Spatial variation in the relative strength of top-down and bottom-up forces: causes and consequences for phytophagous insect populations

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Most ecologists acknowledge that both natural enemies and host-plant resources act in concert to influence populations of insect herbivores. What is poorly known is how the strength of top-down and bottom-up impacts on insect herbivores vary spatially and what factors dictate the relative strength of these forces. We examined spatially-explicit change in top-down and bottom-up impacts along a tidal gradient on the inter-tidal marshes that fringe the Atlantic coast of North America. These marshes are dominated by extensive stands of *Spartina* cordgrass and its associated arthropod food web, comprised mostly of herbivorous planthoppers (*Prokelisia*) and their spider predators. Using "effect sizes" generated from experiments, we show that bottom-up forces dominate in low-marsh habitats and that top-down impacts increase up the elevational gradient. We develop a graphical model that integrates spatial variation in top-down (predation) and bottom-up variables (plant nutrition and vegetation complexity) to make habitat-related predictions concerning herbivore abundance.

Introduction

Despite a long-standing history of controversy, most ecologists now concur that top-down forces (predation) and bottom-up factors (host-plant resources) interact together to impact populations of herbivorous insects (Price *et al.* 1980, Denno & McClure 1983, Hunter & Price 1992, Stiling & Rossi 1997, Rosenheim 1998, Forkner & Hunter 2000, Denno *et al.* 2002). Notably, a recent focus has been to identify factors that mediate the relative strength of natural-enemy and host-plant impacts on insect herbivores (Moran *et al.* 1996, Beckerman *et al.* 1997, Schmitz *et al.* 1997, Denno & Peterson 2000, Forkner & Hunter 2000) and to explore conditions that enhance or reduce bottom-up and top-down forces on food-web dynamics (Polis & Strong 1996, Fagan 1997, Moran & Hurd 1998, Pace *et al.* 1999, Schmitz *et al.* 2000, Halaj & Wise 2001). For instance, habitat structural complexity and features of the herbivores themselves (dispersal strategies and defensive behaviors) can influence the strength of bottom-up and top-

down impacts (Riechert & Bishop 1990, Denno & Peterson 2000, Forkner & Hunter 2000, Denno *et al*. 2002, 2003). Also, a growing number of studies show that plant resources (productivity, nutrition, and vegetation complexity) often mediate the strength of top-down impacts on insect herbivores (Hunter *et al*. 1997, Polis *et al*. 1998, Forkner & Hunter 2000, Denno *et al*. 2002, Haukioja 2005). Top-down impacts are also influenced by interactions among species at higher trophic levels such as intraguild predation or predator facilitation (Moran *et al*. 1996, Fagan 1997, Losey & Denno 1998, Rosenheim 1998, Sih *et al*. 1998, Schoener & Spiller 1999, Finke & Denno 2003, 2004). However, there is growing evidence that antagonistic interactions among predators (interference, cannibalism, and intraguild predation) are moderated in complex-structured vegetation, thereby increasing top-down impacts on insect herbivores (Finke & Denno 2002, Langellotto & Denno 2004, Denno *et al*. in press).

What remains poorly understood is how the strength of top-down and bottom-up factors vary spatially and temporally and what factors underlie the relative strength of these forces (but *see* Walker & Jones 2001, Denno *et al*. 2002, Harrison *et al*. 2005, Roland 2005). The few studies that do exist have focused largely on temporal variation in the strength of top-down and bottom-up forces (Kato 1994, Gratton & Denno 2003). Notably, spatial variation in these forces remains largely unexplored. An ideal approach to this issue is to examine spatially-explicit change in top-down and bottom-up impacts along a landscape gradient where there is known variation in the quality of basal resources and the abundance of natural enemies.

Just such a gradient exists on the inter-tidal marshes that fringe the Atlantic coast of North America, marshes that are dominated by extensive stands of *Spartina* cordgrass and its associated arthropod food web comprised mostly of herbivorous planthoppers (*Prokelisia*) and their invertebrate predators (mostly spiders and predaceous bugs). Along this inter-tidal gradient from low-marsh to high-marsh habitats, there is marked change in the frequency and duration of tidal inundation (Bertness 1991, Denno *et al*. 1996). Variation in tidal flushing in turn results

in spatial differences in nutrient subsidies that affect host plant quality, the amount of detritus (thatch accumulation), and invertebrate predator densities (Denno 1983, Ornes & Kaplan 1989, Bertness 1991, Denno *et al*. 1996), all of which are known to alter the strength of top-down and bottom-up impacts on insect herbivores in this system (Döbel & Denno 1994, Denno *et al*. 2002, 2003, Finke & Denno 2002, 2003, Langellotto & Denno 2004). Along this tidal gradient from low-marsh to high-marsh habitats, host plant quality (nitrogen content) decreases whereas thatch and predators generally increase in abundance (Denno 1983, Ornes & Kaplan 1989, Döbel *et al*. 1990, Denno *et al*. 1996, 2002). In the absence of predators, enhanced plant nitrogen promotes rapid population growth of herbivores and encourages outbreak dynamics (Cook & Denno 1994). Also, invertebrate predators in this system can suppress herbivore populations dramatically under certain circumstances (Döbel & Denno 1994, Finke & Denno 2002). Moreover, thatch encourages the local aggregation of invertebrate predators, enhances their numerical response, and in general intensifies top-down effects on herbivores (Döbel & Denno 1994). Thus, our general expectation was that top-down (predators) and bottom-up forces (plant nutrition and thatch) would interact along the tidal gradient such that planthopper outbreaks would be the paradigm in the low marsh whereas planthopper suppression would be more the norm in high-marsh habitats, especially ones with abundant thatch. Several studies document the frequent occurrence of planthopper outbreaks in low-marsh habitats and their reduced occurrence on the high marsh (Denno 1983, Döbel & Denno 1994, Denno & Peterson 2000). However, it remains unclear whether outbreaks are promoted in the low-marsh because plant quality is high, because predators are rare, or both. Likewise, suppression on the high marsh could result from nitrogen-poor *Spartina*, a more abundant predator complex, the predation-enhancing effects of thatch, or some combination of these impacts. Overall, we expected top-down forces to increase in relative strength moving up tidal gradient. Nonetheless, the relative contribution of each force to spatial variation in planthopper dynamics remains an open question.

To determine spatial differences in the relative effects of top-down and bottom up forces, and to test the hypothesis that predator effects become increasingly stronger along the gradient toward the high marsh, our specific objectives were as follows: First, we verified spatial variation in the quantity and quality of *Spartina* and the abundance of planthoppers and their major invertebrate predators by sampling their populations along the tidal gradient from low-marsh to high marsh habitats. These data will reveal not only where along the gradient planthopper populations are most likely to erupt in relation to *Spartina* resources, but they will further document spatial changes in the abundance of important predators that may underlie patterns of herbivore density. Second, the relative strength of top-down and bottom-up factors on planthopper growth were assessed by reanalyzing the results of factorial experiments conducted both in the laboratory and the field (Döbel 1996, Denno *et al.* 2002). From these experiments, planthopper population growth could be assessed under specific treatment combinations of *Spartina* nutrition, thatch, and spiders that we extracted from the full experiment to represent different high-marsh and low-marsh conditions. Specifically, top-down "effect sizes" of predators on planthopper populations (Effect Size$_{TD}$ = ln[treatment density/control density]) were calculated under different treatment combinations of bottom-up resources (N-rich and N-poor *Spartina* with and without thatch) and were used to assess the suppressing effects of predators in specific habitats (*see* Denno *et al.* 2003). Likewise, the bottom-up effect of plant quality (Effect Size$_{BU}$ = ln[treatment density/control density]) was determined under specific combinations of thatch and predators. Third, the relative strength of the top-down to the bottom-up force (relative effect size) was calculated for separate low-marsh and high-marsh conditions (Denno *et al.* 2003). Results of these "effect-size" analyses will be used here for the first time to explicitly tease apart the relative strength of predation and plant nutrition as they contribute to observed spatial patterns of planthopper outbreak and suppression. Last, we develop a new conceptual model that integrates the information we generate here on spatial variation in top-down and bottom-up forces along

with known temporal variation on the importance of these factors (Gratton & Denno 2003) to make explicit habitat-related predictions concerning herbivore outbreak and suppression as they change throughout the growing season.

Study site and system

Field work was conducted 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, New Jersey, USA. The vegetation of this marsh and other mid-Atlantic marshes is dominated by the perennial cordgrass *Spartina alterniflora*, where it grows in extensive pure stands within the intertidal zone (Denno 1983, Gallagher *et al.* 1988). Within this zone, however, the structure of *Spartina* varies dramatically with elevation due to differences in tidal flooding, nutrient subsidy, and litter (thatch) removal and decay (Denno 1983, Gallagher *et al.* 1988). In tidally subsidized low-marsh habitats, *Spartina* plants accumulate a large standing crop (> 1000 g dry mass m^{-2}), grow vigorously tall (> 1 m), are very nutritious (> 2.5% nitrogen in May), but are often devoid of leaf litter (< 200 g dry mass m^{-2}) because it is carried away by tidewaters (Denno & Grissell 1979, Denno 1983, Ornes & Kaplan 1989, Denno *et al.* 2002). By contrast, in high marsh meadows where nutrient subsidy and tidal flushing are much less, standing crop is low (< 300 g dry mass m^{-2}), plants are dwarfed (< 30 cm), less nutritious (< 1.5% nitrogen in May), but they are frequently engulfed in a dense entanglement of thatch (> 600 g dry mass m^{-2}) (Ornes & Kaplan 1989, Denno *et al.* 2002). Thus, moving up an elevational gradient from low-marsh habitats (tidal creek banks) to high-marsh plateaus (meadows), *Spartina* plants generally decrease in biomass and nitrogen content, but increase in the amount of associated thatch (Denno & Grissell 1979, Denno 1983, Ornes & Kaplan 1989). However, even on the high marsh subtle differences in soil porosity, standing water, and salinity result in the differential decay of dead leaf material and combine to produce a mosaic of habitats that vary in the amount of thatch (Redfield 1972, Gallagher *et*

al. 1988, Denno *et al.* 1996). Notably, *Spartina* growing in meadows accumulates much more thatch than plants occupying mud flats (Redfield 1972, Denno *et al.* 2002). Moreover, *Spartina* plants growing on thatch-free mud flats are often salt-stressed and more nutritious, a situation that results from enhanced evaporation, elevated soil salinity, and the production of nitrogen-containing osmoprotectants such as proline (Redfield 1972, Cavalieri & Huang 1981).

Spartina serves as the only host plant for a variety of insect herbivores, mostly sap-feeders such as planthoppers, leafhoppers and phytophagous mirid bugs (Denno *et al.* 2003). Chewing herbivores such as caterpillars and beetles are not nearly as common in this system. Of the sap-feeders, phloem-tapping *Prokelisia* planthoppers (*P. dolus* and *P. marginata*) are by far the most abundant herbivores on *Spartina*, with adult densities often exceeding several thousand individuals m^{-2} and nymphal densities often reaching more than 10 000 m^{-2} (Denno *et al.* 2000). Host plant nutrition plays an important and direct role in determining the potential for population growth in *Prokelisia* planthoppers. In the absence of predators, planthopper populations grow rapidly and frequently outbreak on nitrogen-rich *Spartina* (Denno 1983, Cook & Denno 1994, Denno & Peterson 2000). Population increases result from a combination of enhanced colonization, oviposition, development rate, survival, and fecundity on plants rich in amino nitrogen (Cook & Denno 1994, Denno *et al.* 2002). The most striking planthopper outbreaks occur annually in low-marsh habitats where they are associated with nitrogen-rich *Spartina* (Denno & Peterson 2000).

A diversity of natural enemies, both invertebrate predators and parasitoids, attack *Prokelisia* planthoppers, but predators are a far more important source of mortality on the mid-Atlantic marshes of North America (Döbel & Denno 1994). Of the invertebrate predators, spiders and heteropterans inflict the most mortality on *Prokelisia* planthoppers (Döbel & Denno 1994, Denno *et al.* 2002, 2003, Finke & Denno 2002, 2003). In particular, the hunting spider *Pardosa littoralis* and the mirid egg predator *Tytthus vagus* can have the most devastating effects on planthopper populations because they are so voracious (Döbel & Denno 1994, Denno *et al.* 2002). Singularly, *Pardosa* can consume up to 70 planthoppers (nymphs or adults) per day and *Tytthus* can kill up to 24 planthopper eggs per day (Döbel & Denno 1994, Finke & Denno 2002). However, *Tytthus* also falls prey to *Pardosa* and intraguild predation can reduce the overall effectiveness of the predator complex in suppressing planthopper populations (Finke & Denno 2002, 2003, Denno *et al.* 2004, Matsumura *et al.* 2004).

Notably though, intraguild predation between *Pardosa* and *Tytthus* is dramatically curtailed in complex-structured habitats with thatch where *Tytthus* finds a spatial refuge from attack (Finke & Denno 2002). Moreover, *Pardosa* and other predators tend to aggregate in thatch-rich habitats independent of the presence of planthopper prey (Langellotto & Denno 2004). Also, *Pardosa* exhibits a strong numerical response to increasing planthopper density, a response that is very much exaggerated in thatchy habitats (Döbel & Denno 1994). Overall, thatch enhances top-down effects on planthoppers by promoting the accumulation of predators, by enhancing their numerical response, and by tempering intraguild predation (Döbel & Denno 1994, Denno *et al.* 2002, Finke & Denno 2002).

Spatial variation in herbivore density and underlying top-down and bottom-up correlates

To determine spatial variation in the abundance of planthoppers (*Prokelisia*) and their major invertebrate predators (*Pardosa* and *Tytthus*), we sampled their populations along the tidal gradient from low-marsh (tidal creek side *Spartina*) to high marsh habitats (meadow *Spartina*) at the Tuckerton field site. Arthropods were sampled at 5 stations along 6 replicated elevational transects (separated by 50 m) running perpendicular to tidal creeks. Samples were taken using a D-vac vacuum sampler (Rincon-Vitova, Ventura, California, USA) (*see* Denno *et al.* 2000) at distances 1, 3, 10, 50, and 100 m from tidal creeks. One sample consisted of five 5-second placements of the sampling head on the marsh surface such that 0.5 m^2 of *Spartina* was vacuumed.

Planthoppers (*Prokelisia* nymphs and adults) and predators (pooled adults and immatures of *Pardosa* and *Tytthus*) were killed in an ethyl-acetate jar, transferred to 95% ethanol sample bottles, and returned to the laboratory where they were counted. Transects were sampled on 17 July 2000 when planthopper adults are most abundant and on 10 August when planthopper nymphs and predators abound (*see* Denno *et al.* 2002).

There was a significant effect of distance from tidal creek (marsh elevation) on the density of planthopper adults ($F_{4,25}$ = 588.91, $P < 0.0001$) and nymphs ($F_{4,25}$ = 357.29, $P < 0.0001$) with both life stages reaching outbreak proportions (> 9000 m^{-2}) in low-marsh *Spartina*; densities were more than one order of magnitude lower (< 500 m^{-2}) in meadows of high-marsh *Spartina* (Fig. 1A and B). Notably, predators showed the opposite pattern whereby both *Pardosa* ($F_{4,25}$ = 3.46, $P = 0.023$) and *Tytthus* ($F_{4,25}$ = 2.740, $P = 0.050$) reached significantly higher densities in high-marsh meadows of *Spartina* than in low-marsh habitats (Fig. 1C and D).

Correlations were performed to determine the spatial relationship between *Prokelisia* planthopper density (log$_{10}$ number of adults m^{-2}), plant quality, the biomass of thatch, and the density of *Pardosa* and *Tytthus* along the transects. Mean planthopper density at the 5 transect stations was correlated with data taken on *Spartina* biomass (g dry mass m^{-2}), thatch (g dry mass m^{-2}), and predator density (log$_{10}$ number of individuals m^{-2}) at the same 5 sampling stations (*see* Denno *et al.* 2002 for details on *Spartina* sampling and biomass determination). The biomass of *Spartina* was used as an expedient surrogate for plant quality (% nitrogen) because the two plant variables are highly associated (*see* Denno *et al.* 2002, Gratton & Denno 2003).

Planthopper adults showed significant positive density relationships with *Spartina* biomass (density = 2.206 + 0.001 × plant biomass, R^2 = 0.911, $P = 0.012$) across the spatial gradient. In contrast, planthoppers were negatively associated with predator density along the gradient, both *Pardosa* (density = 5.137 – 1.217 × *Pardosa* density, R^2 = 0.858, $P = 0.024$) and *Tytthus* (density = 10.637 – 3.339 × *Tytthus* density, R^2 = 0.955, $P = 0.004$). Likewise, planthoppers were also negatively correlated with the biomass
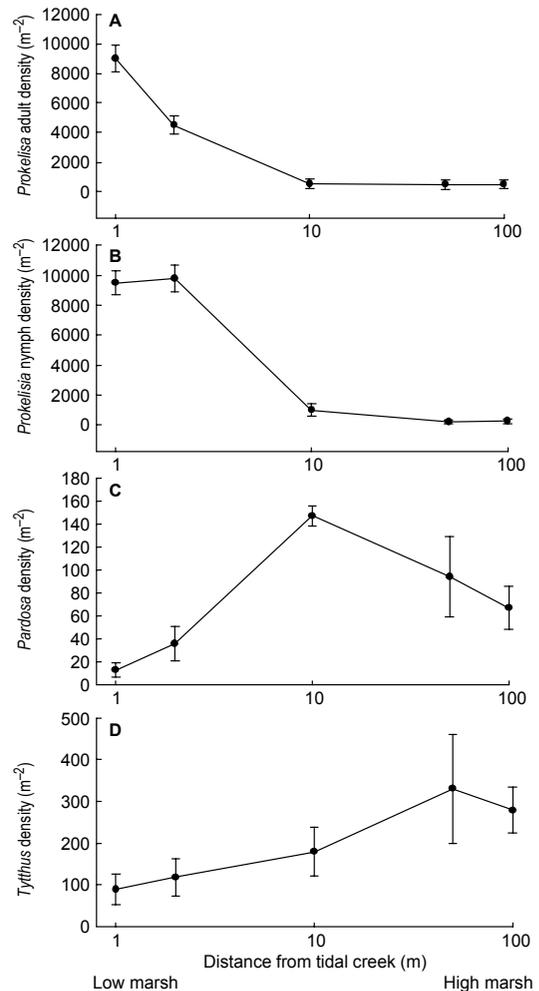
Fig. 1. Density of (**A**) *Prokelisia* planthopper adults, (**B**) *Prokelisia* nymphs, (**C**) the wolf spider *Pardosa*, and (**D**) the planthopper egg predator *Tytthus* along a tidal gradient from low-marsh to high-marsh *Spartina* habitats. Densities (m^{-2}) are measured at five distances (1, 3, 10, 50, and 100 m) from a tidal creek (1 m) in the low marsh to a high-marsh meadow (100 m).

of thatch across the gradient (density = 3.927 – 0.002 thatch biomass, R^2 = 0.786, $P = 0.045$), a correlation that was likely driven by spiders, because spider density was positively related to the amount of thatch in the habitat (spider density = 0.996 + 0.002 × thatch biomass, R^2 = 0.913, $P = 0.011$). The positive relationship between spider density and thatch has been shown in other studies on the same marsh (Döbel & Denno 1994). Thus, the outbreak dynamics of *Prokelisia* planthopper in low marsh *Spartina* may result from

enhanced plant quality, the rarity of predators, or the reduced biomass of thatch that may underlie the rarity of predators in the low marsh. Any one or some combination of these factors may contribute to the observed pattern of planthopper abundance along the marsh gradient.

Spatial variation in the relative strength of top-down and bottom-up forces
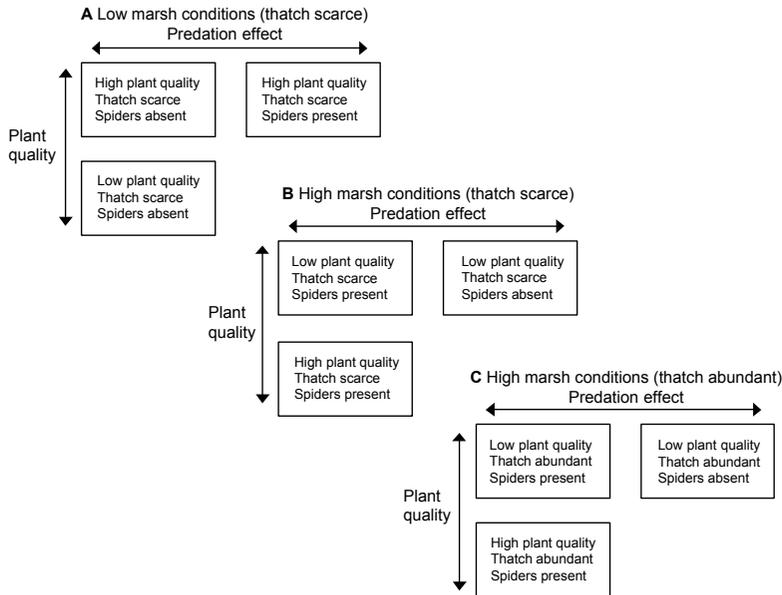
We reanalyzed the results of previously conducted factorial experiments (Döbel 1996, Denno *et al.* 2002) to tease apart the relative effect of top-down (spider predation) and bottom-up forces (*Spartina* quality and thatch) as they might contribute to planthopper population growth along the spatial gradient. From these experiments, planthopper population growth was assessed under specific treatment combinations of *Spartina* nutrition, thatch, and spiders that we extracted from the full experiment to represent different high-marsh and low-marsh conditions. All field experiments were conducted at the Tuckerton field site.

For both the lab and field factorial experiments, 8 treatment combinations of *Spartina* nutrition (high and low), thatch (present and absent), and spider density (high and low) were created by differential fertilization, thatch removal and replacement or not, and spider inclusion or exclusion (*see* Döbel 1996, Denno *et al.* 2002). The levels of spider density, *Spartina* nutrition (%N) and thatch used in these experiments were manipulated specifically to mimic the range of these factors that occur naturally on the marsh (Denno *et al.* 2002). For both lab and field experiments, the effect of the different treatment combinations on planthopper population size was assessed after two months, approximately two full planthopper generations.

From these experiments, "effect sizes" were calculated to assess the relative strength of the different bottom-up and top-down treatment combinations on planthopper population density, and ultimately to determine the relative strength of each force along the landscape gradient (Denno *et al.* 2003). An "effect size" is simply the natural log of the density of planthoppers in the treatment over their density in the control

(ln[treatment density/control density]). Thus, an effect size of zero constitutes no treatment effect, a positive effect size denotes higher planthopper densities in the treatment relative to the control as might occur when plant nutrition is enhanced, and a negative effect size results when planthopper densities are lower in the treatment than the control as might occur when predator density is augmented. The significance of the various treatment effects relative to controls was determined from analyses of variance (Döbel 1996, Denno *et al.* 2002, 2003). The "relative effect" of top down (TD = spider predation) and bottom-up (BU = *Spartina* quality) factors on planthopper population size was also determined, where "relative effect size" = ln[|Effect Size$_{TD}$|/|Effect Size$_{BU}$|]. A positive relative effect size connotes a stronger top-down than bottom-up effect (Effect$_{TD}$ > Effect$_{BU}$), whereas a negative relative effect size suggests a stronger bottom-up effect (Effect$_{BU}$ > Effect$_{TD}$).

Spider and plant quality effects on planthopper population size were compared under three different sets of conditions representing distinct low marsh and high marsh scenarios (Fig. 2). For the low marsh situation (Fig. 2A), plant quality effects (high versus low *Spartina* nitrogen content) were compared in the absence of spiders when thatch was scarce, a variable state typical of low-marsh habitats. Spider effects (present *vs.* absent) were compared under conditions of high plant quality and scarce thatch, also characteristic of the low marsh. Because thatch varies on the high marsh, spider and plant quality effects were determined under two regimes, when thatch was abundant and when it was scarce. In high marsh habitats devoid of thatch (e.g., the *Spartina* surrounding mud pan habitats; Fig. 2B), plant quality effects were determined in the presence of spiders and the scarcity of thatch. Spider effects were determined under conditions of low plant quality and the absence of thatch. In thatch-rich habitats on the high marsh (e.g., *Spartina* meadows; Fig. 2C), plant quality effects were assessed under conditions of abundant thatch and spiders, whereas spider effects were assessed holding plant quality low and thatch abundant. Treatment means from both our lab (Fig. 3) and field experiments (Fig. 4) were used to calculate top-down (spider predation) and bottom-up (*Spartina* qual-

A Low marsh conditions (thatch scarce)
Predation effect

| High plant quality Thatch scarce Spiders absent | High plant quality Thatch scarce Spiders present |

Plant quality

| Low plant quality Thatch scarce Spiders absent |

B High marsh conditions (thatch scarce)
Predation effect

| Low plant quality Thatch scarce Spiders present | Low plant quality Thatch scarce Spiders absent |

Plant quality

| High plant quality Thatch scarce Spiders present |

C High marsh conditions (thatch abundant)
Predation effect

| Low plant quality Thatch abundant Spiders present | Low plant quality Thatch abundant Spiders absent |

Plant quality

| High plant quality Thatch abundant Spiders present |

Fig. 2. Low-marsh and high-marsh conditions under which spider predation and plant quality effects on planthopper populations were assessed experimentally in the lab and field. For the low marsh situation (**A**), plant quality effects (high versus low *Spartina* nitrogen content) were compared in the absence of spiders and when thatch was scarce, two variable states typical of low-marsh habitats. Spider effects (present *vs.* absent) were compared under conditions of high plant quality and the scarcity of thatch, two variable states also characteristic of the low marsh. On the high marsh, spider and plant quality effects were determined under two regimes, when thatch was scarce (**B**) and when it was abundant, the usual case (**C**). In high marsh habitats devoid of thatch (e.g., the *Spartina* surrounding mud pan habitats), plant quality effects were determined in the presence of spiders and the scarcity of thatch. Spider effects were determined under conditions of low plant quality and the absence of thatch. In thatch-rich habitats on the high marsh (e.g., *Spartina* meadows), plant quality effects were assessed under conditions of abundant thatch and spiders, whereas spider effects were assessed holding plant quality low and thatch abundant.

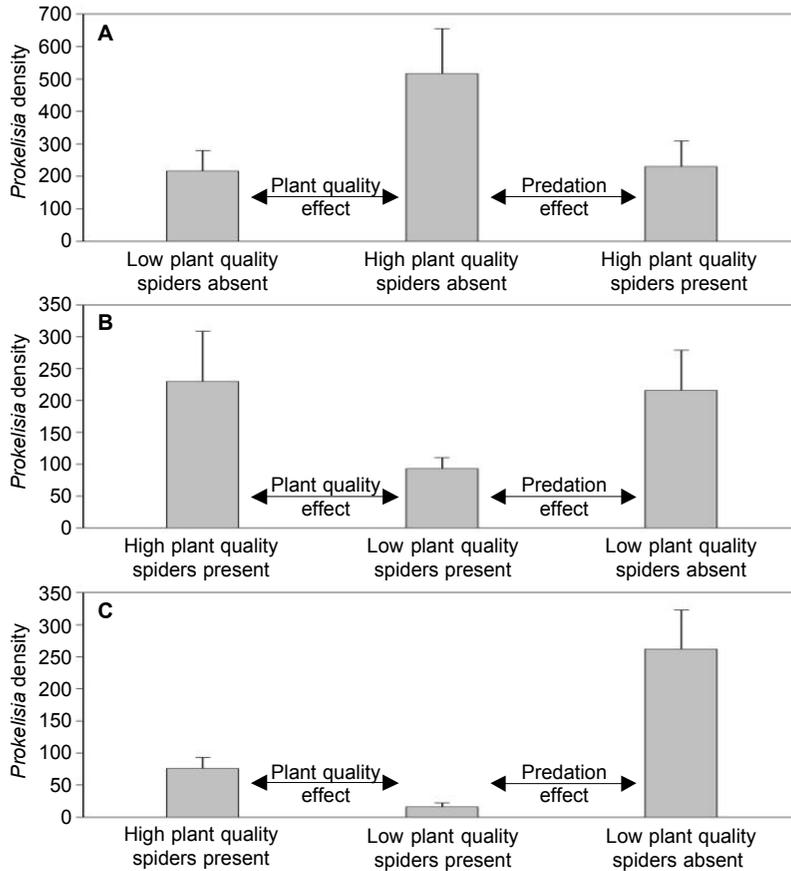ity) effect sizes as well as their relative effects on planthopper populations.

Results

Laboratory experiment

There were significant top-down (predation) and bottom-up (*Spartina* quality) effects on planthopper populations in all three habitat scenarios (Fig. 5), as evidenced by the significant *P* values (effect size significantly different from zero). However, the relative strength (effect size) of the two forces changes across habitat types (Fig. 5): plant quality effects prevail under low-marsh conditions (negative relative effect size) and under high-marsh conditions in the absence of thatch, whereas predation effects are relatively stronger under high-marsh conditions in the presence of

thatch. Thus, thatch dramatically shifts the paradigm to top-down control on the high marsh.

Field experiments

Results were similar when field data were analyzed. There were significant bottom-up effects on planthopper populations under the three habitat conditions, but top-down effects were significant only under high-marsh scenarios both when thatch was absent and present (Fig. 6). Relative effect sizes show that plant nutritional effects were strongest in the low marsh and decrease under high marsh conditions, and that thatch once again promotes top-down suppression under high marsh conditions (Fig. 6). Overall, top-down forces were shown to be stronger under confined cage conditions in the lab than the in the field (compare Figs. 5 and 6) where

Fig. 3. Mean (± SEM) planthopper densities resulting in cages from different treatment combinations of host-plant quality (high or low), spider predation (present or absent), and thatch (present or absent) used in a laboratory experiment (data extracted from Denno *et al.* 2002). Treatment means were generated under three scenarios: (**A**) low-marsh conditions without thatch, (**B**) high-marsh conditions (thatch scarce), and (**C**) high-marsh conditions (thatch abundant) (*see* Fig. 2); and were used to calculate top-down (spider predation) and bottom-up (*Spartina* quality) effect sizes as well as their relative effects on planthopper populations (*see* Fig. 5). Arrows indicate specific means that were used to calculate plant-quality and predation effect sizes.

prey are better able to escape predators by emigration (Cronin *et al.* 2004). Likewise, bottom-up effects were stronger under predator-reduced conditions in the field than in the lab (compare low-marsh condition in Figs. 5 and 6), because adult planthoppers were able to colonize nutrient-rich plants in the field (Denno *et al.* 2002).

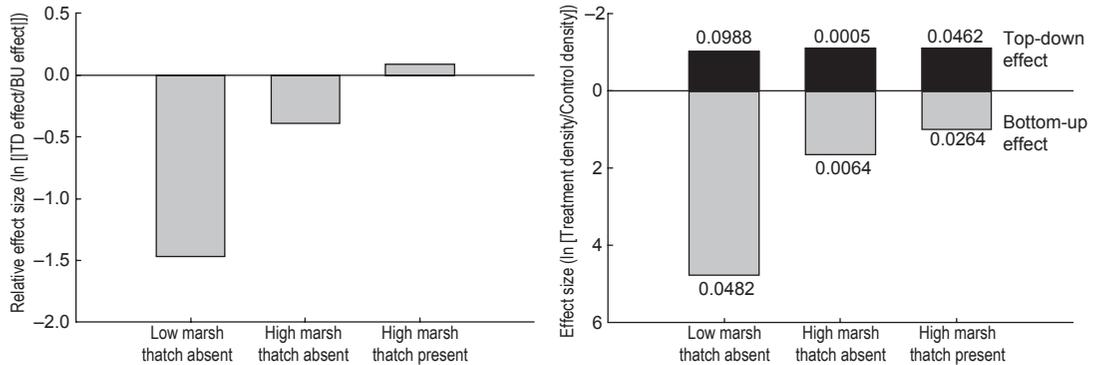## Consensus and interpretation of effect sizes

Altogether, our data suggest that the relative strength of top-down and bottom-up forces reverses along the habitat gradient with plant nutritional factors dominating in the low marsh and with predation increasing in strength on the high marsh, especially in thatch-rich habitats. This said, it is important to realize that the levels of spider density, *Spartina* nutrition, and thatch used in these experiments represented high and low ambient values. Local variation in these variables will alter both the absolute and relative strength of top-down and bottom-up impacts. Had we used other spider densities, plant qualities, or levels of thatch in our experiments, the magnitude of resulting effect sizes would most certainly change. Moreover, our analyses assume additivity of forces and one can ask if non-linearities (e.g., density-dependent effects) exist. Indeed they do, but we do not expect that our overall conclusion will change as a consequence. For example, over the range of *Spartina* qualities used in our experiments (1%–3% nitrogen), planthopper population growth is positively and linearly related to plant nitrogen content (Huberty 2005). Also, density effects on several components of planthopper fitness (survival, development rate, and body size) are linear across a wide range of densities, whereas density effects on dispersal are not (Denno & Roderick 1992). Dispersal in planthoppers is density-dependent and

Fig. 4. Mean (± SEM) planthopper densities (m^{-2}) resulting from different treatment combinations of host-plant quality (high or low), spider predation (present or absent), and thatch (present or absent) used in field experiments (data extracted from Döbel 1996, Denno *et al.* 2002). Treatment means were generated under three scenarios: (**A**) low-marsh conditions without thatch, (**B**) high-marsh conditions (thatch scarce), and (**C**) high-marsh conditions (thatch abundant) (*see* Fig. 2); and were used to calculate top-down (spider predation) and bottom-up (*Spartina* quality) effect sizes as well as their relative effects on planthopper populations (*see* Fig. 6). Arrows indicate specific means that were used to calculate plant-quality and predation effect sizes.
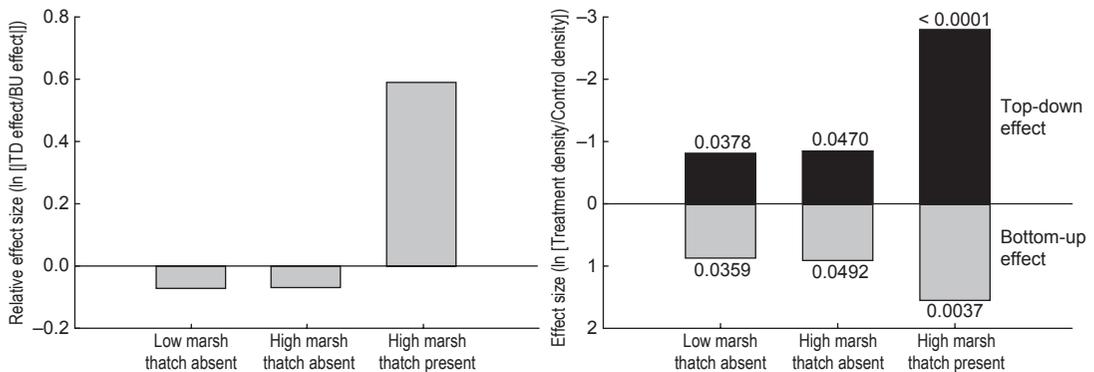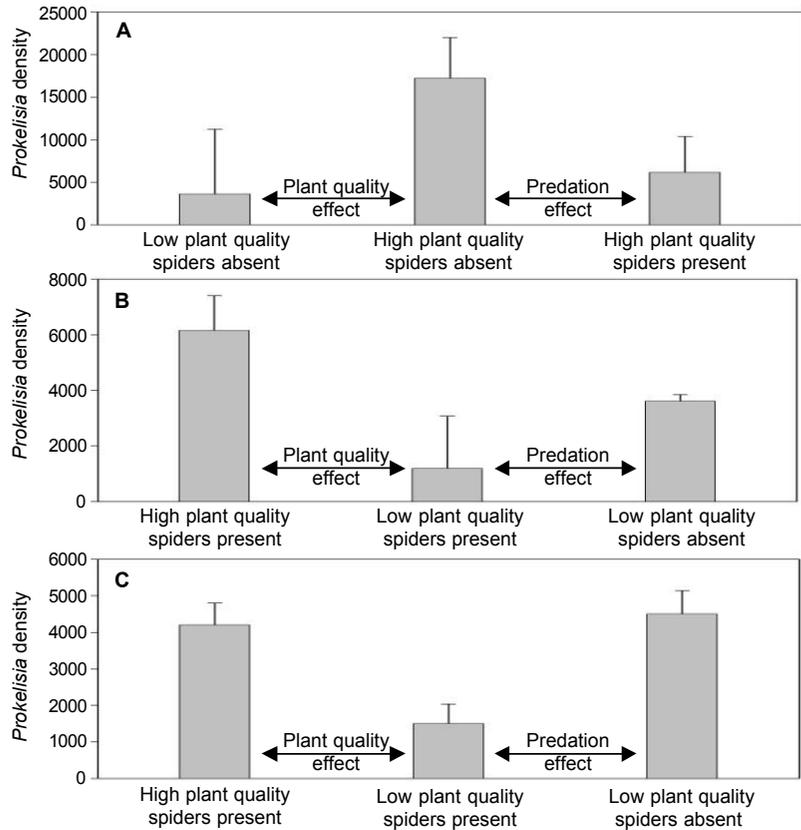
Fig. 5. Effect size (right panel; ln[treatment density/control density]) of bottom-up (plant-quality) and top-down (spider-predation) treatments on the population density of planthoppers. Effect sizes were generated under three scenarios in the laboratory designed to mimic real-world situations: low-marsh conditions without thatch and high-marsh conditions in the absence and presence of thatch (*see* Fig. 3 for treatment means used to calculate effect sizes). *P* values above and below bars indicate the significance of the top-down and bottom-up treatments relative to controls for each sap-feeder species (pre-planned contrasts) and for the community at large. Relative effect size (left panel; [|Effect size$_{TD}$|/|Effect Size$_{BU}$|]) of the top-down (spider predation) and bottom-up (plant quality) treatments on planthopper population density under the same three marsh scenarios. A relative effect size value of 0 indicates that planthopper density was influenced equally by top-down and bottom-up treatments, positive values indicate that top-down effects had a relatively greater impact on planthopper density than bottom-up effects, and negative values indicate that bottom up effects were stronger.

Fig. 6. Effect size (right panel; ln[treatment density/control density]) of bottom-up (plant-quality) and top-down (spider-predation) treatments on the population density of planthoppers. Effect sizes were generated under three scenarios in the field at Tuckerton New Jersey: low-marsh conditions without thatch and high-marsh conditions in the absence and presence of thatch (*see* Fig. 4 for treatment means used to calculate effect sizes). *P* values above and below bars indicate the significance of the top-down and bottom-up treatments relative to controls for each sap-feeder species (pre-planned contrasts) and for the community at large. Relative effect size (left panel; [|Effect size$_{TD}$|/|Effect Size$_{BU}$|]) of the top-down (spider predation) and bottom-up (plant quality) treatments on planthopper population density under the same three marsh scenarios. A relative effect size value of 0 indicates that planthopper density was influenced equally by top-down and bottom-up treatments, positive values indicate that top-down effects had a relatively greater impact on planthopper density than bottom-up effects, and negative values indicate that bottom up effects were stronger.

non-linear because migratory adults with wings are produced above a certain density threshold. Thus, bottom-up effects calculated on the basis of ambient densities in the field may be underestimated if emigrants resulting from population outbreaks on nitrogen-rich plants are not taken into account. However, this possibility did not appear to mask the observed pattern of a very strong bottom-up effect of plant quality on planthopper populations under predator-free conditions (low marsh) in the field (Fig. 6).

Likewise, effects of spider predation (*Pardosa*) on planthoppers are not linear given that cannibalism intensifies with increasing spider density (Langellotto & Denno 2004). This likely explains why spiders are more effective at suppressing planthoppers in thatch-rich habitats where cannibalism is reduced (Döbel & Denno 1994). Moreover, *Pardosa* exhibits a saturating functional response to increasing planthopper density in thatch-free habitats, whereas it shows a Type III functional response under thatchy conditions (Döbel & Denno 1994). Thus, planthopper suppression by *Pardosa* is density-dependent over a range of densities (those we used in our experiments) in thatch, but planthoppers readily escape predator controls under the same density

conditions when thatch is rare (Figs. 6 and 7). Despite these density-dependent effects, some of which are evaluated in our design (lab versus field), we feel that the levels of top-down and bottom-up variables used in our analyses are representative, and thus the emerging effect sizes adequately reflect spatial changes in the relative strength of these forces across major habitats on the marsh.

Conceptual model

Here we develop a simple conceptual model that describes spatial and temporal changes in the relative strength of top-down and bottom-up factors as they affect planthopper population dynamics, and predicts where and when planthopper outbreaks are most likely to occur on the marsh. The spatial aspects of the model are based on assessments of the relative strength of predation, *Spartina* quality, and the abundance of thatch as they change between low-marsh and high-marsh habitats to influence planthopper dynamics (Figs. 5 and 6, Cavalieri & Huang 1981, Döbel & Denno 1994, Döbel 1996, Denno *et al.* 2002, Finke & Denno 2002, 2003, Langellotto
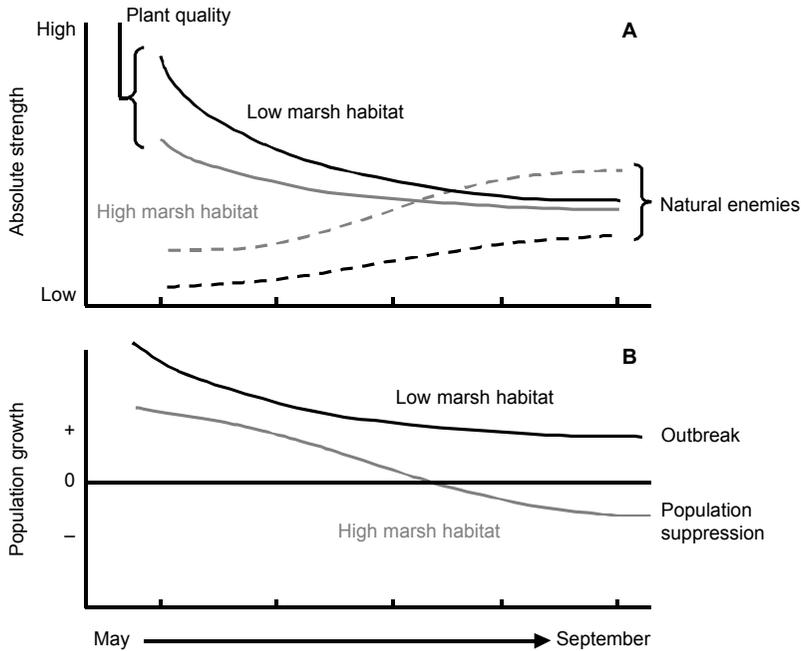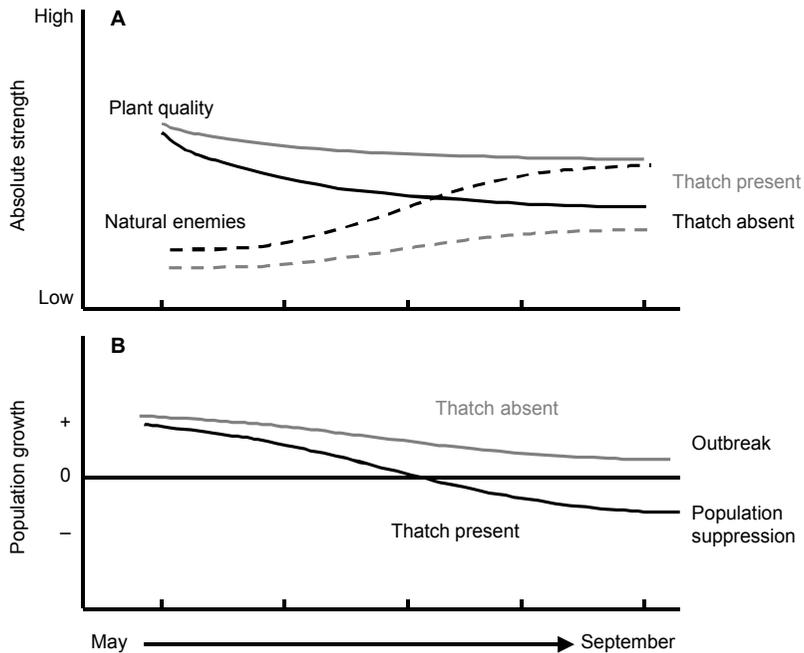
Fig. 7. Conceptual model comparing seasonal changes in (**A**) the strength of bottom-up (plant quality, solid lines) and top-down (predation, dashed lines) forces in low-marsh (black lines) and high-marsh (gray lines) habitats and (**B**) their interactive effects on planthopper population growth (outbreak versus suppression). Factor strengths and population responses are predicted assuming thatch-rich conditions in the high marsh habitat. High plant quality and scarce predators promote planthopper outbreaks in low-marsh habitats early in the season. Late in the season, low plant quality, abundant predators, and reduced intraguild predation combine to suppress planthopper populations in high-marsh habitats.

& Denno 2004). Temporal (seasonal) changes in the strength of these factors as they bear on planthopper dynamics were extracted from the literature (Denno 1983, Döbel *et al.* 1990, Denno & Peterson 2000, Gratton & Denno 2003).

The strength of bottom-up (plant quality) and top-down factors (predation) is compared between low-marsh and high-marsh habitats and during the course of the growing season (Fig. 7A). Also, the interactive effects of the two forces are shown as they either promote planthopper outbreaks or suppression (Fig. 7B). Predicted effects are shown assuming an abundance of thatch on the high marsh (e.g., as occurs in *Spartina* meadow habitats). In the low marsh during spring, plant quality is high, predators are rare (Fig. 7A) and the probability for outbreak is high (Fig. 7B). As the season progresses, plant quality declines, but predators never become very abundant and the chance for outbreak remains quite high, albeit lower than earlier in the year.

On the high marsh in spring, plant quality is rather high, predators are more abundant than in low marsh habitats (Fig. 7A), but their densities at this time are too low to suppress planthoppers and outbreaks can occur (Fig. 7B). Later in the year, plant quality plummets, predator populations build to their highest levels, and planthopper populations are effectively suppressed. Notably, thatch promotes predator aggregation and minimizes intraguild predation (provides spatial refuges for intraguild prey) further enhancing top-down impacts in high marsh meadow habitats later in the season.

The scenario is much different on the high marsh in the absence of thatch, which commonly occurs in the *Spartina* surrounding mud pans (Fig. 8). As above (Fig. 7), the presence of thatch coupled with nitrogen-poor *Spartina* and abundant predators enhances top-down impacts and herbivore suppression, especially late in the season (Fig. 8). In contrast, when thatch is absent

Fig. 8. Conceptual model comparing seasonal changes in (**A**) the strength of bottom-up (plant quality, solid lines) and top-down (predation, dashed lines) forces and (**B**) their interactive effects on planthopper population growth (outbreak versus suppression). Factor strengths and population responses are compared between high-marsh habitats with thatch (black lines) and without thatch (gray lines). In thatch-rich habitats late in the season, low plant quality and the abundance of predators result in planthopper suppression. At the end of the season in thatch-free habitats, plants become salt stressed, plant quality increases due to the production of N-containing osmoprotectants, and predators fail to aggregate; the result is an increased probability for planthopper outbreak.

higher rates of evaporation increase soil salinity, *Spartina* becomes salt stressed, and plant quality goes up due to the production of N-containing osmoprotectants (Fig. 8A). Also, predators avoid thatch-free habitats and the risk of predation is relaxed. Moreover, the few predators that do occur in such thatch-poor habitats are more likely to engage in intraguild predation leading to reduced risk of predation for planthoppers. Thus, the paradigm shifts back to bottom-up control in thatch-poor habitats on the high marsh where outbreaks can occur (Fig. 8B).

For future research considerations, this model suggests that in order to refine our understanding of the interactive effects of top-down and bottom-up forces on herbivores that it will be critical to capture spatial variation in the driver variables in any experimental/sampling design. This approach is particularly critical late in the growing season when spiders are abundant and the abundance of thatch, even at a small spatial

scale, mediates the direction and magnitude of predator impacts.

Synthesis and broader implications

In the *Spartina* system, spatial variation in the relative strength of top-down and bottom-up forces results from an interplay among allochthonous nutrient inputs, predator subsidies from neighboring habitats, discrepant dispersal abilities of the herbivores and predators, and a seasonal environment that resets the stage for interaction every winter. Winter destruction of the standing crop of low-marsh *Spartina* habitats relegates herbivores and predators to high-marsh habitats, the only sites that allow for successful overwintering (Denno & Grissell 1979, Döbel *et al.* 1990, Denno *et al.* 1996). In spring, regrowth of the perennial *Spartina* occurs in all habitats,

but is particularly vigorous in low-marsh habitats due to greater marine subsidies of nutrients. At this time, low-marsh *Spartina* remains unexploited by planthoppers and their predators that are situated hundreds of meters away in protective habitats on the high marsh (Denno *et al*. 1996). Moreover, *Pardosa* spiders overwinter further away in neighboring upland habitats and must travel greater distances to colonize low-marsh *Spartina* (Döbel *et al*. 1990, D. Lewis & R. F. Denno unpubl. data). As the season progresses, populations of both planthoppers and predators (e.g., spiders) grow and disperse from high-marsh to low-marsh habitats, but planthoppers are tremendously advantaged in this colonization process due to their superior dispersal capability (Döbel & Denno 1994, Denno *et al*. 1996). *Prokelisia* planthoppers undergo interhabitat migrations moving from overwintering sites to low-marsh *Spartina* where they colonize this habitat *en masse* (Denno 1988). By contrast, *Pardosa*, which is relegated to ground dispersal with rare bouts of ballooning spiderlings, lags far behind in its colonization of low-marsh *Spartina* (Döbel *et al*. 1990, D. Lewis & R. F. Denno unpubl. data). Thus, even though *Pardosa* can aggregate in areas of high planthopper density at a local spatial scale, its reduced powers of dispersal compared to planthoppers hinders its ability to track planthopper populations and decouples predator–prey dynamics at the landscape spatial scale (Döbel & Denno 1994). The long-term average is strong bottom-up control and planthopper outbreak dynamics in the low marsh and greater top-down suppression on the high marsh. The gradient results because subsidies of basal nutrients and predators enter the system differentially and because winter disturbance resets the spatial landscape on which flight-capable herbivores are better able to track spatial changes in favorable resources than are ground foraging predators.

One can ask if there is evidence from other systems for spatial gradients or mosaics in the strength of bottom-up versus top-down forces on insect herbivores. Notably, there is heightened awareness that the movement of nutrients and basal resources across habitat boundaries can strongly influence herbivore dynamics (Polis *et al*. 1996, Ostfeld & Keesing 2000). For exam-

ple, nutrient runoff from agricultural habitats, marine-derived detritus in littoral habitats, wind-blown detritus into low-productivity habitats, and leaf-fall in streams can enhance consumer abundance, boost predator densities, and alter food-web interactions (Seely 1991, Polis & Hurd 1995, 1996, Polis *et al*. 1997, McCormick *et al*. 2002, Ostfeld & Keesing 2000). Moreover, the incursion of predators from one habitat to another can alter species interactions dramatically and either stabilize or destabilize predator–prey dynamics (Fagan *et al*. 1999, Halaj *et al*. 2000, Jeffries 2000, Post *et al*. 2000, Cantrell *et al*. 2001, Nakano & Murakami 2001, Holt 2002, Murakami & Nakano 2002, Cronin *et al*. 2004, Denno *et al*. in press). Also, deploying refuge habitats in agricultural ecosystems assumes that significant predator incursions will occur across habitat boundaries and result in enhanced biological control (Landis *et al*. 2000, Frampton *et al*. 1995, Symondson *et al*. 2002). For many of these studies, there is a strong directional entry of subsidies into the focal system resulting in gradients of primary productivity, host plant quality, and/or predator density. Also, habitat edges, the nature of the landscape matrix in which focal habitats are nested, and habitat fragmentation can differentially affect the flow of basal resources, herbivores and predators across habitat boundaries (Fagan *et al*. 1999, Cronin 2003, Cronin *et al*. 2004, Morris *et al*. 2005, Roland 2005, Tscharntke *et al*. 2005, van Nouhuys 2005, Denno *et al*. in press). Thus, landscape-level variation in the relative strength of bottom-up and top-down effects on herbivores is likely to be a common characteristic of many systems.

Environmental disturbance (e.g., fire, storms, cold snaps, drought, stream discharge events, and pollutants) is also likely to alter the relative strength of bottom-up versus top-down forces and create gradients or mosaics of differential impact on herbivores across landscapes. For herbivores at large including vertebrates, however, it is not clear whether disturbance will alter top-down or bottom-up effects. There are examples in which disturbance selectively reduces the density or efficiency of predators, thus relaxing risk of predation (Menge & Sutherland 1987, Peckarsky *et al*. 1990, Whitman & Grange 1998). In contrast, disturbance can weaken herbivores making them

more susceptible to predation (Kiffney 1996, Hamilton 2000, Mech *et al.* 2001).

However, for smaller insect herbivores, disturbance seems to promote bottom-up control. For example, for herbivorous insects on small Caribbean islands, violent storms promote regrowth making plants more susceptible to attack, a phenomenon that does not occur on nearby protected islands (Spiller & Agrawal 2003). Notably, spider and lizard predators were eliminated on exposed islands. Thus, the post-storm paradigm was very much bottom-up centric. In the *Spartina* system, exposed low-marsh plants incur greater tidal flooding and wave action during storms than high-marsh plants. Such disturbance advantages mobile planthoppers over predators because they can both withstand tidal flooding and more easily recolonize disturbed habitats (Throckmorton 1989, D. Lewis & R. F. Denno unpubl.). Under these conditions on nutrient-rich *Spartina*, the default is bottom-up control. In general, when disturbance creates open sites or temporary habitats, a colonization strategy is favored for herbivores to exploit such habitats (Denno *et al.* 1996). For small insect herbivores, mobility both promotes escape from natural enemies and allows for the colonization of nutrient-rich host plants, a strategy that results in much stronger bottom-up effects (Wissenger 1997, Denno & Peterson 2000). The larger body size and reduced mobility of arthropod predators as compared with those of their prey tend to result in lagged numerical responses, decoupled predator–prey dynamics, and diminished top-down impact (Döbel & Denno 1994).

More often than not for herbivorous insects, plants set the stage on which natural enemies interact (Denno & McClure 1983, Hunter & Price 1992, Forkner & Hunter 2000, Gruner 2004). Our *Spartina* system certainly supports this notion as bottom-up impacts tend to dominate in most habitats and during most seasons (Denno *et al.* 2002, 2003, Gratton & Denno 2003). Moreover, when predator effects are important, they are often mediated by bottom-up factors such as plant nutrition and thatch (Döbel & Denno 1994, Denno *et al.* 2002). This is no truer than when viewed in a spatial context, as it was the local presence of plant-derived thatch on the high marsh that shifted the scenario from bottom-up to top-down control (Figs. 5 and 6). We argue here for a greater emphasis on studying plant-herbivore-predator interactions across spatially complex landscapes. This said, however, we suspect that a bottom-up paradigm will emerge repeatedly in many habitats given the small size, superior dispersal ability, and high reproductive rate of many insect herbivores as compared with those of their predators.

Acknowledgements

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