Sap-feeding insect communities as indicators of habitat fragmentation and nutrient subsidies

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Abstract

Upland salt marsh vegetation is particularly prone to habitat fragmentation and nutrient run-off due to coastal development and nearby agriculture. By examining how communities of sap-feeding insects respond to natural variation in plant-patch size and an experimental nutrient addition we explored how species with particular life history traits (e.g. dispersal ability and over-wintering style) might be used to indicate the effects of habitat fragmentation (patch area) and nitrogen subsidies on food webs. Sap-feeders that were superior dispersers or over-wintered in concealed microhabitats persisted well in small patch sizes. In contrast, species that were both immobile and over-wintered in exposed stages were more sensitive to decreasing patch size. Furthermore, mobile sap-feeders colonized and established populations on nitrogen-subsidized patches more rapidly than less mobile taxa. Thus, patterns in community composition (mobile vs. sedentary sap-feeders) can be used as key indicators of both habitat fragmentation and allochthanous nitrogen subsidies. Both patch size and nutrient subsidy altered trophic structure with a higher predator to herbivore ratio occurring in small compared to large patches and in control compared to nitrogen-subsidized habitats where herbivore outbreaks occurred. Our data suggest that conserving large habitat patches and minimizing nitrogen input is critical for maintaining sap-feeder diversity and preserving food-web structure.

Introduction

Assessing the impact of habitat fragmentation on the structure and diversity of local food webs and surrounding landscapes has been the focus of much attention (Radeloff et al. 2000; Fahrig 2003; Reed 2004; Tscharntke and Brandl 2004). Habitat fragmentation results in both habitat loss and fractionation and affects not only the survival and fitness of populations within fractionated habitat patches (Zabel and Tscharntke 1998), but it can also strongly impact populations in the surrounding habitat matrix by altering the flow of materials and organisms across landscape and habitat boundaries (Fagan et al. 1999; Bowne and Bowers 2004; Murphy & Lovett-Doust 2004). For example, terrestrial systems, especially agricultural ones, often export nutrients due to fertilization in excess of crop uptake (Vitousek et al. 1997; Mazerolle and Villard 1999; Valiela and Cole 2002). The regulation of nutrient fluxes and the relative effect of agricultural subsidies across landscapes may depend on the spatial structure and dimensions of adjoining habitats (Pickett and Cadenasso 1995; Polis et al. 1997; Valiela and Cole 2002). The dissection of large habitats into smaller

more isolated patches can reduce dispersal among patches (Steffan-Dewenter and Tscharntke 2002), diminish survival within patches (Young and Clarke 2000) and lead to inbreeding and increased extinction rates (Soulé 1987; Crnokrak and Roff 1999). Furthermore, fractionation of critical boundary habitats can increase nutrient runoff across the landscape that can in turn lead to altered competitive interactions between species (Levine et al. 1998), increased invasion success in the boundary habitat (Silliman and Bertness 2004), and altered trophic structure of food-webs at the landscape spatial scale (Mazerolle and Villard 1999; Valiela et al. 2004).

The impact of habitat fragmentation on food web dynamics depends on both the spatial configuration of the resulting patches and the surrounding matrix as well as the life history traits of the component species (Harrison and Bruna 1999; Debinski and Holt 2000; Biedermann 2004). For example, the number (Kareiva 1987), size (MacArthur and Wilson 1967; McIntyre and Wiens 1999), and distance between patches (Sousa 1984; Zabel and Tscharntke 1998; Marsh et al. 2004) will determine differentially both patch quality and matrix effects for resident species depending upon their dispersal ability, competitive ability, and life-history strategy (Steffan-Dewenter and Tscharntke 2002; Marsh et al. 2004). Because the landscape-level consequences of habitat fragmentation are potentially far-reaching and difficult to assess, many studies have advocated the use of indicator species, or indicator communities (Kremen et al. 1993; Carignan and Villard 2002) to predict the impact of habitat fragmentation on biodiversity (Ledig 1992; Fahrig 2003), food web structure (Laurance et al. 2002), and ecosystem function (Scheffer et al. 2001).

By examining how communities comprised largely of sap-feeding herbivores (Hemiptera: Auchenorrhyncha and Heteroptera) respond to natural variation in host plant-patch size and nutrient subsidies we explore how variation in particular life history traits (e.g. dispersal ability and over-wintering style) might be used to indicate the effects of habitat fragmentation on food-web structure and dynamics at the landscape scale (Novotny 1994; Nickel and Hildebrandt 2003). Delphacid planthoppers in particular make ideal indicators of fragmentation effects because many species are monophagous and feed only on a few related plant species, usually grasses (Wilson et al. 1994). Moreover, their host plants often grow in pure stands facilitating the study of habitat-area effects without the confounding influence of mixed vegetation (Denno 1983, 1994). Also, sap-feeding herbivores exhibit a wide range of inter-specific variation in dispersal ability (migratory vs. sedentary) as well as overwintering style (concealed versus exposed eggs or nymphs) (Denno et al. 1981; Denno and Perfect 1994). We argue that dispersal and over-wintering style are key traits in the context of a species' persistence in a patch because together they directly affect relative colonization and extinction rates (Novotny 1994). Furthermore, there is remarkable variation across sap-feeder species in their response to the nutrient subsidy of their host plants (Cook and Denno 1994; Denno et al. 2003), providing the opportunity to identify which species might be better indicators of altered nutrient dynamics. In this report we describe the sensitivity of several common species of sap-feeding insects to decreasing host plant-patch size and altered nutrient conditions on a mid Atlantic salt marsh. Further, we provide evidence that changes in sap-feeder abundance can have large impacts on food web dynamics by impacting the population biology their main predators: spiders, mirid bugs and hymenopteran parasitoids. In this context we evaluate the suitability of sap-feeders as indicators of food web stability and wetland health (Nickel and Hildebrandt 2003).

Study system

Spatial distribution of salt marsh vegetation

Salt marsh vegetation along the Atlantic coast of North America has a characteristic zonal distribution with the various plant species sorting out along an elevation gradient in relation to soil porosity, waterlogging, oxygenation, salinity, and tidal inundation (Redfield 1972; Gallagher et al. 1988; Denno et al. 1996; Bertness and Pennings 2000). Vegetation along the upland fringe coastal marshes, which is reached by only the highest tides, is characterized by a zone of woody shrubs (e.g. the composites *Iva frutescens* and *Baccharis halimifolia* and myrtles in the genus *Myrica*) (Bertness and Pennings 2000). Down the elevation gradient,

upland vegetation gives way to a narrow zone of *Juncus* and then to the perennial cordgrass *Spartina patens* (Bertness and Pennings 2000). *S. patens* occupies a zone of well-drained habitats on the high marsh where it often grows in expansive monocultures that are consistently flooded by high tides (Bertness 1991; Bertness and Pennings 2000). At slightly lower elevations, the intertidal marsh is dominated by another cordgrass, *Spartina alterniflora*, that also grows in extensive pure stands that directly abut *S. patens* (Redfield 1972; Bertness 1991). Many marshes are characterized by huge expanses of *S. patens* (>3 ha) that abruptly intergrade into vast meadows of *S. alterniflora* (Warren and Niering 1991). However, variation in topographical relief of the marsh surface can result in an archipelago of *S. patens* islands ranging in size from just a few square meters to enormous patches (>3 ha) in a sea of *S. alterniflora* (Denno et al. 1981). Because patches of all sizes are closely intermixed within the archipelago of *S. patens* islands, we did not specifically examine the effects of patch isolation or habitat connectivity on arthropod community structure. However, this configuration of patch sizes provides an ideal, naturally occurring opportunity to assess the consequences of patch size effects on the community of insect herbivores specializing on *S. patens* (Raupp and Denno 1979; Denno et al. 1981).

The assemblage of resident herbivores on Spartina cordgrasses and their natural enemies

The most abundant herbivores on *S. alterniflora* and *S. patens* are host-specific sap-feeders and include planthoppers, leafhoppers, and mirid bugs whose combined densities can exceed 50,000 individuals/m^2 and account for >90% of herbivore biomass (Hemiptera: Delphacidae, Cicadellidae and Miridae, respectively) (Denno et al. 1981, 2000; Denno 1983). Chewing herbivores such as caterpillars, beetles, and orthopterans are far less abundant (Denno et al. in press).

In *S. alterniflora*, two multivoltine planthopper species (*Prokelisia marginata* and *P. dolus*: Delphacidae) are by far the most abundant herbivores where they frequently reach outbreak densities (>5000 adults/m^2) (Denno et al. 1996, 2000). These two planthoppers both over-winter as nymphs nestled in the litter layer of their host plant

in meadows of short-form *S. alterniflora*. Two other multivoltine planthoppers are far less abundant, *Delphacodes penedetecta* that over-winters as nymphs in the thatch and *Megamelus nr lobatus* that overwinters as eggs embedded in the host plant (Denno 1983). All four planthopper species are wing dimorphic with both flight-capable (macropters) and flightless adults (brachypters) in the same population (Denno et al. 1991, 1996). However, the proportion of flight-capable adults varies tremendously across species and reflects their dispersal ability (Denno et al. 1991). On Atlantic marshes, *P. marginata* is a highly migratory species (>90% adults are macropterous), whereas *P. dolus* (<20% macroptery), *D. penedetecta* (<5% macroptery) and *M. nr lobatus* (<2%) are quite sedentary (Denno et al. 1991, 1996). The leafhopper *Sanctanus aestuarium* and the mirid bug *Trigonotylus uhleri* (Hemiptera: Miridae) are moderately abundant, bivoltine, over-winter as embedded eggs, and are also very mobile (Denno 1983).

The assemblage of herbivores on *S. patens* is very similar taxonomically to that on *S. alterniflora*. The two most abundant herbivores in *S. patens* are delphacid planthoppers, the bivoltine *Tumidagena minuta* and the multivoltine *Delphacodes detecta*, both of which over-winter as nymphs in the highly-developed litter layer of their host plant (Denno et al. 1981; Denno 1983). Two other less common, bivoltine planthoppers, the delphacid *Megamelus lobatus* and the issid *Aphelonema simplex* (Hemiptera: Issidae) over-winter as eggs, embedded eggs in the case of the delphacid and exposed eggs for the issid (Denno et al. 1981). Two leafhoppers are infrequent, the univoltine *Amplicephalus simplex* and the bivoltine *Destria bisignata*, both of which over-winter as embedded eggs (Denno et al. 1981). There is also tremendous variation in dispersal capability among these sap-feeders (Novotny 1994) as evidenced by the incidence of macroptery in populations, with *Am. simplex* being the most mobile (100%), followed by *D. detecta* (<20%), *M. lobatus* (<3%), *T. minuta* (<<1%), *Ap. simplex* (<<1%), and *D. bisignata* (0% in females) (Denno et al. 1981, 1991).

The most abundant natural enemies of planthoppers and leafhoppers in the *Spartina* system are web-building and hunting spiders (Döbel et al. 1990, 2002). In *S. alterniflora* the most abundant hunting spiders are *Pardosa littoralis* (Araneae:

Lycosidae) and *Clubiona saltitans* (Clubionidae) and the most common web-builders are *Grammonota trivittata* (Linyphiidae) and *Dictyna altamira* (Dictynidae) (Döbel et al. 1990). In *S. patens*, *Pardosa littoralis* also occurs abundantly as does another hunting spider *Sitticus palustris* (Salticidae); common web-builders in this habitat are *Dictyna altamira* and *Hyposinga variabilis* (Araneidae) (Döbel et al. 1990). The major natural enemy of planthopper eggs are predaceous mirid bugs (Hemiptera: Miridae), *Tytthus vagus* that feeds selectively on the eggs of both *Prokelisia* species in *S. alterniflora* and *Tytthus alboornatus* that attacks the eggs of *Tumidagena minuta* and perhaps *Delphacodes detecta* in *S. patens* (Denno 1983). The nymphal parasitoid *Haplogonatopus* sp. (Hymenoptera: Dryinidae) attacks the active stages of *T. minuta* (Denno et al. 1981).

Disturbance and the altered structure of salt marsh vegetation

Intertidal salt marshes exist as a fringing ecosystem along much of the Atlantic coast of North America (Redfield 1972; Bertness 1991; Bertness and Pennings 2000; Weinstein and Kreeger 2000). The upland marsh is particularly prone to habitat fragmentation due to coastal development (Bertness et al. 1999; Bertness et al. 2004), and historical 'ditching' of high marsh *S. patens* for mosquito abatement reasons (Bertness et al. 2004). Because planthoppers differ in their dispersal ability and overwintering habitat, fragmentation in upland sections of the salt marsh may preferentially affect less mobile plant hopper species.

Furthermore, the increasing proximity of agricultural lands and human development to salt marshes has promoted nitrogen runoff, a situation that is exacerbated by the removal of upland vegetation (Bertness et al. 1999; Valiela and Cole 2002; Bertness et al. 2004). Thus, habitat fragmentation in the upland marsh may affect planthopper food webs both in the fractionated habitat and in the adjoining low marsh habitat that is subjected to increased nitrogen subsidies (Valiela et al. 2004). In general, most planthoppers, including salt marsh species, survive better, develop quicker, and exhibit enhanced fecundity on nitrogen-rich host plants (reviewed in Cook and Denno 1994). However, not all planthopper and leafhopper species respond equally to elevated host plant nitrogen (Prestidge 1982; Denno et al. 2003; Huberty 2005). Thus, certain species (mobile ones) may be differentially affected by nitrogen-subsidized plants, a notion that we explore in this report.

Methods

Study site

The effects of habitat fragmentation (patch size) and nutrient subsidy on sap-feeder abundance were studied in the field on an expansive intertidal marsh in the Great Bay-Mullica River estuarine system at the end of Great Bay Boulevard and just north of the Rutger's University Marine Station, Tuckerton, Ocean County, New Jersey (39°30.8′ N, 74°19.0′ W). The vegetation at this site is dominated by *Spartina patens* on the high marsh and *S. alterniflora* in the intertidal zone where they both grow in extensive pure stands. *S. patens* grows in an archipelago of patches that range from enormous expanses (>3 ha) to very small 'islands' (<2 m^2), all surrounded or abutted by *S. alterniflora* meadows.

Effects of habitat fragmentation on the sap-feeder community in S. patens

To determine the relationship between habitat fragmentation (the area of *S. patens* patches) and the abundance of sap-feeding herbivores and their invertebrate predators, patches in three patch-size categories were sampled at the Tuckerton field site. Five replicate patches in each of three size categories (small = <50 m^2, medium = $51–225$ m^2, and large = $226–3000$ m^2) were randomly selected for arthropod sampling from the expansive archipelago of patches. The area of each patch was determined from GPS coordinates using a manual range finder. Samples were taken using a D-vac vacuum sampler (0.093 m^2 sampling head) on four sampling dates during 1999 (24 June, 8 July, 21 July, 24 August, 1999), and five dates in 2000 (13 June, 29 June, 11 July, 2 August, and 16 August). In an attempt to subject patches to a similar sampling effort, one sample was taken from small patches, two from medium-sized patches, and three from large patches. One sample consisted of four

10-s placements of the vacuum head on the marsh surface for a total sampling area of 0.372 m^2/ sample. All arthropods were killed in ethyl-acetate jars, transferred to jars of 90% ethyl-alcohol, and censused. In both 1999 and 2000, adults of the sap-feeder species and their major predators were identified and censused. In 1999, however, only the predators *T. alboornatus* and *P. littoralis* were identified to species level and all other spiders were pooled. In 2000, spiders were further divided into hunting spiders and web-builders and counted, as were the number of *T. minuta* parasitized by the dryinid wasp *Haplogonatopus* sp.

Correlation analysis was used to assess the relationship between: (1) patch size (log$_{10}$ area in m^2) and herbivore density (log$_{10}$ number/m^2 of each sap-feeder species), (2) patch size and herbivore richness (number of sap-feeder species), (3) patch size and the density of specialist predators (*T. alboornatus* and *Haplogonatopus* sp.), (4) patch size and the density of generalist predators, and (5) patch size and the ratio of all pooled spiders to all pooled sap-feeding herbivores. To determine if patch size affected the ability of specialized predators and parasitoids to track populations of their prey/host, correlations were also performed between the density of *T. minuta* (log$_{10}$ number/m^2) and the density of *T. alboornatus* and *Haplogonatopus* sp. (log$_{10}$ number/m^2).

Responses of sap-feeders and their natural enemies to nitrogen subsidy in S. alterniflora

To determine the effect of nitrogen subsidy on the nitrogen content of *Spartina alterniflora* and the population size of associated sap-feeders (mostly planthoppers), we conducted a fertilization experiment (completely randomized design) in a high marsh meadow habitat at our field site. Fertilizer [ammonium nitrate (N–P–K: 34–0–0)] was either added (4 plots) or withheld (4 plots) from 4.0 m^2 field plots for a total of 8 experimental units. Each fertilized plot received seven applications of the fertilizer mixture at a rate of 60 g/m^2/date, applied biweekly from June to August 2001. To equalize initial arthropod densities, all field plots were defaunated three times using a D-vac vacuum sampler (10, 16, and 25 June 2001). Planthoppers and spiders could freely colonize all field plots following the final defaunation on 25 June 2001. The effect of

the treatments on planthopper population size (number/m^2) was assessed by collecting arthropods with a D-vac (0.093 m^2 sampling head) on four dates (30 June, 8 July, 5 August, and 17 August 2001). Arthropods were transferred to jars containing 95% ethanol, and returned to the laboratory where they were counted. To assess the extent to which fertilizer addition treatments enhanced the nitrogen content of plant tissue, all above ground plant material within a randomly placed 0.047 m^2 wire quadrat frame was collected from each field plot on 20 August 2001. Plant biomass (dry g/m^2) and nitrogen content (%N) of each plot was assessed by separating live plant tissue from dead, drying it to constant biomass, and grinding it to 1 mm granules in a Wiley Mill, before analyzing it in a CHN automated analyzer (University of Maryland, Soil Testing Laboratory).

The effect of fertilization on the density of the numerically dominant planthoppers (pooled macropterous and bracypterous adults of *P. marginata* and *P. dolus*), predators (pooled spiders), and the ratio of predators to prey (density of predators/ density of sap-feeders) was assessed using two-way ANOVA on log-transformed densities (N + 1 individuals per m^2) with sample date, fertilization treatment, and date × treatment interaction as fixed effects. Because of naturally large seasonal fluctuations in insect densities this variance was more appropriate than the covariance structures in a repeated measures analysis. The effect of the nitrogen subsidy on the density of less dominant sap-feeders (*Delphacodes penedetecta*, *Megamelus lobatus*, *Sanctanus aestuarium*, and *Trigonotylus uhleri*) and total sap-feeder richness is reported for 17 August 2001, a sample date when all herbivores occurred in study plots. Treatment effects on plant parameters were examined using ANOVA for each dependent variable: nitrogen (%), live biomass (log-transformed g per m^2). All means (± SEM) are reported untransformed and effect sizes are calculated as [ln(density in fertilizer treatment/density in control treatment)] (see Denno et al. 2003).

Results

Effects of habitat fragmentation on the sapfeeder-natural enemy assemblage in S. patens

The most abundant herbivores in *S. patens* were the delphacid planthoppers *T. minuta* and *D. detecta*,

followed by the leafhoppers *Am. simplex* and *D. bisignata*, the delphacid *M. lobatus*, and the issid *Ap. simplex* (Table 1). Most herbivores and the specialized egg predator *T. alboornatus* were nearly twice as abundant in 2000 than in 1999. Notable exceptions were the issid *Aphelonema simplex*, which was far more abundant in 1999, and spiders including the hunting spider *Pardosa littoralis* that were only slightly more abundant in 2000 (Table 1).

Densities of two (*T. minuta* and *Ap. simplex*) of the six sap-feeders were consistently related to the size of *S. patens* patches. *T. minuta* and *Ap. simplex* had very low incidence of macropterous adults (0.002 ± 0.0005% and 0.003 ± 0.0007%, respectively). Furthermore, positive relationships between patch size and density occurred on several dates during 1999 and 2000, with more significant relationships found during the portion of the season when *T. minuta* and *Ap. simplex* were most abundant (July and August) and during the year when each sap-feeder was most abundant (2000 for *T. minuta* and 1999 for *Ap. simplex*) (Table 2, Figure 1a and b). The densities of the planthoppers *D. detecta* (Figure 1c) and *M. lobatus* and the leafhoppers *Am. simplex* and *D. bisignata* (Figure 2a and b) were unrelated to patch size on most sample dates (Table 2). Furthermore, there was no relationship between the percent macroptery and patch size ($r^2 = 0.00009$, $p = 0.97$) in *D. detecta*, the most mobile of the planthopper species (13.3 ± 0.04% macroptera). Sap-feeder richness was weakly related to patch area with significant positive correlations occurring on one date in 1999 and on three dates in 2000 (Table 2). This relationship was driven largely by the consistent absence of *Ap. simplex* and the occasional absence of *T. minuta* on the smallest patches (Figure 1a and b).

During both years and on most sample dates, the density of the specialized egg predator *T. alboornatus* was positively and significantly related to patch size, as was the number of *T. minuta* parasitized by *Haplogonotopus* sp. (Table 2, Figure 3a and b). The positive relationship between patch size and the density of these two specialized natural enemies probably results because the densities of both are highly correlated with that of their host/prey *T. minuta* (Figure 4a and b) and because the density of *T. minuta* itself is so positively related to patch size (Figure 1a). In contrast to the specialists, densities of the generalist wolf-spider predator *Pardosa littoralis* and the pooled densities of all other spiders were generally not significantly related to patch size Table 2, Figure 5a). On several dates during 2000, the density of web-building spiders (mostly the sheet-web builder *Grammonota trivittata*) was negatively correlated with patch size (Table 2, Figure 5b). Predator-prey ratios (pooled spiders/pooled sap-feeders) were negatively related to patch size on all dates and significantly so on several dates (Table 2, Figure 6). This pattern likely resulted because the most abundant herbivore (*T. minuta*) showed positive density relationships with patch size (Figure 1a) whereas the most abundant spider (*P. littoralis*) and spiders at large (pooled total) showed no relationship (Table 2, Figure 5a). Thus, spiders were relatively more abundant than herbivores on small patches and relatively less so on large patches.

Responses of sap-feeders and their natural enemies to nitrogen subsidy in S. alterniflora

At the end of the season the most abundant sap-feeder in *S. alterniflora* was *P. marginata* followed by its congener *P. dolus* and then *D. penedetecta*, *T. uhleri*, *M. lobatus*, and *S. aestuarium*. In general, sap-feeder species were more abundant in nitrogen-subsidized plots compared to controls, however, the magnitude of the fertilization effect depended on the mobility of the sap-feeder species. Only the mobile taxa (*P. marginata*, *S. aestuarium*, and *T. uhleri*) showed a significant population increase on nitrogen-subsidized plots whereas the sedentary taxa (*P. dolus*, *D. penedetecta*, and *M. lobatus*) did not (Table 3; Figure 7). Effect sizes [ES = ln(fertilized treatment density/control density)] for the mobile taxa ($ES_{Pm} = 1.62$, $ES_{Sa} = 2.00$, $ES_{Tu} = 1.32$) were also significantly higher than those for the sedentary sap-feeders ($ES_{Pd} = 0.17$, $ES_{Dp} = 0.99$, $ES_{Ml} = 0.41$) ($t_4 = 3.52$, $p = 0.023$; Figure 7). The elevated densities of sap-feeders in fertilized versus control plots was likely attributable to the increase in leaf nitrogen content from 1.4 ± 0.04% N to 2.4 ± 0.04% ($F_{1,6} = 9.52$, $p = <0.0001$) and above-ground live biomass from 372.9 ± 16.13 g/m² to 206.6 ± 16.9 g/m² ($F_{1,6} = 3.56$, $p = 0.006$).

Table 1. Density (mean $\pm$ SEM/m^2) of sap-feeding herbivores and their predators and parasitoids sampled in patches of *Spartina patens* during 1999 and 2000 on a salt marsh near Tuckerton, New Jersey, USA.

1999 Taxon	June 24	July 8	July 21	August 24	Season mean
Herbivores					
Planthoppers					
Tumidagena minuta	5.4 ± 1.2	217.6 ± 55.2	446.0 ± 88.3	50.2 ± 12.7	179.8 ± 34.1
Delphacodes detecta	10.6 ± 5.7	18.1 ± 4.1	13.8 ± 3.3	56.2 ± 19.2	24.7 ± 5.6
Megamelus lobatus	21.6 ± 4.7	5.5 ± 1.4	2.3 ± 0.8	49.9 ± 15.7	19.8 ± 4.7
Aphelonema simplex	9.4 ± 2.7	2.4 ± 0.8	1.2 ± 0.5	9.6 ± 3.5	5.6 ± 1.2
Leafhoppers					
Amplicephalus simplex	25.5 ± 4.4	16.9 ± 2.8	12.4 ± 1.9	0.5 ± 0.4	13.8 ± 1.8
Destria bisignata	9.2 ± 1.9	5.2 ± 1.7	4.8 ± 1.4	5.5 ± 1.5	6.2 ± 0.8
All sap-feeders	81.7 ± 11.1	265.8 ± 57.0	480.5 ± 91.6	171.8 ± 33.4	249.9 ± 33.7
Sap-feeder richness	4.5 ± 0.2	4.8 ± 0.2	4.3 ± 0.2	4.4 ± 0.1	4.5 ± 0.1
Predators					
Tytthus alboornatus	73.6 ± 24.5	102.9 ± 27.1	143.6 ± 39.4	189.6 ± 41.5	127.4 ± 17.5
Pardosa littoralis	120.9 ± 17.5	75.0 ± 12.3	196.4 ± 16.2	89.5 ± 9.1	120.5 ± 9.2
Other spiders	31.1 ± 5.9	57.7 ± 7.4	103.9 ± 23.0	51.3 ± 6.0	61.0 ± 7.1
All spiders	152.0 ± 18.5	132.7 ± 11.4	300.3 ± 20.8	140.8 ± 10.9	181.5 ± 11.9
All predators	225.6 ± 34.4	235.7 ± 30.7	443.9 ± 37.7	330.4 ± 46.0	308.9 ± 21.6

2000 Taxon	June 13	June 29	July 11	August 2	August 16	Season mean
Herbivores						
Planthoppers						
T. minuta	17.3 ± 3.4	77.1 ± 18.7	1231.9 ± 210.0	194.1 ± 47.3	7.1 ± 2.1	305.5 ± 68.8
D. detecta	7.3 ± 4.4	81.9 ± 11.3	92.0 ± 13.1	19.3 ± 4.5	10.8 ± 3.1	42.3 ± 5.6
M. lobatus	5.7 ± 2.2	29.5 ± 8.2	18.3 ± 5.0	1.8 ± 0.7	4.8 ± 0.8	12.0 ± 2.3
Ap. simplex	1.1 ± 0.6	0.8 ± 0.4	0.7 ± 0.4	0.6 ± 0.4	0.7 ± 0.4	0.8 ± 0.2
Leafhoppers						
Am. simplex	3.3 ± 1.5	66.2 ± 11.2	45.9 ± 6.9	7.0 ± 1.4	0.3 ± 0.2	24.5 ± 4.0
D. bisignata	7.7 ± 1.6	29.5 ± 5.3	31.9 ± 6.5	4.4 ± 1.4	3.9 ± 1.8	15.5 ± 2.3
All sap-feeders	42.4 ± 7.2	284.9 ± 26.7	1420.6 ± 207.9	227.3 ± 50.3	27.6 ± 6.6	400.6 ± 73.6
Sap-feeder richness	3.6 ± 0.2	5.2 ± 0.1	5.0 ± 0.1	3.9 ± 0.2	3.1 ± 0.3	4.2 ± 0.1
Predators and Parasitoids						
T. alboornatus	220.7 ± 42.2	197.0 ± 39.1	550.4 ± 62.87	455.4 ± 63.5	237.4 ± 86.2	332.2 ± 31.4
P. littoralis	71.2 ± 10.3	123.2 ± 7.8	181.6 ± 18.21	145.8 ± 9.9	162.6 ± 16.1	136.9 ± 7.2
Other spiders	48.3 ± 14.3	59.8 ± 11.2	131.0 ± 59.1	71.1 ± 16.0	58.1 ± 6.7	73.6 ± 13.0
Hunting spiders	5.9 ± 1.5	9.1 ± 2.3	11.1 ± 2.0	12.8 ± 2.7	17.2 ± 3.3	11.2 ± 1.2
Web-builders	36.9 ± 14.0	37.2 ± 9.6	47.4 ± 22.0	39.4 ± 16.4	16.7 ± 6.5	35.5 ± 6.5
All spiders	119.5 ± 20.6	182.9 ± 12.3	312.6 ± 53.9	216.8 ± 20.4	220.7 ± 19.8	210.5 ± 14.7
All predators	340.9 ± 40.2	405.4 ± 37.6	871.4 ± 83.0	680.9 ± 62.0	46.6 ± 81.4	551.8 ± 36.0
Dryinids*	0.7 ± 0.3	25.4 ± 13.3	8.4 ± 1.4	8.6 ± 2.0	2.6 ± 1.1	9.1 ± 2.8

*Number of *T. minuta* parasitized by the dryinid wasp *Haplogonatopus* sp.

Further evidence that mobility was an important contributor to a sap-feeder's response to nitrogen subsidy is seen by comparing the densities of the two wing-dimorphic congeners *P. marginata* and *P. dolus* throughout the season (Figure 8). *P. marginata*, a predominately macropterous species, rapidly colonized fertilized plots, attained much higher densities there compared to controls ($F_{1,24} = 13.35$, $p = 0.001$), and reached its highest densities at the end of the season (Figure 8).

The significant increase in macropter density ($F_{1,24} = 13.06$, $p = 0.001$) but not brachypter density ($F_{1,24} = 2.71$, $p = 0.11$) on fertilized plants emphasizes the important contribution of colonization to this species' dramatic response to nitrogen-enriched plants (Figure 8a and b). In contrast, *P. dolus*, a predominately brachypterous species, colonized at much slower rate, and its overall density was not significantly affected by the fertilization treatment ($F_{1,24} = 0.73$, $p = 0.40$;
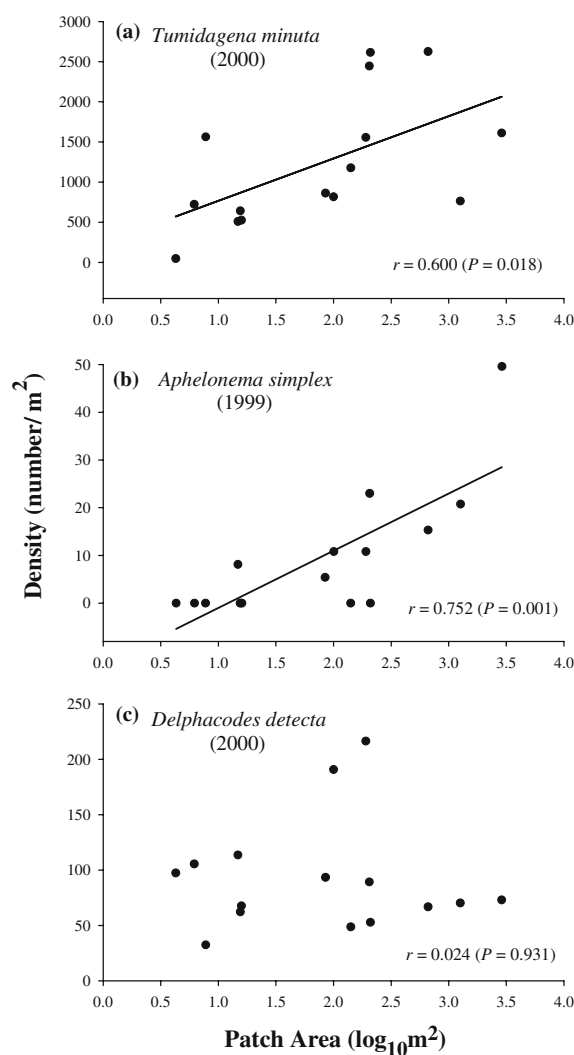
Figure 1. Relationship between the density (number/m^2) of the planthoppers (a) *Tumidagena minuta* (b) *Aphelonema simplex*, and (c) *Delphacodes detecta* and the patch area of their host plant *Spartina patens* (log$_{10}$ m^2). Relationships were generated from data taken on 11 July 2000, 24 August 1999, and 11 July 2000 for *T. minuta*, *Ap. simplex*, and *D. detecta*, respectively.

Table 4, Figure 8c and d). In general, effect sizes were greater for macropters (ES$_{Pm}$ = 1.77 and ES$_{Pd}$ = 2.44) than brachypters (ES$_{Pm}$ = 0.81 and ES$_{Pd}$ = 0.10) of both species, further highlighting the importance of the flight-capable morph when assessing population responses to host-plant nitrogen (Figure 8). Overall, however, the difference in wing-form composition between the two congeneric planthoppers determined its ability to selectively colonize subsidized field plots. Despite differences in dispersal ability among species, sap-feeder richness was significantly higher on fertil-

ized (6 ± 0.0 species) than unfertilized plots (3.75 ± 0.38 species; Table 3).

Spiders selectively colonized fertilized plots ($F_{1,24}$ = 6.73, p = 0.02) and reached significantly higher densities than in non-fertilized control plots (Table 5, Figure 9a). The positive response of spiders to plant nitrogen probably resulted from a strong numerical response to increased prey density in fertilized plots (mostly *P. marginata*) as evidenced by the significant correlation between predator and prey density (r = 0.64, p < 0.0001). Although spider densities

Table 2. Correlations (product-moment coefficients) between the density (log number per m^2) of various herbivore and predator taxa and the size of their host plant patch (log area of *Spartina patens* patch in m^2) generated from samples taken during 1999 and 2000 and 2 on a salt marsh near Tuckerton, New Jersey, USA.

1999

Taxon	June 24	July 8	July 21	August 24
Herbivores				
Planthoppers				
Tumidagena minuta	0.548 (**p** = 0.034)	0.404 (p = 0.136)	0.589 (**p** = 0.021)	0.331 (p = 0.229)
Delphacodes detecta	−0.024 (p = 0.932)	0.401 (p = 0.139)	0.506 (p = 0.054)	0.333 (p = 0.226)
Megamelus lobatus	−0.108 (p = 0.700)	0.146 (p = 0.604)	0.131 (p = 0.641)	−0.185 (p = 0.508)
Aphelonema simplex	0.550 (**p** = 0.034)	0.483 (p = 0.068)	0.679 (**p** = 0.005)	0.752 (**p** = 0.001)
Leafhoppers				
Amplicephalus simplex	0.201 (p = 0.474)	−0.110 (p = 0.697)	−0.301 (p = 0.276)	−0.364 (p = 0.182)
Destria bisignata	−0.047 (p = 0.869)	−0.322 (p = 0.241)	0.261 (p = 0.310)	0.342 (p = 0.212)
All sap-feeders	0.028 (p = 0.921)	0.255 (p = 0.359)	0.612 (**p** = 0.015)	0.236 (p = 0.397)
Sap-feeder richness	0.278 (p = 0.153)	0.285 (p = 0.285)	0.374 (**p** = 0.050)	0.360 (p = 0.065)
Predators				
Tytthus alboornatus	0.487 (p = 0.066)	0.655 (**p** = 0.008)	0.615 (**p** = 0.015)	0.677 (**p** = 0.006)
Pardosa littoralis	−0.135 (p = 0.631)	−0.390 (p = 0.151)	0.044 (p = 0.876)	−0.006 (p = 0.984)
Other spiders	−0.185 (p = 0.510)	0.118 (p = 0.675)	−0.560 (**p** = 0.030)	−0.212 (p = 0.448)
All spiders	−0.19 (p = 0.497)	−0.405 (p = 0.135)	−0.646 (**p** = 0.009)	−0.179 (p = 0.522)
All predators	0.138 (p = 0.624)	0.366 (p = 0.180)	0.247 (p = 0.375)	0.555 (**p** = 0.032)
Predator/Prey ratio				
All spiders/all sap-feeders	−0.371 (p = 0.174)	−0.242 (p = 0.384)	−0.527 (**p** = 0.044)	−0.429 (p = 0.111)

2000

Taxon	June 13	June 29	July 11	August 2	August 16
Herbivores					
Planthoppers					
T. minuta	0.606 (**p** = 0.017)	0.271 (p = 0.328)	0.600 (**p** = 0.018)	0.769 (**p** = 0.0)	0.832 (**p** = 0.001)
D. detecta	−0.079 (p = 0.780)	0.247 (p = 0.374)	0.024 (p = 0.931)	0.262 (p = 0.345)	0.175 (p = 0.532)
M. lobatus	−0.463 (p = 0.082)	0.186 (p = 0.507)	0.638 (**p** = 0.010)	0.311 (p = 0.260)	0.062 (p = 0.825)
Ap. simplex	0.230 (p = 0.409)	0.480 (P = 0.070)	0.531 (**p** = 0.042)	0.479 (p = 0.071)	0.464 (p = 0.081)
Leafhoppers					
Am. simplex	−0.043 (p = 0.880)	−0.265 (p = 0.340)	−0.116 (p = 0.682)	0.109 (p = 0.699)	0.188 (p = 0.502)
D. bisignata	0.238 (p = 0.394)	0.268 (p = 0.335)	0.274 (p = 0.324)	0.321 (p = 0.243)	0.528 (**p** = 0.043)
All sap-feeders	−0.009 (p = 0.976)	0.085 (p = 0.762)	0.635 (**p** = 0.011)	0.777 (**p** = 0.001)	0.506 (p = 0.055)
Sap-feeder richness	0.172 (p = 0.390)	0.512 (**p** = 0.006)	0.451 (**p** = 0.018)	0.239 (p = 0.229)	0.499 (**p** = 0.08)
Predators					
T. alboornatus	0.589 (**p** = 0.021)	0.749 (**p** = 0.001)	0.553 (**p** = 0.032)	0.504 (**p** = 0.050)	0.524 (**p** = 0.045)
P. littoralis	−0.540 (**p** = 0.038)	0.244 (p = 0.381)	0.136 (p = 0.630)	−0.307 (p = 0.265)	0.041 (p = 0.884)
Hunting spiders	−0.062 (p = 0.827)	0.572 (**p** = 0.026)	0.225 (p = 0.420)	0.458 (p = 0.086)	0.576 (**p** = 0.025)
Web-builders	−0.464 (p = 0.081)	−0.681 (**p** = 0.005)	−0.620 (**p** = 0.0142)	−0.398 (p = 0.142)	−0.360 (p = 0.187)
All spiders	−0.622 (**p** = 0.013)	−0.399 (p = 0.141)	−0.489 (p = 0.064)	−0.391 (p = 0.149)	−0.010 (p = 0.973)
All predators	0.282 (p = 0.309)	0.431 (p = 0.109)	0.275 (p = 0.321)	0.362 (p = 0.185)	0.611 (**p** = 0.016)
Dryinids*	0.622 (**p** = 0.013)	−0.392 (**p** = 0.149)	−0.301 (**p** = 0.275)	0.567 (**p** = 0.027)	0.172 (**p** = 0.540)
Predator/Prey ratio					
All spiders/all sap-feeders	−0.531 (**p** = 0.041)	−0.349 (p = 0.203)	−0.549 (**p** = 0.034)	−0.682 (**p** = 0.005)	−0.052 (p = 0.854)

Significant *p* values are bolded for emphasis.

*Number of *T. minuta* parasitized by the dryinid wasp *Haplogonatopus* sp.

increased in fertilized plots Figure 9b), populations of sap-feeders, particularly *P. marginata*, increased dramatically (Figures 7 and 8) suggesting that spiders did not effectively suppress planthopper populations. The lower ratio of spider density to sap-feeder density in fertilized
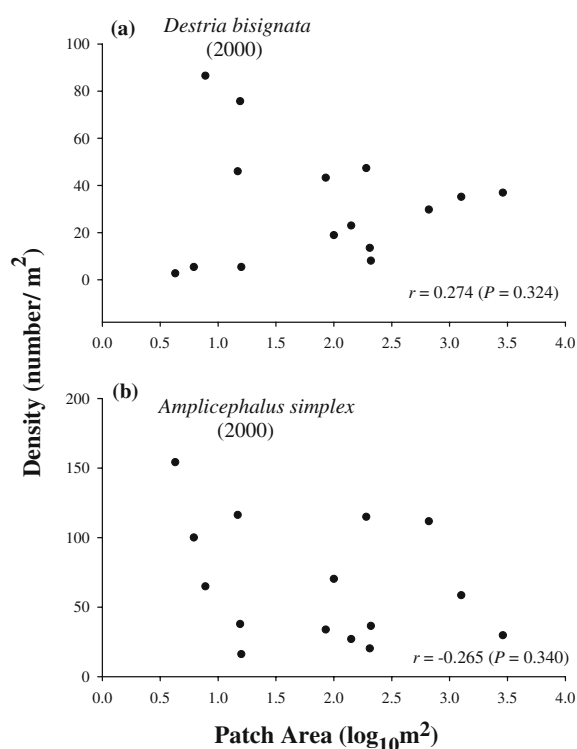
Figure 2. Relationship between the density (number/m^2) of the leafhoppers (a) *Destria bisignata* and (b) *Amplicephalus simplex* and the patch area of their host plant *Spartina patens* (log$_{10}$ m^2). Relationships were generated from data taken on 11 July and 29 June 2000 for *D. bisignata* and *Am. simplex*, respectively.

plots compared to non-fertilized plots further corroborates the relaxed predation pressure in the treatment plots on the dominant herbivores (Table 5, Figure 9b).

Discussion

Effects of habitat fragmentation on the sapfeeder-natural enemy assemblage in S. patens

Patch/habitat size (the area occupied by an herbivore's host plant) is an important driver of biodiversity at both geographic and local spatial scales (Rey 1981). Larger patches of host plants often support more species of herbivores for a variety of reasons, including increased habitat heterogeneity, increased encounter rate, and reduced probability of extinction (Root 1973; Rey 1981; Kareiva 1987; Connor et al. 2000). As patch size decreases, some herbivores simply become rare and disappear altogether below a certain critical patch size (Hanski 1999; McIntyre and

Wiens 1999; Hanski and Ovaskainen 2000). By defaunating 'islands' of *Spartina alterniflora* in the Gulf of Mexico and monitoring recolonization, Rey (1981) was able to show that immigration rates increased and extinction rates declined with island area. Certain combinations of life history traits (e.g. high dispersal and concealed overwintering stages) may favor colonization and persistence on isolated and small patches (Mazerolle and Villard 1999; Fahrig 2003). Consequently, species with specific life history styles may be over- or under-represented on large or small patches of hosts, and thus be better or worse indicators of habitat loss.

Some, but not all herbivore species show positive abundance-area relationships and the exceptions underscore the need to consider the unique responses of specific herbivores to changes in vegetation texture (Kareiva 1983). Several factors affect an herbivore's response to changing host patch size and thus alter any abundance-area relationship. These include (1) the diet breadth of the herbivore, (2) the mobility of the herbivore, (3)
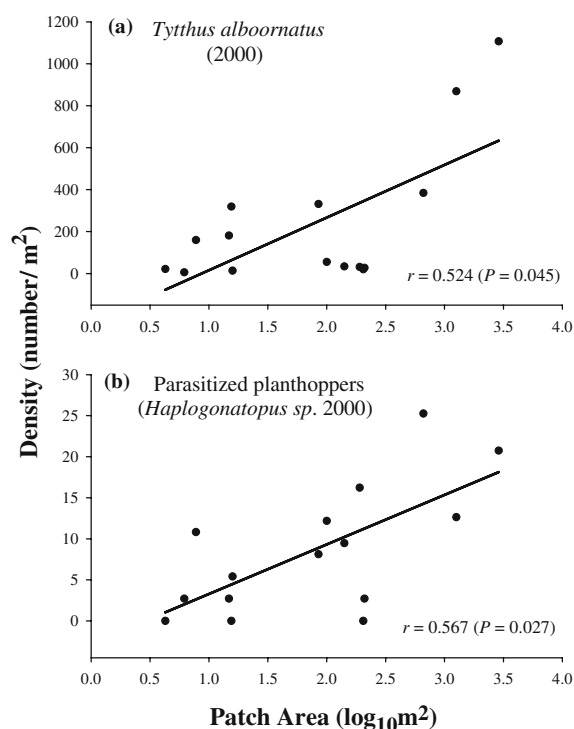
Figure 3. Relationship between the density (number/m^2) of the (a) egg predator *Tytthus alboornatus* and (b) the dryinid wasp *Haplogonatopus* sp. and the patch area of *Spartina patens* (log$_{10}$ m^2). Relationships were generated from data taken on 16 and 2 August 2000 for *T. alboornatus* and *Haplogonotopus*, respectively. Both of these species are specialized natural enemies of the planthopper *T. minuta*.

the quality, density, and size of host plants as they vary with patch area, (4) the nature of the matrix habitat within which patches are nested, (5) edge effects, and (6) the number of parasites, predators, and pathogens as they vary with patch size (Root 1973; Kareiva 1983; Denno 1994; Fagan et al. 1999; Cronin 2003). Here we emphasize that the causal mechanisms underlying abundance-patch area relationships are best elucidated by examining the life history traits of the specific herbivores.

In the *Spartina patens* system, only two species of planthoppers (*T. minuta* and *Ap. simplex*) showed positive relationships with patch area (Figure 1a and b), whereas the other four sap-feeders did not (Table 2). Both area-responsive species were considerably rarer on patches less than 100 m^2, suggesting a relatively small critical patch size for persistence. These results are largely consistent with the results reported in previous studies in salt marsh systems that have examined the effect of patch size on density of these herbivores on *S. patens* (Raupp and Denno 1979;

Denno et al. 1981). Relative abundance of sap-feeders within the community was not a good predictor of a species' response to variation in patch size, as *T. minuta* and *Ap. simplex* were the most and least common species in the assemblage respectively. One can ask what characteristics these area-responsive species share and the other non-responsive sap-feeders lack? Two life history traits, namely dispersal ability and over-wintering style, likely combine to influence colonization and extinction dynamics, and thus contribute to abundance-area patterns. Both *T. minuta* and *Ap. simplex* are poor dispersers (>99% of adults in populations are brachypterous) and both species over-winter as exposed stages (Denno et al. 1981; Denno 1983). Thus, neither species is likely an effective colonizer of vacant patches nor should they persist through harsh winters as well as species that over-winter as concealed eggs embedded into plant tissues. We argue here that colonization rates are lower on small patches and that extinction rates are higher, both of which contribute to
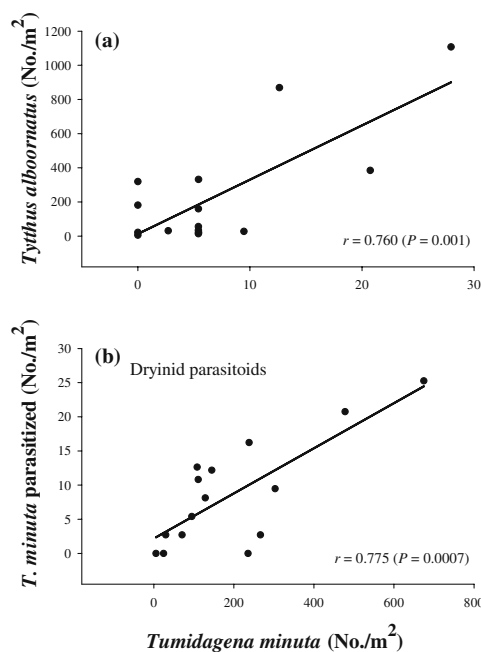
Figure 4. Relationship between the density (number/m^2) of (a) the egg predator *Tytthus alboornatus* and (b) the dryinid wasp *Haplogonatopus* sp. and the density of their host planthopper *Tumidagena minuta* in patches of *Spartina patens*. Relationships were generated from data taken on 16 and 2 August 2000 for *T. alboornatus* and *Haplogonotopus*, respectively.

lower densities. Extinction rates should be particularly high on small islands for 'exposed species' because there is less protective leaf litter during the winter season, a resource that many planthoppers require to successfully over-winter (Denno et al. 1981; Denno 1994).

Species with the opposite combination of life history traits (high mobility coupled with concealed eggs during winter) should have the best chance for success on small patches and be least responsive to habitat fragmentation. The only species with this combination of traits, the leafhopper *Amplicephalus simplex*, showed no significant effects of patch area on population size (Table 2, Figure 2b). Species with one or the other but not both high mobility and concealed over-wintering stages were also relatively unaffected by patch size. For example, species with moderate colonizing ability ($\sim$20% macropterous adults) and exposed over-wintering stages (*Delphacodes detecta*), or species with poor colonizing ability (>95% brachypters) and concealed over-wintering stages (*M. lobatus* and *D. bisignata*), were similarly abundant across the patch-area gradient (Table 2, Figures 1c and 2a). The non-significant

relationship between macroptery (%) in *D. detecta* and patch size further indicates that this species is able to disperse across habitat patches of all sizes (e.g. macropters were not relatively more abundant on large patches). Apparently, either increased persistence during winter or enhanced colonizing ability is sufficient to preclude strong patch-size effects on population density.

Other factors, specifically natural enemies, may act selectively in small patches and fragmented landscapes resulting in reduced populations of certain sap-feeders. The key to determining predator impacts along a patch-size gradient is knowing how food resources, habitat edges, and background matrix integrate to affect the immigration-emigration dynamic of both predators and prey (Denno et al. 2002; Cronin 2003; Cronin et al. 2004). Typically, the specialized predators of planthoppers exhibit strong numerical responses and aggregate in habitats where prey is most abundant (Döbel et al. 1990). This appears to be the case in the *S. patens* system where there is a strong positive relationship between the density of *Tytthus alboornatus* and *Haplogonatopus* sp. and their planthopper host *Tumidagena minuta* across
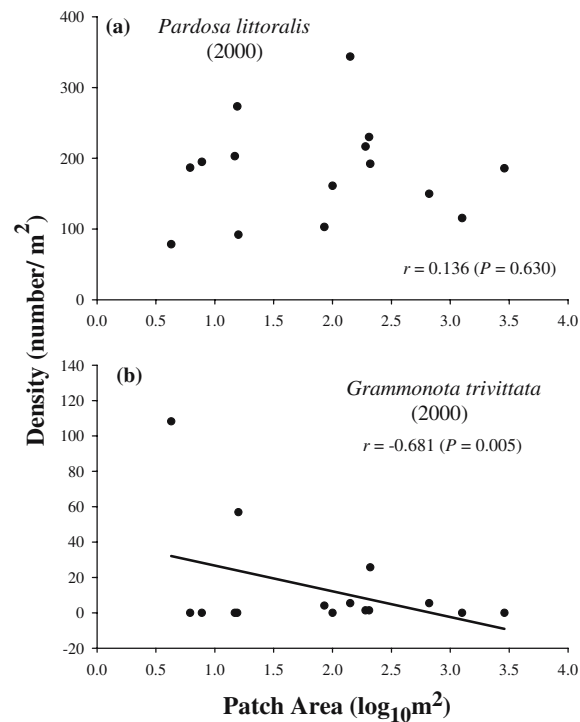
Figure 5. Relationship between the density (number/m^2) of (a) the wolf spider *Pardosa littoralis* and (b) the sheet web-building spider *Grammonota trivittata* and the patch area of *Spartina patens* (log$_{10}$ m^2). Relationships were generated from data taken on 11 July and 29 June 2000 for *P. littoralis* and *G. trivittata*, respectively.
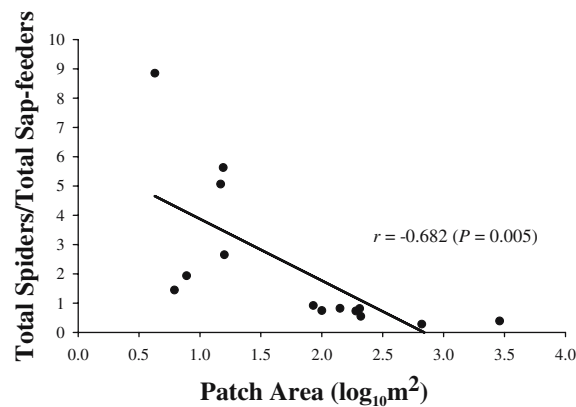

Figure 6. Relationship between the ratio of spider density (pooled total) to sap-feeder density (pooled total) and the patch area of *Spartina patens* (log$_{10}$m^2). The relationship was generated from data taken on 2 August 2000.

the patch-size gradient (Figure 4). Although this pattern supports a strong aggregative response and the ability of these natural enemies to effectively track populations of their planthopper host, it does not suggest that the reduced densities of *T. minuta* in small patches are attributable to these specialist natural enemies because all are rare in small patches (Figures 1a and 3).

Alternatively, generalist predators such as spiders may contribute in part to the lower densities of *T. minuta* and *Ap. simplex* in small patches. For example, densities of the web-building spiders such

Table 3. ANOVA results for the effect of nitrogen subsidy on the density (pooled nymphs and adults/m^2) of mobile (*P. marginata*, *T. uhleri*, and *S. aestuarium*) and sedentary sap-feeder species (*P. dolus*, *D. penedetecta*, and *M. lobatus*), and on sap-feeder richness in experimental plots of *Spartina alterniflora* on a salt marsh near Tuckerton, New Jersey, USA.

		Mobile species						Sedentary species						
	df*	*Prokelisia marginata*		*Santanus aestuarium*		*Trigonotylus uhleri*		*Prokelisia dolus*		*Delphacodes penedetecta*		*Megamelus lobatus*		Species richness
Effect	1,6	F	p	F	p	F	p	F	p	F	p	F	p	F p
Treatment	1,6	5.52	**0.05**	11.49	**0.01**	3.62	0.11	0.19	0.67	1.99	0.21	0.38	0.56	3 **0.01**

Significant *p* values are bolded for emphasis.
*Degrees of freedom (numerator, denominator).

Table 4. ANOVA results for the effect of nitrogen subsidy on the density (number/m^2) of adults (pooled wing forms), macropters, and brachypters of *Prokelisia marginata* and *P. dolus* in experimental plots of *Spartina alterniflora* on a salt marsh near Tuckerton, New Jersey, USA.

		Prokelisia marginata						*Prokelisia dolus*						
		Adults		Macropters		Brachypters		Adults		Macropters		Brachypters		
Effect	df*	F	p	F	p	F	p	F	p	F	p	F	p	
Treatment (Trt)	1, 24	13.35	**0.001**	13.06	0.001	2.71	0.11	0.73	0.40	2.7	0.11	0.14	0.71	
Time	3,24	2.05	**0.013**	1.37	0.27	60.89	**< 0.0001**	15.27	**< 0.0001**	3.04	*0.05*	19.33	**< 0.0001**	
Trt × Time	3,24	0.18	**0.90**	0.20	0.89	0.33	0.80	0.85	0.47	1.82	0.17	0.09	0.97	

Significant *P* values are bolded for emphasis.
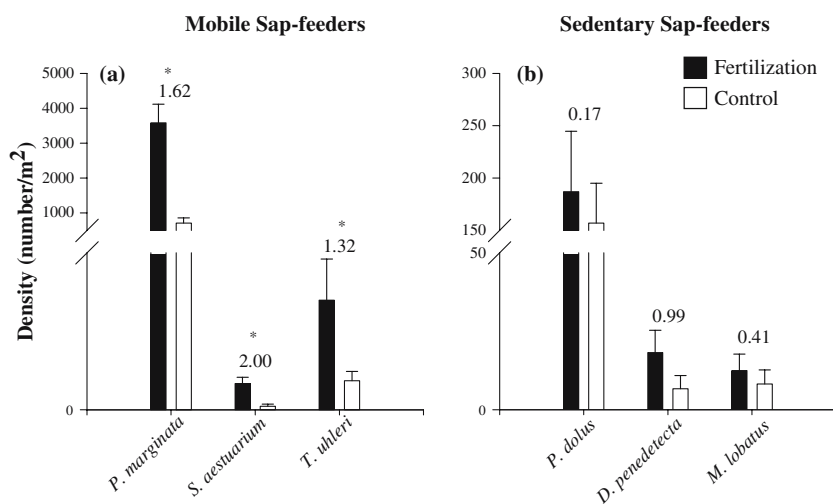*degrees of freedom (numerator, denominator).

Figure 7. Effect of nitrogen fertilization on (a) the density (mean ± SEM number/m^2) of the mobile sap-feeder taxa *Prokelisia marginata*, *Sanctanus aestuarium*, and *Trigonotylus uhleri* and (b) the sedentary sap-feeder taxa *P. dolus*, *Delphacodes penedetecta* and *Megamelus lobatus* in plots of *Spartina alterniflora*. Asterisks indicate a significantly higher population density in fertilized than control plots ($p < 0.05$). Effect sizes for each species are shown above bars.

as *Grammonota trivittata* can be higher in small patches of *S. patens* (Figure 5b), and probably results from their incursion from surrounding *S. alterniflora* habitat where they can be very abundant (Döbel et al. 1990). In fact, predator impacts can be greater in small patches or fragmented landscapes when habitat edges are permeable and generalist predators freely colonize from the sur-
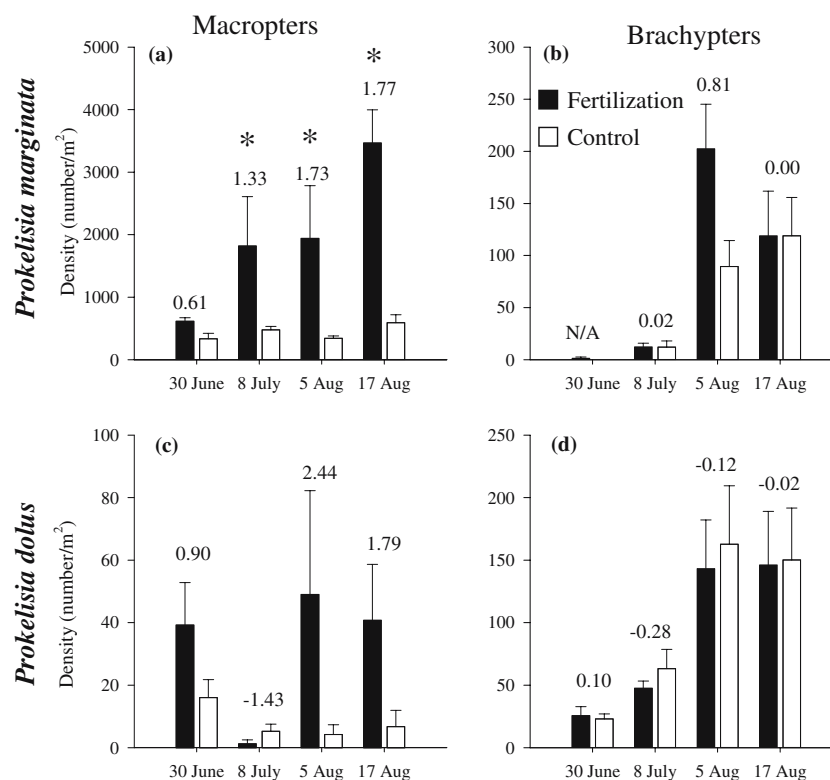
Figure 8. Effect of nitrogen fertilization on the density (mean ± SEM number/m^2) of (a) macropters and (b) brachypters of *Prokelisia marginata* and the density of (c) macropters and (d) brachypters of *P. dolus* in plots of *Spartina alterniflora*. Asterisks indicate a significantly higher population density in fertilized than control plots ($p < 0.05$). Effect sizes for each wing form are shown above bars.

Table 5. ANOVA results for the effect of nitrogen subsidy on the density (number/m^2) of spiders and the ratio of predators to prey (density of predators/density of sap-feeders) in experimental plots of *Spartina alterniflora* on a salt marsh near Tuckerton, New Jersey, USA.

		Spiders		Predator:Prey	
Effect	df*	F	p	F	p
Treatment (Trt)	1,24	6.73	**0.016**	3.12	0.09
Time	3,24	7.93	**0.0008**	6.25	**0.001**
Trt × Time	3,24	2.13	0.12	0.01	0.99

Significant *p* values ($p < 0.05$) are bolded for emphasis.
*degrees of freedom (numerator, denominator).

rounding matrix (Zabel and Tscharntke 1998; Cronin et al. 2004; Denno et al. in press). However, *G. trivittata* is not a particularly voracious predator of planthoppers (Döbel et al. 1990), and it is unlikely that it contributes much to the strong density-area relationship exhibited by *T. minuta*. Nonetheless, overall predation pressure from spiders is greater in small compared to large patches of *S. patens* Figure 6), and mortality inflicted by

spiders cannot be ruled out as contributing to the reduced number of certain planthoppers in small patches.

Data from the *S. patens* system suggests that many species of sap-feeders are not particularly responsive to changes in patch size. For those that respond to patch size, densities are lower on small host plant patches. Patterns of abundance and persistence on small patches, and thus the extent to

which a species may act as an indicator of habitat loss, can be predicted by life-history characteristics such as the combination of low mobility and exposed over-wintering stages that reflect a species' inability to colonize and persist on small patches. Thus, to maximize biodiversity in this wetlands system it becomes critical to retain large patches in the matrix, a habitat management strategy that will become increasingly more challenging as development fragments the upper marsh Bertness et al. 1999, 2004; Valiela et al. 2004).

Responses of sap-feeders and their natural enemies to nitrogen subsidy in S. alterniflora

The effect of nitrogen fertilization on the density of resident herbivores in nitrogen-limited terrestrial systems has been studied extensively (Mattson 1980; White 1993; Awmack and Leather 2002). Most female planthoppers selectively oviposit on nitrogen-rich plants, and macropterous adults selectively colonize nitrogen-subsidized plants (Denno and McClure 1980; Denno et al. 2002, 2003). However, the magnitude of the sap-feeder response to nitrogen-rich host plants depends on species-specific variations in mobility and life history traits (Prestidge 1982; Denno et al. 2002, 2003).

Our results suggest that mobile species, either dimorphic species with a high proportion of macropterous adults (e.g. *P. marginata)* or monomorphic species that are entirely flight capable (*T. uhleri* and *S. aestuarium*), are better indicators of a short-term nutrient pulse than are less mobile species with a high proportion of flightless adults in the population (e.g. *P. dolus* and *M. lobatus*). For example, macropters of *P. marginata* and adults of *S. aestuarium* and *T. uhleri* rapidly colonized plants of *Spartina alterniflora* that experienced a short-term nitrogen subsidy (Figures 7 and 8). This contrasted with the weaker density responses of the less mobile sap-feeders (Figures 7 and 8) whose marsh-wide populations were dominated by flightless adults. Besides *P. marginata*, other highly mobile species of planthoppers (e.g. *Javesella pellucida, Nilaparvata lugens,* and *Saccharosydne saccharivora*) often exhibit outbreak dynamics when they are able to synchronize reproduction with high host nitrogen content by migrating to more nutritious plants (Denno and

Peterson 2000). Moreover, when such species experience nitrogen-deficient host plants, their reproduction is often drastically curtailed (Cook and Denno 1994; Denno and Peterson 2000). Consequently, species with high dispersal ability should be over-represented on nitrogen-rich patches of plants and may be more sensitive indicators of nutrient run-off.

It is not surprising that colonization ability influenced a sap-feeder's response to elevated plant nitrogen because our experiment was conducted in defaunated plots. Although this approach may identify a species' ability to respond to a short-term pulse of nitrogen subsidy, one could argue that given sufficient time even the less mobile species will ultimately exhibit elevated densities on nitrogen enriched host plants. Indeed this is the case and has been shown for several sedentary species of planthoppers including those on the salt marsh (reviewed in Denno and Peterson 2000; Denno et al. 2002). Given that nutrient subsidies (run-off events) can occur as sporadic 'pulses' (Holmgren et al. 2001) or exist as a continuous allochthonous input (Polis et al. 1997; Ostfeld and Keesing 2002), one can ask how sap-feeder communities might help elucidate the occurrence and nature of such events? Again, mobility proves to be key.

When *Spartina alterniflora* is subjected to a one-time nitrogen subsidy, effects on the sap-feeder community carry over for several years before dissipating (Gratton and Denno 2003). For example, populations of the mobile *P. marginata* and *T. uhleri* remain significantly higher for up to 3 years following a nutrient pulse before their densities equalize with controls. In particular, *T. uhleri* is sensitive to diminishing plant nitrogen because its density plummets as the effects of the nitrogen subsidy wear thin (see Haddad et al. 2000; Gratton and Denno 2003). Thus, during the short time following a nutrient pulse (1–3 years), the sap-feeder community is swamped by highly responsive mobile species and this composition is indicative of nutrient pollution despite increases in the density of less mobile species (Figures 7 and 8); (Gratton and Denno 2003). There is building evidence that planthoppers using dispersal (escape and colonization) as a strategy to cope with deteriorating plant nitrogen (as opposed to feeding compensation) are far more sensitive to changing plant nitrogen content than are sedentary species
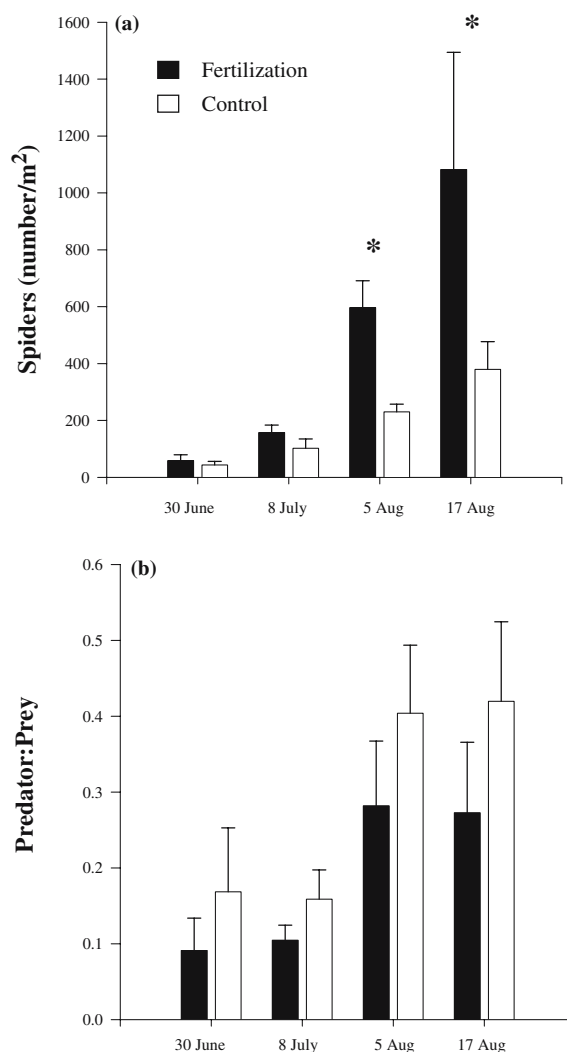
Figure 9. Effect of nitrogen fertilization on (a) the density (mean $\pm$ SEM number/m^2) of spiders and (b) on the ratio of predators to prey (density of predators/density of sap-feeders) in plots of *Spartina alterniflora*.

(Denno et al. 2000; Huberty 2005). Thus, even under a regime of continuous nitrogen subsidy, a community dominated by mobile sap-feeders is expected.

Although increased nitrogen uptake by plants can increase the number of coexisting species, and thus increase biodiversity in herbivorous insect communities, altered plant competitive interactions and outbreak densities of a few mobile members of the sap-feeder community likely reduce food web stability and diversity over longer time periods (Haddad et al. 2000; Bailey et al. 2004). Although predaceous spiders showed a significant numerical response to increased prey

densities on nitrogen-enriched *S. alterniflora* Figure 9a), they were unable to exert sufficient top-down control to preclude outbreak dynamics in the abundant sap-feeders (Figures 7a and 8a). This notion is supported by the fact that prey density remained high and predator-to-prey ratio low throughout the growing season in nitrogen-subsidized plots. There is also evidence from other studies that one-time nutrient subsidies in this system propagate to higher trophic levels for several years (Holmgren et al. 2001; Gratton and Denno 2003). For instance, populations of generalist spiders and the planthopper egg-predator *Tytthus vagus* remain elevated for 2 years follow-

ing a nitrogen subsidy (Gratton and Denno 2003). However, an even stronger population response by the mobile sap-feeders resulted in a lower predator to prey ratio (Figure 9b); (Gratton and Denno 2003). Overall, nitrogen subsidies appear to promote the escape of sap-feeders from predator controls and an increased probability for sap-feeder outbreaks especially in mobile species.

Conclusions

Species-specific variation in life history traits of sap-feeding herbivores make this community of terrestrial insects ideal indicators of food-web response to habitat fragmentation and subsequent nutrient run-off into adjoining habitats (McGeoch 1998; Carignan and Villard 2002; Valiela and Cole 2002; Nickel and Hildebrandt 2003; Biedermann 2004). Although quantifying habitat loss in area is relatively uncomplicated, understanding the relative impact of habitat loss and fragmentation on food webs and ecosystem function is far less clear (Radeloff et al. 2000; Fahrig 2003; Reed 2004; Tscharntke and Brandl 2004). Furthermore, because of the monetary cost associated with measuring nutrient concentrations such as nitrogen, in ground water, soils, and plants, insects are often used as biological indicators of altered nitrogen concentrations (Carignan and Villard 2002). Although insects have long been used as indicators of nutrient pollution in aquatic systems (Wright et al. 1984; Heino et al. 2003), only a few terrestrial insects have been considered as indicator species, perhaps because of the taxonomic and ecological complexity of factors that affect their population size (McGeoch 1998). The taxonomy (e.g. (O'Brien and Wilson 1985; Wilson et al. 1994), life history (Denno et al. 1981), and ecology (e.g. (Waloff 1980) of planthoppers and their relatives are fairly well known making them ideal candidates as indicator species in grass-dominated habitats where they abound (Wilson et al. 1994).

Acknowledgements

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