

Increased primary production shifts the structure and composition of a terrestrial arthropod community

GINA M. WIMP,^{1,2,6} SHANNON M. MURPHY,³ DEBORAH L. FINKE,⁴ ANDREA F. HUBERTY,⁵ AND ROBERT F. DENNO^{2,7}

¹Biology Department, Georgetown University, Washington, D.C. 20057 USA

²Department of Entomology, University of Maryland, College Park, Maryland 20742 USA

³Department of Biological Sciences, University of Denver, Denver, Colorado 80208 USA

⁴Division of Plant Sciences, University of Missouri, Columbia, Missouri 65211 USA

⁵USDA/APHIS/BRS, 4700 River Road, Unit 147, Riverdale, Maryland 20737 USA

Abstract. Numerous studies have examined relationships between primary production and biodiversity at higher trophic levels. However, altered production in plant communities is often tightly linked with concomitant shifts in diversity and composition, and most studies have not disentangled the direct effects of production on consumers. Furthermore, when studies do examine the effects of plant production on animals in terrestrial systems, they are primarily confined to a subset of taxonomic or functional groups instead of investigating the responses of the entire community. Using natural monocultures of the salt marsh cordgrass *Spartina alterniflora*, we were able to examine the impacts of increased plant production, independent of changes in plant composition and/or diversity, on the trophic structure, composition, and diversity of the entire arthropod community. If arthropod species richness increased with greater plant production, we predicted that it would be driven by: (1) an increase in the number of rare species, and/or (2) an increase in arthropod abundance. Our results largely supported our predictions: species richness of herbivores, detritivores, predators, and parasitoids increased monotonically with increasing levels of plant production, and the diversity of rare species also increased with plant production. However, rare species that accounted for this difference were predators, parasitoids, and detritivores, not herbivores. Herbivore species richness could be simply explained by the relationship between abundance and diversity. Using nonmetric multidimensional scaling (NMDS) and analysis of similarity (ANOSIM), we also found significant changes in arthropod species composition with increasing levels of production. Our findings have important implications in the intertidal salt marsh, where human activities have increased nitrogen runoff into the marsh, and demonstrate that such nitrogen inputs cascade to affect community structure, diversity, and abundance in higher trophic levels.

Key words: *allochthonous subsidies; ANOSIM; arthropod community structure; biodiversity; detritivore; herbivore; NMDS; nutrient runoff; parasitoid; predator; primary production; Spartina alterniflora.*

INTRODUCTION

Since the Industrial Revolution, human activities have doubled nitrogen pools, with profound consequences for terrestrial and aquatic ecosystems (Vitousek et al. 1997). Increases in nutrient availability often lead to increased biomass of primary producers (Gruner et al. 2008, Cardinale et al. 2009), which in turn has extended effects on animal communities (Kirchner 1977, Strauss 1987, Siemann 1998, Forkner and Hunter 2000, Haddad et al. 2000, Cebrian et al. 2009). Production and diversity may follow any number of relationships, including a dome-shaped (unimodal), negative, U-shaped, monotonically increasing, or no relationship depending on the trophic

level and/or taxonomic group examined (Groner and Novoplansky 2003). Theory and empirical data have demonstrated a dome-shaped relationship between production and diversity in plant communities (Bakelaar and Odum 1978, Rosenzweig and Abramsky 1993, Tilman and Pacala 1993, Whittaker and Heegaard 2003, Gillman and Wright 2006), which suggests that species interactions under high production constrain diversity (Leibold 1999). Animal diversity, however, often increases monotonically with production, without a corresponding decrease at high production levels as seen in plant communities (Waide et al. 1999, Mittelbach et al. 2001).

Several factors may contribute to an increase in animal consumer diversity (we define species richness as our measure of diversity) under high plant production, including: (1) the persistence of rare species, (2) an increasing diversity of feeding niches the habitat may support, (3) density-dependent responses of predator

Manuscript received 16 July 2009; revised 8 March 2010; accepted 12 March 2010; final version received 9 April 2010. Corresponding Editor: J. T. Cronin.

⁶ E-mail: gmw22@georgetown.edu

⁷ Deceased.

and parasitoid species, and (4) a reduction in herbivore competition via top-down control from a diverse predator/parasitoid species pool. First, increases in plant quality (percentage nitrogen) may allow rare nitrogen-sensitive species to persist (Mattson 1980, Prestidge and McNeill 1982, Huberty and Denno 2006a, b). Additionally, higher plant production may increase the population growth rate of animal consumers, and populations with higher abundances would be less prone to extinction due to disturbance (DeAngelis 1994). Second, an increase in plant production expands the diversity and abundance of feeding niches and thus may support additional consumer species (Hurd et al. 1971, Hurd and Wolf 1974, Moran 1980, Lawton 1983, Strauss 1987, Elkinton et al. 1996, Polis and Hurd 1996, Stiling and Rossi 1997, Polis et al. 1998, Siemann 1998, Forkner and Hunter 2000, Haddad et al. 2000, Ostfeld and Keesing 2000, Denno et al. 2002, Gratton and Denno 2003). However, because plant species richness and production often covary (Stevens et al. 2004, Suding et al. 2005, Hillebrand et al. 2007), and plant species richness affects animal diversity independently of changes in production (Murdoch 1972), it is difficult to determine which of these factors causes the arthropod community response when production is experimentally manipulated (Kirchner 1977, Siemann 1998, Haddad et al. 2000, 2001, Pearson et al. 2008). This is not to say that there are not important effects of nutrient loading on plant community composition and diversity that cascade to higher trophic levels (see Kirchner 1977, Tilman 1987, Tilman and Pacala 1993, Siemann 1998, Haddad et al. 2000, Pearson et al. 2008). However, the way in which food-web structure is altered through trophic dynamics that extend solely from enhanced plant production, and not from changes in plant community composition, has not yet been investigated for an entire terrestrial arthropod community. Notably, the pattern of increased animal diversity with increasing levels of production may be the result of rare specialist herbivores (and their respective specialist predators/parasites) responding to an increase in the abundance and quality of their preferred host plant species. Yet, alterations in plant production without a simultaneous change in plant diversity and/or composition could mean that new species would be added to the community from a relatively smaller species pool, which may have negligible effects on overall arthropod diversity. Without isolating the effects of plant production, independent of plant diversity, it is impossible to determine the singular importance of production for arthropod community structure. Third, by promoting increased herbivore density, enhanced plant production and quality often encourage a greater diversity of predators and parasitoids via density-dependent responses (Abrams 1995, Siemann 1998). Last, an increase in predator/parasitoid diversity could feed back to affect herbivore diversity if: (1) the dominant herbivores were the most susceptible to predation/parasitism (Leibold 1996) and/or (2) pred-

tors/parasitoids shift their feeding preferences in accordance with prey abundance (Murdoch 1969).

Here we study the impacts of nutrient inputs on arthropod community composition and diversity in a salt marsh that is dominated by a single plant species, the cordgrass *Spartina alterniflora* (hereafter *Spartina*). By working in natural plant monocultures (*Spartina*-dominated wetlands) the cascading effects of nutrient subsidies on consumers will be driven entirely by changes in primary production and plant nitrogen, not plant diversity (see Denno et al. 2002). The use of a natural monoculture will thereby preclude two explanations for an increase in animal species diversity due to increased primary production: an increase in plant species diversity or a change in plant community composition. If animal species richness increases linearly with plant production in this natural monoculture, there are a limited number of hypotheses that would explain such an increase. Specifically, an increase in plant production could lead to an increase in animal species richness due to: (1) the addition of rare species, (2) an increase in the density of arthropods the habitat is able to support, or (3) an increase in both rare species and arthropod density. While these hypotheses are not the only explanation for the relationship between plant production and animal consumer diversity in a natural monoculture, we did not manipulate predator/parasitoid diversity or abundance, and were therefore not able to directly test top-down effects on herbivore diversity.

The study presented here is one of a few detailed assessments of the response of the entire arthropod community to plant production, not only in the salt marsh system, but also in the production/diversity literature (but see Gruner and Taylor 2006). Most studies that have examined the relationship between production and diversity have been limited to particular taxonomic or functional groups (Lightfoot and Whitford 1987, Moon and Stiling 2002, 2003, Gratton and Denno 2003, Kaspari et al. 2003, Krauss et al. 2007), which can make the application of theoretical predictions difficult as most theory encompasses species richness at the level of entire trophic levels or guilds, not just specific taxa (Tilman 1982, Leibold 1996). Our study examines the response of 100 arthropod species, spanning multiple functional and trophic groups, to plant production in an attempt to reconcile theoretical predictions with empirical data.

MATERIALS AND METHODS

Study site and organisms

We conducted experimental manipulations at an expansive salt marsh near Tuckerton, New Jersey, USA (39°30.8' N, 74°19.0' W) that is dominated by natural monocultures of *Spartina alterniflora* (Denno et al. 2002). Unlike many salt marshes along the Atlantic Coast, the Tuckerton site is not bordered by extensive agricultural fields, golf courses, or urban development, thereby making this system ideal for testing the effects of

nutrient inputs on arthropod communities in a marsh that is not already heavily affected by anthropogenic nutrient-loading. Additionally, the diverse arthropod fauna associated with *Spartina* allows us to examine the effects of nutrient inputs on multiple trophic levels and feeding groups (Appendix A). Furthermore, the arthropod community on *Spartina* has been characterized and relationships among the dominant species have been described in previous studies (Appendix A).

Nutrient manipulations

We manipulated nutrient levels using a one-way design with three levels of nitrogen addition (none, low addition, high addition) in order to examine the effects of increasing levels of plant percentage nitrogen and production on arthropod community structure and diversity. Our fertilization levels captured the highest possible fertilization levels found on the marsh; any further increase in fertilization leads to *Spartina* dieback (G. M. Wimp, unpublished data). We established 42 2×2 m plots in the high marsh, and plots were haphazardly chosen to represent one of the three different nitrogen treatments. We added nitrogen (ammonium nitrate) and phosphate (superphosphate to aid in nitrogen uptake) five times during the course of the *Spartina* growing season (24 May, 11 June, 24 June, 5 July, and 30 July 2002) in the following manner: control plots received no nutrient addition, low addition plots received 8 g/m² ammonium nitrate and 2.75 g/m² superphosphate, and high addition plots received 45 g/m² ammonium nitrate and 15 g/m² superphosphate for each date. In this study, we focus on N rather than P inputs because *Spartina* marshes are N-limited (Mendelssohn 1979a, b) and N-limitation has been shown to have a greater impact than P-limitation for *Spartina* consumers (Huberty and Denno 2006b).

Arthropod and plant samples

For each plot, we assessed arthropod density and diversity four times during the growing season (16 June, 27 June, 12 July, and 12 August 2002); we used a D-vac suction sampler (Rincon-Vitova Insectaries, Ventura, California, USA) with a large suction head (0.093 m²), and we sampled each plot by placing the head in two locations within the plot for two five-second periods. We stored all of the arthropods that we collected from the D-vac samples in ethanol and later sorted, counted, and identified all individuals to either genus or species with the assistance of taxonomic experts (see *Acknowledgments*).

To measure treatment effects on the nitrogen and carbon content of *Spartina*, we collected plant snips (15–20 *Spartina* culms per plot) at the time of arthropod sampling, dried them in a drying oven at 60°C for three days, ground them in a Wiley mill, and then sent our plant samples to the Cornell Stable Isotope Laboratory for analyses (information available online).⁸ We mea-

sured plant biomass and height near the end of the growing season (15 August) in 0.047-m² quadrats (Denno et al. 2002) by sorting the quadrat samples into live and dead plant material and measuring the height of living culms. For the live plant material, we washed it with deionized water, dried it in a drying oven at 60°C for three days, and then weighed it.

Statistical analyses

Due to the fact that our plant variables were likely correlated, we assessed treatment effects on plant nitrogen, C:N ratio, plant height, and biomass with a MANOVA. We square-root transformed arthropod species richness and abundance data to meet normality and equality of variance assumptions, then analyzed these data using a repeated-measures ANOVA with fertilization level as the between-subjects factor and time as the within-subjects factor. Because response variables from consecutive time periods may be highly correlated relative to response variables from nonconsecutive time periods, we specifically assigned the variance/covariance structure in our repeated-measures analysis to account for correlations among response variables that were closer together in time. We used separate one-way ANOVAs with a sequential Bonferroni for multiple comparisons in order to test for differences among treatments for each time period.

After we examined the effects of fertilization treatment on arthropod richness, we investigated the factors that may account for this relationship. We explored the relationship between arthropod diversity and plant production for the different trophic groups (i.e., herbivores, detritivores, predators, parasitoids, and algivores). If increasing plant production (biomass) results in a greater diversity and abundance of feeding niches (Moran 1980, Lawton 1983, Siemann 1998, Haddad et al. 2000), we should find an increase in species richness across trophic groups. Even though we have three treatment levels (control, low addition, and high addition), we had enough variation in production such that we were able to examine the relationship between plant production and arthropod diversity using linear regression. To determine whether the relationship between plant production and arthropod diversity was monotonically increasing or dome-shaped, we included linear and quadratic terms in our regression model. We then examined the improvement in fit using a quadratic term with Akaike's Information Criterion (AIC). We performed regression analyses with a sequential Bonferroni correction to account for previous comparisons of species richness and abundance. To test whether an increase in species richness for each trophic group was driven by an increase in trophic abundance, we performed individual-based rarefaction (Gotelli and Colwell 2001). Rarefaction curves were generated by repeatedly resampling the average number of species represented in a sample from a pool of 14 samples for each treatment type (control, low addition, and high

⁸ <http://www.cobsil.com/index.php>

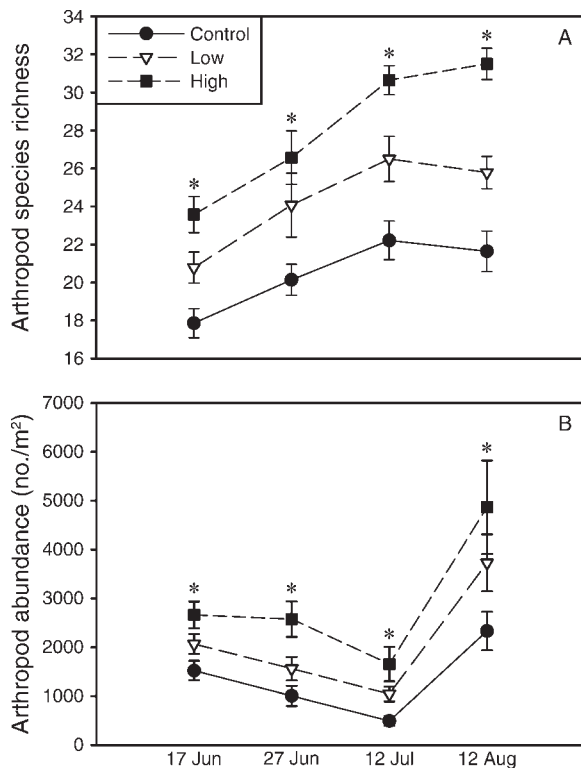


FIG. 1. Effects of three levels of nitrogen addition (control, low, and high) on (A) species richness and (B) abundance of arthropods associated with *Spartina alterniflora* in a salt marsh near Tuckerton, New Jersey, USA (all values are means \pm SE). Richness is measured as the actual number of species. An asterisk indicates significant differences ($P < 0.05$) among treatments within a time period.

addition). This resampling procedure allowed us to generate the expected number of species recorded (S_{obs} or Mao Tau) with an increasing number of individuals on a per sample basis.

In addition to impacts on species richness, changes in production may also impact species composition. We therefore examined arthropod species composition across the different nitrogen manipulation treatments using NMDS (nonmetric multidimensional scaling), which is a robust ordination technique for community data that compares differences in species composition among plots (Minchin 1987). We used the overall abundance of each species across all time periods for our analysis, so time was not included as a factor. By summing across time periods, we were able to examine patterns of species assortment among our treatments that were robust to seasonal changes in species abundance through time. We used the ordination program DECODA (Database for Ecological Community Data; Minchin 2001) to create a dissimilarity matrix among treatments using the Bray-Curtis dissimilarity coefficient (Faith et al. 1987) and then tested for differences in community composition among treatments using ANOSIM (analysis of similarity; Warwick

et al. 1990). We determined the percentage contribution that each arthropod species made to the overall dissimilarity among nitrogen treatments using similarity percentages (SIMPER; Clarke and Warwick 2001). We determined the maximum correlation between host plant biomass per plot and the configuration of points (i.e., the arthropod community found within the same plots) using vector analysis (Minchin 1987, Faith and Norris 1989). If we found differences in species composition as production increased, this could be explained by the addition of rare species (Abrams 1995). We therefore examined the number of species in each plot that accounted for $<1\%$ of overall arthropod abundance and compared differences in the number of rare species across fertilization treatments using a one-way ANOVA for each trophic group (herbivores, predators, parasitoids, and detritivores).

RESULTS

Effects of plant production on arthropod abundance, diversity, and composition

We found a significant effect of fertilization level on live *Spartina* biomass/m², plant percentage nitrogen, C:N ratio, and plant height (Wilks' $\lambda = 0.389$, $F_{6,74} = 50.21$, $P < 0.001$; Appendix B). Biomass increased in low and high addition treatments, by 33% and 52%, respectively, relative to controls. Importantly, fertilization did not change plant species composition and *Spartina* remained a monoculture even with increased available nitrogen.

We found a significant increase in arthropod species richness in response to both nitrogen addition ($F_{2,39} = 23.878$, $P < 0.001$) and sampling date ($F_{3,117} = 31.039$, $P < 0.001$), but no interaction between nitrogen addition and sampling date ($F_{6,117} = 0.986$, $P = 0.438$; Fig. 1). Species richness in low and high addition plots increased, by 13% and 23%, respectively, relative to controls. Similarly, we found a significant increase in arthropod abundance with nitrogen addition ($F_{2,39} = 8.487$, $P = 0.001$; Fig. 1) and sampling date ($F_{3,117} = 49.873$, $P < 0.001$), but no interaction between nitrogen addition and sampling date ($F_{6,117} = 0.517$, $P = 0.718$). Arthropod abundance increased in low and high addition plots, by 38% and 54%, respectively, relative to controls.

We found a linear, positive relationship between plant biomass and species richness, for four major arthropod trophic groups: herbivores ($R^2 = 0.282$, $F_{1,40} = 15.72$, $P < 0.001$), detritivores ($R^2 = 0.445$, $F_{1,40} = 33.34$, $P < 0.001$), predators ($R^2 = 0.385$, $F_{1,40} = 25.07$, $P < 0.001$), and parasitoids ($R^2 = 0.225$, $F_{1,40} = 11.64$, $P < 0.001$; Fig. 2). Plant biomass, however, did not affect the species richness of algivores ($R^2 = 0.046$, $F_{1,40} = 1.92$, $P = 0.174$; Fig. 2). Moreover, we did not find an improvement in fit using regressions that included a quadratic term to describe the relationship between biomass and species richness for each of the trophic groups (Appendix C). Using individual-based rarefaction curves, we

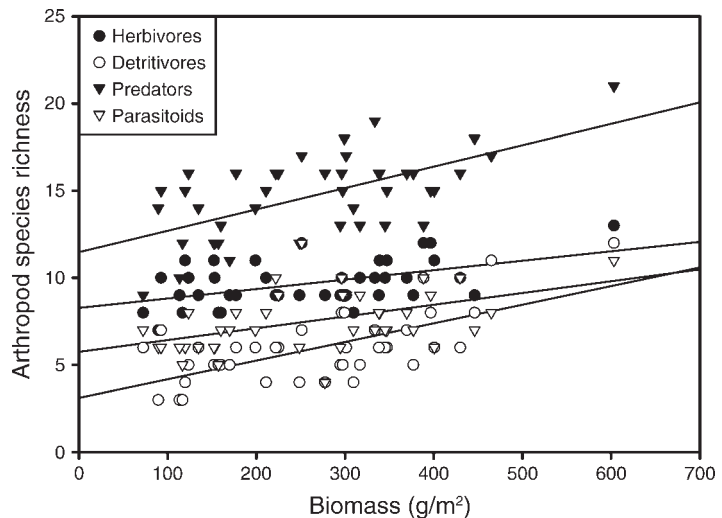


FIG. 2. Relationship between primary production (biomass) and species richness for herbivores, detritivores, predators, and parasitoids associated with *Spartina alterniflora*. Richness is measured as the actual number of species. Biomass includes only *Spartina*; the aboveground dry mass was measured for the entire plant.

found that greater herbivore species richness in fertilization treatments was driven by an increase in arthropod abundance, but this relationship disappeared when we standardized species richness for the number of individuals found in a plot (Appendix D). This result indicated that greater herbivore diversity in fertilization plots was due to an increase in plant resources. Notably, species richness for detritivores, predators, and parasitoids remained elevated in fertilization plots relative to controls even when we standardized for the number of individuals found in a plot (Appendix D).

We found that nitrogen addition significantly altered arthropod community composition for all three nitrogen addition treatments (ANOSIM $R = 0.4156$, $P < 0.001$; Fig. 3). We used vector analysis to examine the relationship between plant biomass (production) and the NMDS configuration and found a significant correlation (vector maximum $R = 0.7963$, $P < 0.001$), which suggests that arthropod community composition responds to a gradient of plant biomass. Additionally, using SIMPER, we found that species from a broad array of trophic groups contributed to compositional differences among treatment groups. The percentage contribution to compositional differences among treatments was: 3–33% for herbivores (*Prokelisia marginata*, *P. dolus*, and *Delphacodes penedetector*), 1–3% for algivores (*Orchestia grillus* and *Ameronothrus marinus*), 2–3% for saprophages (*Incertella* sp.), 3–12% for web-building spiders (*Gramminota trivittata*, *Eperigone* sp.), 1–3% for specialist predators (e.g., *Tytthus vagus*), 1% for generalist predators (e.g., *Pentacora* sp.), 1% for intraguild predators (*Pardosa littoralis*), and 1% for third- (*Leptopilina* sp.) and fourth- (e.g., *Baeus* sp.) trophic-level parasitoids (Appendix E). Furthermore, each of the species that contributed to compositional differences among treatment groups appeared to be positively affected by nitrogen addition (Appendix F). Finally, in low- and high-addition plots, we found an

11–39% increase in the number of rare predators, a 60–67% increase in the number of rare parasitoids, and a 60–71% increase in the number of rare detritivores relative to controls, but no change in the number of rare herbivores (Appendix G).

DISCUSSION

We predicted and found that nitrogen addition significantly increased plant biomass and percentage nitrogen, which in turn enhanced both arthropod species richness and abundance. Higher plant production (biomass) was correlated with an increase in herbivore, predator, parasitoid, and detritivore diversity. Previous studies have found that fertilization leads to changes in plant species diversity and composition, but in this experiment and a four-year nutrient press experiment (S. M. Murphy and G. M. Wimp, *unpublished data*), *Spartina* remains a monoculture despite continued fertilization. Our results demonstrate that in a natural monoculture, where enhanced production does not alter plant diversity or composition, greater production leads to increases in animal diversity.

Fertilization not only affected arthropod species richness and abundance, but also altered arthropod species composition (Fig. 3). Notably, changes in arthropod composition occurred in both the low- and high-addition treatments relative to controls, which indicates that even relatively low inputs of nutrients to salt marshes may restructure the associated arthropod community. Although changes in composition were driven largely by herbivores, species of detritivores, algivores, parasitoids, and web-building spiders also accounted for changes in arthropod community composition among fertilization treatments (Appendix E).

We examined trophic-level responses to fertilization and found an increase in species richness with greater plant production. If greater plant production led to an increase in arthropod consumer diversity, we predicted

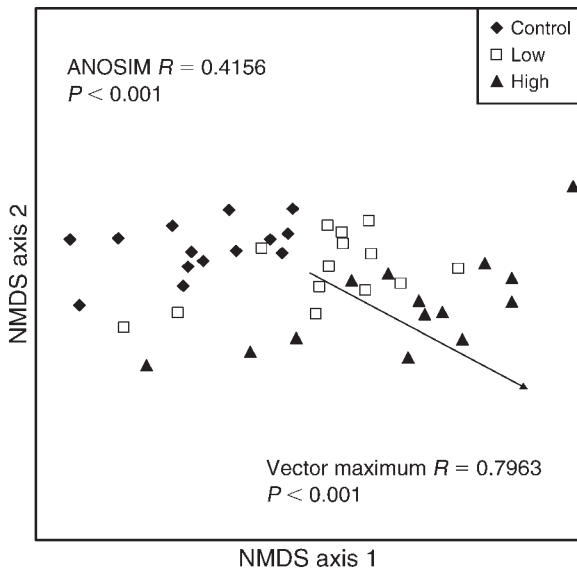


FIG. 3. Composition of the arthropod community associated with *Spartina alterniflora* subjected to three levels of nitrogen addition (control, low, and high). The composition of the arthropod community differed significantly among the three nitrogen treatments. Compositional dissimilarity was based on 100 different arthropod species (Appendix A). Shown is the two-dimensional representation of the arthropod community found in 42 nitrogen treatment plots. Vector analysis (arrow) indicates that differences in arthropod community composition were correlated with *Spartina* biomass. Dissimilarities were computed between all plots, and the NMS (nonmetric multidimensional scaling) ordination is a representation of these dissimilarities in Euclidean two-dimensional space. ANOSIM stands for analysis of similarity.

that such a response was likely driven by two mechanisms that might act singly or in concert: (1) an increase in the abundance of rare species and/or (2) an increase in the density of arthropods that the habitat is able to support. For herbivores, the increase in species richness could not be explained by an increase in the number of rare herbivore species. Instead, the increase in herbivore species richness with plant production was driven by herbivore abundance (Appendix D). *Spartina* has a relatively high silica content and grows under high levels of salt stress, both of which limit the herbivore community to a group of specialized phloem-feeders (Denno and Roderick 1990, Bertness 1991, Norris and Hackney 1999), and may constrain the number of herbivorous species that can feed on *Spartina*. Although the high silica content of *Spartina* likely constrains herbivore diversity, similar bottom-up constraints, such as plant trichomes and secondary chemicals, affect herbivores across a wide array of systems (Lambert et al. 1995, Becerra 1997, Mutikainen et al. 2000).

Primary consumers, such as herbivores, were not the only feeding group affected by plant production; we also found an increase in both predator and parasitoid

species richness with an increase in plant production. Indeed, predator diversity exhibited one of the strongest responses to increased plant production (Fig. 2). However, predator species richness was not driven solely by the well-established relationship between abundance and species richness (Bunge and Fitzpatrick 1993, Srivastava and Lawton 1998); rarefied species accumulation curves showed that predator species richness was greatest in high fertilization plots, even after predator abundance was taken into account (Appendix D). Previous studies in the same system have found that fertilization leads to a decrease in emigration and an increase in reproduction for the dominant predator species (Denno et al. 2002). Additionally, by increasing prey diversity and abundance, the increase in plant production may have expanded the diversity of predator and parasitoid feeding niches in much the same way that plant production increases niche diversity for herbivores (Kneitel and Miller 2002). Specifically, generalist predators often thrive in low-production habitats and because generalists overlap in resource use, the community supports fewer overall species (Srivastava and Lawton 1998). However, when resources are more abundant in high-production habitats, both generalist and specialist species may coexist, which leads to greater overall species richness (Srivastava and Lawton 1998). In support of previous findings, we found an increase in the number of rare predator and parasitoid species with higher levels of plant production (Appendix G). Specifically, although generalist predators were numerically dominant in low production habitats (*Eperigone* sp., *G. trivittata*), specialist predators (*T. vagus*) and parasitoids (*Baeus* sp., *Leptopilina* sp.) became increasingly more abundant in high-production habitats (Appendix F). Notably, whether increased species richness in relation to production was caused by greater arthropod abundance or rare species (e.g., Yee and Juliano 2007, Yee et al. 2007) depended on the trophic level examined. Greater herbivore species richness with higher production was due to an increase in herbivore abundance, but greater species richness for detritivores, predators, and parasitoids was due to an increase in the number of rare species.

Our study demonstrates that plant production, without an associated change in plant composition or diversity, increases arthropod species richness and abundance, and alters community composition. By examining the entire arthropod community, we were able to determine that each trophic group responds to greater production, but the factors that explain such an increase vary according to trophic group. These results are not only important to our understanding of the relationship between production and consumer diversity, but also because numerous terrestrial systems are currently experiencing an increase in allocthonous nitrogen input from anthropogenic sources (Vitousek et al. 1997). For salt-marsh habitats in particular, marshes that have not been directly destroyed by human

development have been drastically altered by nitrogen enrichment (Bertness et al. 2002, Valiela et al. 2004). Previous studies have found that anthropogenic increases in nitrogen runoff to salt marshes can alter the structure of the vegetation community (Bertness et al. 2002, 2004); our results demonstrate that nutrient addition to these systems affects higher trophic level consumers as well. Even though arthropod species richness was greater in high production plots, by altering species composition, nitrogen enrichment may feed back to affect ecosystem processes through arthropod consumer effects on standing crop biomass and nutrient cycling. Future experiments should therefore aim to test the separate and combined effects of plant production and plant diversity on consumers using factorial experiments, as well as the long-term effects of nutrient loading on animal communities.

ACKNOWLEDGMENTS

We thank the following systematists for their generous help with our identifications: V. Behan-Pelletier, M. Buffington, J. Davidson, M. Gates, E. Grissell, and M. Yoder. We thank members of the D.C. PIG, a plant-insect discussion group composed of members from D.C.-area universities and institutions, for comments that improved this manuscript, especially M. Douglas, D. Gruner, A. Howard, D. Lewis, J. Lill, E. Lind, H. Mallory, D. Uma, and M. Weiss. This research was supported by National Science Foundation Grants DEB-9903601 and DEB-0313903 to R. F. Denno.

LITERATURE CITED

- Abrams, P. A. 1995. Monotonic or unimodal diversity-productivity gradients: what does competition theory predict? *Ecology* 76:2019–2027.
- Bakelaar, R. G., and E. P. Odum. 1978. Community and population level responses to fertilization in an old-field ecosystem. *Ecology* 59:660–665.
- Becerra, J. X. 1997. Insects on plants: macroevolutionary chemical trends in host use. *Science* 276:253–256.
- Bertness, M. D. 1991. Zonation of *Spartina patens* and *Spartina alterniflora* in a New England salt marsh. *Ecology* 72:138–148.
- Bertness, M. D., P. J. Ewanchuck, and B. R. Silliman. 2002. Anthropogenic modification of New England salt marsh landscapes. *Proceedings of the National Academy of Sciences USA* 99:1395–1398.
- Bertness, M. D., B. R. Silliman, and R. Jeffries. 2004. Salt marshes under siege. *American Scientist* 92:54–61.
- Bunge, J., and M. Fitzpatrick. 1993. Estimating the number of species: a review. *Journal of the American Statistical Association* 88:364–373.
- Cardinale, B. J., D. M. Bennett, C. E. Nelson, and K. Gross. 2009. Does productivity drive diversity or vice versa? A test of the multivariate productivity-diversity hypothesis in streams. *Ecology* 90:1227–1241.
- Cebrian, J., J. B. Shurin, E. T. Borer, B. J. Cardinale, J. T. Ngai, M. D. Smith, and W. F. Fagan. 2009. Producer nutritional quality controls ecosystem trophic structure. *PLoS ONE* 4:1–5.
- Clarke, K. R., and R. M. Warwick. 2001. Change in marine communities: an approach to statistical analysis and interpretation. Second edition. Plymouth Marine Laboratory, Plymouth, UK.
- DeAngelis, D. L. 1994. Relationships between the energetics of species and large-scale species richness. Pages 263–272 in C. G. Jones and J. H. Lawton, editors. Linking species and ecosystems. Chapman and Hall, New York, New York, USA.
- Denno, R. F., C. Gratton, M. A. Peterson, G. A. Langellotto, D. L. Finke, and A. F. Huberty. 2002. Bottom-up forces mediate natural-enemy impact in a phytophagous insect community. *Ecology* 83:1443–1458.
- Denno, R. F., and G. K. Roderick. 1990. Population biology of planthoppers. *Annual Review of Entomology* 35:489–520.
- Elkinton, J. S., W. M. Healy, J. P. Buonaccorsi, G. H. Boettner, A. M. Hazzard, H. R. Smith, and A. M. Liebhold. 1996. Interactions among gypsy moths, white-footed mice, and acorns. *Ecology* 77:2332–2342.
- Faith, D. P., P. R. Minchin, and L. Belbin. 1987. Compositional dissimilarity as a robust measure of ecological distance. *Vegetatio* 69:57–68.
- Faith, D. P., and R. H. Norris. 1989. Correlation of environmental variables with patterns of distribution and abundance of common and rare freshwater macroinvertebrates. *Biological Conservation* 50:77–98.
- Forkner, R. E., and M. D. Hunter. 2000. What goes up must come down? Nutrient addition and predation pressure on oak herbivores. *Ecology* 81:1588–1600.
- Gillman, L. N., and S. D. Wright. 2006. The influence of productivity on the species richness of plants: a critical assessment. *Ecology* 87:1234–1243.
- Gotelli, N. J., and R. K. Colwell. 2001. Quantifying biodiversity: procedures and pitfalls in the measurement and comparison of species richness. *Ecology Letters* 4:379–391.
- Gratton, C., and R. F. Denno. 2003. Inter-year carryover effects of a nutrient pulse on *Spartina* plants, herbivores, and natural enemies. *Ecology* 84:2692–2707.
- Groner, E., and A. Novoplansky. 2003. Reconsidering productivity-diversity relationships: directness of productivity estimates matters. *Ecology Letters* 6:695–699.
- Gruner, D. S., J. E. Smith, E. W. Seabloom, S. A. Sandin, J. T. Ngai, H. Hillebrand, W. S. Harpole, J. J. Elser, E. E. Cleland, M. E. S. Bracken, E. T. Borer, and B. M. Bolker. 2008. A cross-system synthesis of consumer and nutrient resource control on producer biomass. *Ecology Letters* 11:740–755.
- Gruner, D. S., and A. D. Taylor. 2006. Richness and composition of arboreal arthropods affected by nutrients and predators: a press experiment. *Oecologia* 147:714–724.
- Haddad, N. M., J. Haarstad, and D. Tilman. 2000. The effects of long-term nitrogen loading on grassland insect communities. *Oecologia* 124:73–84.
- Haddad, N. M., D. Tilman, J. Harstad, M. E. Ritchie, and J. M. H. Knops. 2001. Contrasting effects of plant richness and composition on insect communities: a field experiment. *American Naturalist* 158:17–35.
- Hillebrand, H., D. S. Gruner, E. T. Borer, M. E. S. Bracken, E. E. Cleland, J. J. Elser, W. S. Harpole, J. T. Ngai, E. W. Seabloom, J. B. Shurin, and J. E. Smith. 2007. Consumer versus resource control of producer diversity depends on ecosystem type and producer community structure. *Proceedings of the National Academy of Sciences USA* 104:10904–10909.
- Huberty, A. H., and R. F. Denno. 2006a. Trade-off in investment between dispersal and ingestion capability in phytophagous insects and its ecological implications. *Oecologia* 148:226–234.
- Huberty, A. H., and R. F. Denno. 2006b. Consequences of nitrogen and phosphorus limitation for the performance of two phytophagous insects with divergent life-history strategies. *Oecologia* 149:444–455.
- Hurd, L. E., M. V. Mellinger, L. L. Wolf, and S. J. McNaughton. 1971. Stability and diversity at three trophic levels in terrestrial successional ecosystems. *Science* 173:1134–1136.
- Hurd, L. E., and L. L. Wolf. 1974. Stability in relation to nutrient enrichment in arthropod consumers of old-field

- successional ecosystems. *Ecological Monographs* 44:465–482.
- Kaspari, M., M. Yuan, and L. Alonso. 2003. Spatial grain and the causes of regional diversity gradients in ants. *American Naturalist* 161:459–477.
- Kirchner, T. 1977. The effects of resource enrichment on the diversity of plants and arthropods in a shortgrass prairie. *Ecology* 58:1334–1344.
- Kneitel, J. M., and T. E. Miller. 2002. Resource and top-predator regulation in the pitcher plant (*Sarracenia purpurea*) inquiline community. *Ecology* 83:680–688.
- Krauss, J., S. A. Härril, L. Bush, R. Husi, L. Bigler, S. A. Power, and C. B. Müller. 2007. Effects of fertilizer, fungal endophytes, and plant cultivar on the performance of insect herbivores and their natural enemies. *Functional Ecology* 21:107–116.
- Lambert, L., R. M. McPherson, and K. E. Espelie. 1995. Soybean host plant resistance mechanisms that alter abundance of whiteflies (Homoptera: Alydidae). *Environmental Entomology* 24:1381–1386.
- Lawton, J. H. 1983. Plant architecture and the diversity of phytophagous insects. *Annual Review of Entomology* 28:23–39.
- Leibold, M. A. 1996. A graphical model of keystone predation: effects of productivity on abundances, incidence and ecological diversity in communities. *American Naturalist* 147:784–812.
- Leibold, M. A. 1999. Biodiversity and nutrient enrichment in pond plankton communities. *Evolutionary Ecology Research* 1:73–95.
- Lightfoot, D. C., and W. G. Whitford. 1987. Variation in insect densities on desert creosotebush: is nitrogen a factor? *Ecology* 68:547–557.
- Mattson, W. J. 1980. Herbivory in relation to plant nitrogen content. *Annual Review of Ecology and Systematics* 11:119–161.
- Mendelssohn, I. A. 1979a. The influence of nitrogen level, form, and application method on the growth response of *Spartina alterniflora* in North Carolina. *Estuaries* 2:106–112.
- Mendelssohn, I. A. 1979b. Nitrogen metabolism in the height forms of *Spartina alterniflora* in North Carolina. *Ecology* 60:574–584.
- Minchin, P. R. 1987. Simulation of multidimensional community patterns: towards a comprehensive model. *Vegetatio* 71:145–156.
- Minchin, P. R. 2001. DECODA (Database for Ecological Community Data), version 3.0, Australian National University. Distributed by ANUTECH Party, Canberra, Australian Capital Territory, Australia.
- Mittelbach, G. G., C. F. Steiner, S. M. Scheiner, K. L. Gross, H. L. Reynolds, R. B. Waide, M. R. Willig, S. I. Dodson, and L. Gough. 2001. What is the observed relationship between species richness and productivity? *Ecology* 82:2381–2396.
- Moon, D. C., and P. Stiling. 2002. The effects of salinity and nutrients on a tritrophic salt marsh system. *Ecology* 83:2465–2476.
- Moon, D. C., and P. Stiling. 2003. The influence of legacy effects and recovery from perturbations in a tritrophic salt marsh complex. *Ecological Entomology* 28:457–466.
- Moran, V. C. 1980. Interaction between phytophagous insects and their *Opuntia* hosts. *Ecological Entomology* 5:153–164.
- Murdoch, W. W. 1969. Switching in general predators: experiments on predator specificity and stability of prey populations. *Ecological Monographs* 39:335–354.
- Murdoch, W. W. 1972. Diversity and pattern in plants and insects. *Ecology* 53:819–829.
- Mutikainen, P., M. Walls, J. Ovaska, M. Keinänen, R. Julkanen-Tiitto, and E. Vapaavouri. 2000. Herbivore resistance in *Betula pendula*: effect of fertilization, defoliation, and plant genotype. *Ecology* 81:49–65.
- Norris, A. R., and C. T. Hackney. 1999. Silica content of a mesohaline tidal marsh in North Carolina. *Estuarine, Coastal and Shelf Science* 49:597–605.
- Ostfeld, R. S., and F. Keesing. 2000. Pulsed resources and community dynamics of consumers in terrestrial ecosystems. *Trends in Ecology and Evolution* 15:232–237.
- Pearson, C. V., T. J. Massad, and L. A. Dyer. 2008. Diversity cascades in alfalfa fields: from plant quality to agroecosystem diversity. *Environmental Entomology* 37:947–955.
- Polis, G. A., and S. D. Hurd. 1996. Allochthonous input across habitats, subsidized consumers, and apparent trophic cascades: examples from the ocean-land interface. Pages 275–285 in G. A. Polis and K. O. Winemiller, editors. *Food webs: integration of patterns and dynamics*. Chapman and Hall, New York, New York, USA.
- Polis, G. A., S. D. Hurd, C. T. Jackson, and F. Sanchez-Piñero. 1998. Multifactor population limitation: variable spatial and temporal control of spiders on Gulf of California Islands. *Ecology* 79:490–502.
- Prestidge, R. A., and S. McNeill. 1982. The role of nitrogen in the ecology of grassland Auchenorrhyncha (Homoptera). *Symposium of the British Ecological Society* 22:257–281.
- Rosenzweig, M. L., and Z. N. Abramsky. 1993. How are diversity and productivity related? Pages 52–65 in R. E. Ricklefs and D. Schluter, editors. *Species diversity in ecological communities: historical and geographical perspectives*. University of Chicago Press, Chicago, Illinois, USA.
- Siemann, E. 1998. Experimental tests of effects of plant productivity and diversity on grassland arthropod diversity. *Ecology* 79:2057–2070.
- Srivastava, D. S., and J. H. Lawton. 1998. Why more productive sites have more species: an experimental test of theory using tree hole communities. *American Naturalist* 152:510–529.
- Stevens, C. J., N. B. Dise, J. O. Mountford, and D. J. Gowing. 2004. Impact of nitrogen deposition on the species richness of grasslands. *Science* 303:1876–1879.
- Stiling, P., and A. M. Rossi. 1997. Experimental manipulations of top-down and bottom-up factors in a tri-trophic system. *Ecology* 78:1602–1606.
- Strauss, S. Y. 1987. Direct and indirect effects of host-plant fertilization on an insect community. *Ecology* 68:1670–1678.
- Suding, K. N., S. L. Collins, L. Gough, C. Clark, E. E. Cleland, K. L. Gross, D. G. Milchunas, and S. Pennings. 2005. Functional- and abundance-based mechanisms explain diversity loss due to N fertilization. *Proceedings of the National Academy of Sciences USA* 102:4387–4392.
- Tilman, D. 1982. Resource competition and community structure. Princeton University Press, Princeton, New Jersey, USA.
- Tilman, D. J. 1987. Secondary succession and the pattern of plant dominance along experimental nitrogen gradients. *Ecological Monographs* 57:189–214.
- Tilman, D., and S. Pacala. 1993. The maintenance of species richness in plant communities. Pages 13–25 in R. E. Ricklefs and D. Schluter, editors. *Species diversity in ecological communities: historical and geographical perspectives*. University of Chicago Press, Chicago, Illinois, USA.
- Valiela, I., D. Rutecki, and S. Fox. 2004. Salt marshes: biological controls of food webs in a diminishing environment. *Journal of Experimental Marine Biology and Ecology* 300:131–159.
- Vitousek, P. M., J. D. Aber, R. W. Howarth, G. E. Likens, P. A. Matson, D. W. Schindler, W. H. Schlesinger, and D. G. Tilman. 1997. Human alteration of the global nitrogen cycle: sources and consequences. *Ecological Applications* 7:737–750.
- Waide, R. B., M. R. Willig, C. F. Steiner, G. Mittelbach, L. Gough, S. I. Dodson, G. P. Juday, and R. Parmenter. 1999. The relationship between productivity and species richness. *Annual Review of Ecology and Systematics* 30:257–300.

- Warwick, R. M., K. R. Clarke, and Suharsono. 1990. A statistical analysis of coral community responses to the 1982–1983 El Nino in the Thousand Islands, Indonesia. *Coral Reefs* 8:171–179.
- Whittaker, R. J., and E. Heegaard. 2003. What is the observed relationship between species richness and productivity? *Comment. Ecology* 84:3384–3390.
- Yee, D. A., and S. A. Juliano. 2007. Abundance matters: a field experiment testing the more individuals hypothesis for richness–productivity relationships. *Oecologia* 153:153–162.
- Yee, D. A., S. H. Yee, J. M. Kneitel, and S. A. Juliano. 2007. Richness–productivity relationships between trophic levels in a detritus-based system: significance of abundance and trophic linkage. *Oecologia* 154:377–385.

APPENDIX A

List of arthropod species recorded during the nitrogen manipulation experiment (*Ecological Archives* E091-233-A1).

APPENDIX B

Effects of nitrogen addition on plant parameters (*Ecological Archives* E091-233-A2).

APPENDIX C

Effects of *Spartina alterniflora* biomass on trophic group richness (*Ecological Archives* E091-233-A3).

APPENDIX D

Sample-based rarefaction curves estimating species richness according to the number of individuals found within a plot (*Ecological Archives* E091-233-A4).

APPENDIX E

Percentage contribution of different arthropod species to compositional dissimilarities among nitrogen treatments (*Ecological Archives* E091-233-A5).

APPENDIX F

Abundance of species that made the greatest contribution to dissimilarity among nitrogen treatments (*Ecological Archives* E091-233-A6).

APPENDIX G

Effects of fertilization on rare species (*Ecological Archives* E091-233-A7).