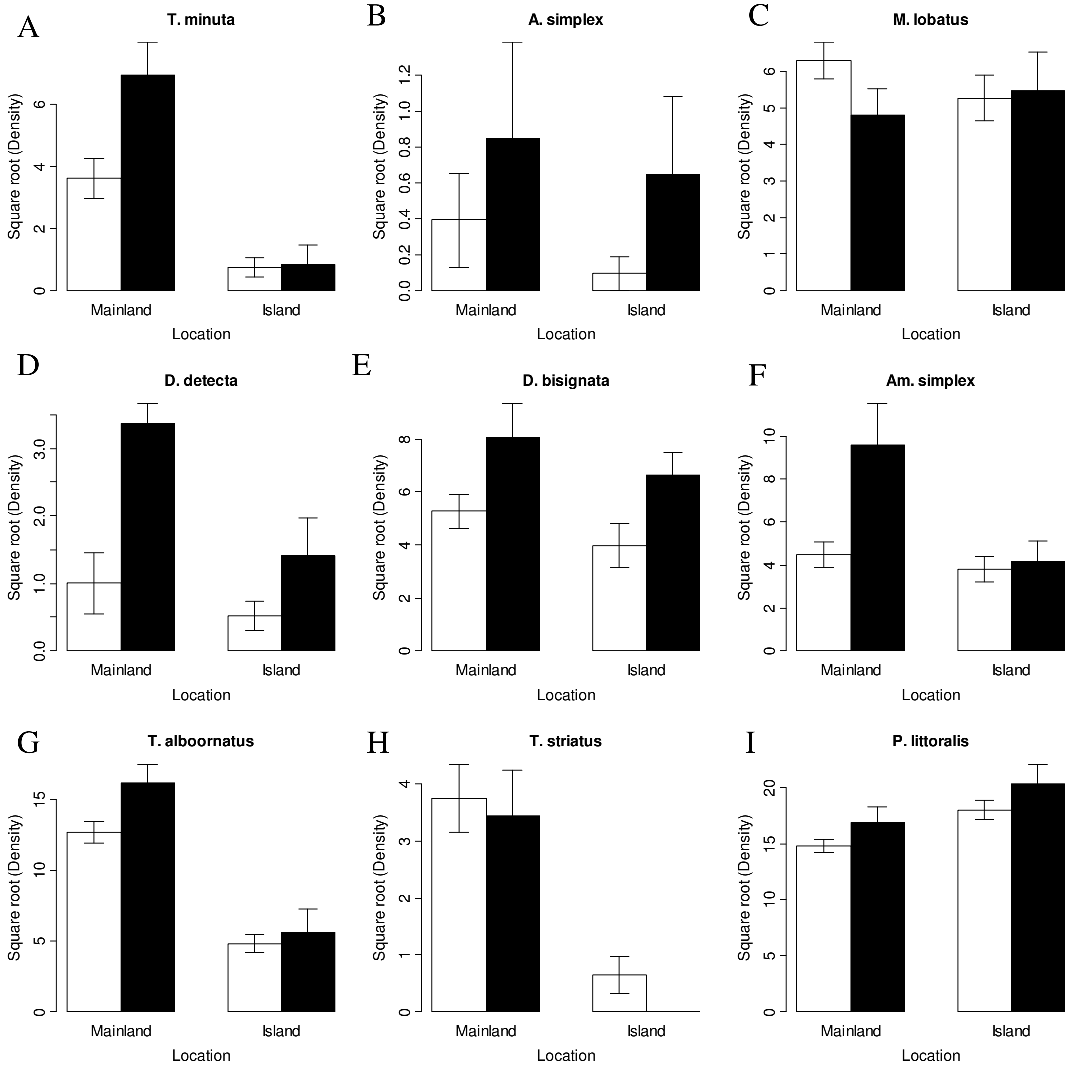
Logistic regression of the presence of each species as a function of patch size (A) and patch connectivity (B). Repeated measures analysis of all survey dates was conducted first, followed by the more conservative response variable of whether a species was ever present on a patch during the 7 surveys ('Any Date'). Results for all species are presented for the repeated measures analysis of patch size; only species for which b_1 was significant are presented for the remaining analyses. Parameter estimates are presented (± SE) The patch size and level of connectivity for 90% probability of patch occupancy were calculated from these parameters (see text).

Test	Species	b_0	b_1	p	90% Threshold
A) Patch Size					Minimum Patch Size ($\log_{10}m^2$)
Repeated Measures					
	A. simplex	-2.47 (± 0.62)	0.98 (± 0.24)	< 0.001	1.45
	Am. simplex	-1.18 (± 0.91)	0.94 (± 0.25)	< 0.001	0.14
	D. bisignata	0.083 (± 0.61)	1.68 (± 0.33)	< 0.001	-0.68
	D. detecta	-0.19 (± 0.56)	1.65 (± 0.24)	< 0.001	-0.53
	Haplogonatopus sp.	-3.61 (± 0.67)	1.32 (± 0.22)	< 0.001	1.94
	M. lobatus	1.66 (± 0.82)	1.07 (± 0.22)	< 0.001	-2.54
	P. littoralis	16.61 (± 8.85)	-0.17 (± 4.80)	0.97	
	T. alboornatus	-0.44 (± 0.71)	2.83 (± 0.51)	< 0.001	-0.22
	T. minuta	0.50 (± 0.72)	1.22 (± 0.23)	< 0.001	-1.28
	T. striatus	-2.71 (± 0.52)	2.08 (± 0.34)	< 0.001	0.79

Any Date					
	A. simplex	-0.18 (± 0.52)	1.06 (± 0.47)	0.0241	-0.83
	Am. simplex	0.81 (± 0.64)	1.71 (± 0.92)	0.0615	-1.09
	Haplogonatopus sp.	-1.57 (± 0.60)	1.44 (± 0.44)	0.0011	0.36
	T. alboornatus	1.57 (± 0.90)	4.65 (± 2.57)	0.0698	-0.56
	T. striatus	-0.59 (± 0.58)	1.85 (± 0.66)	0.0047	-0.25
B) Connectivity					Minimum Connectivity ($\log_{10}$IFM)
Repeated Measures					
	A. simplex	-2.75 (± 0.86)	0.30 (± 0.13)	0.024	5.72
	D. detecta	0.56 (± 0.76)	0.24 (± 0.11)	0.027	-6.79
	T. minuta	0.82 (± 0.87)	0.24 (± 0.10)	0.022	-7.8
	T. striatus	-2.34 (± 0.98)	0.43 (± 0.18)	0.014	2.98
Any Date					
	A. simplex	-0.59 (± 0.84)	0.31 (± 0.16)	0.056	-1.49

Appendix B: Pre-defaunation effects of patch size and fertilization

Effects of patch size (mainland, island) and treatment (fertilized or unfertilized) on densities of nine arthropod species on patches of *Spartina patens* in pre-defaunation samples (11 July 2006). A-C brachypterous herbivores (<1% long-winged individuals); D-F, herbivores with higher levels of macroptery (D, *D. detecta*: 14%, E, *D. bisignata*: 50%; F, *Am. simplex*: 100%); G-I, predatory species. Pre-defaunation samples were collected on 11 July 2006. Mainland patches were > 100 m^2 in area, islands were < 10 m^2. Open bars are unfertilized, filled bars are fertilized plots. Error bars are ± 1 SE. Note differences in y-axes across species due to differences in relative abundance.



Appendix C: Studies of trophic interactions in fragmented habitats

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Appendix D: Vote count of trophic interactions in fragmented habitats

The effect of habitat fragmentation and related variables on the occurrence of trophic interactions. For increases in the fragmentation variable (leftmost column), the response of the trophic interaction was categorized as positive (+) if the interaction occurred significantly more frequently, negative (-) if it occurred significantly less frequently, different (d) if the result was significant but was inconsistently related to levels of the fragmentation variable, and non-significant (n..s) if variation in the fragmentation variable did not affect the frequency of the interaction. Results are presented for herbivory, parasite-host, parasitoid-host, predator-prey, other two-species interactions, and three or more species interactions.

Fragmentation variable	Herbivory				Parasite-Host				Parasitoid-Host				Predator-Prey				Other 2-Species			Three-Plus Sp				
	d	-	+	n.s.	d	-	+	n.s.	d	-	+	n.s.	d	-	+	n.s.	-	+	n.s.	d	-	+	n.s.	*Total*
patch size	3	22	21	38	3	3	6	19		5	15	21	2	9	5	11	9	6	9	2	1	7	8	*225*
patch connectivity		2	14	31			1	1		4	10	18		1	3	1	1	2				1	3	*93*
dist. from edge	2	18	6	7		5	3	7		7	5	8		10	3	16		1	3					*101*
fragmentation		2	9	2		6	1	16			1	1	1	1	6	6		2			2	2	2	*60*
matrix	9			8				2	14			24	4			6								*67*
proport. habitat		10	7	14		8	1	3		6	7	49		6	1	9								*121*
habitat diversity				3							5	12		1		2								*23*
other						2	2	1					1	2		2						1	1	*12*
Grand Total	*14*	*54*	*57*	*103*	*3*	*24*	*14*	*49*	*14*	*22*	*43*	*133*	*8*	*30*	*18*	*53*	*10*	*11*	*12*	*2*	*3*	*11*	*14*	*702*

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