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

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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 (Gruner and Novopolskky 2003). Theory and empirical data have demonstrated a dome-shaped relationship between production and diversity in plant communities (Bakerlaar 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.
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) predators/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 x 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 Acknowledgements).

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 measured 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 Akaiake’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)
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’ λ = 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 ($F_{3,39} = 8.487$, $P = 0.001$; 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
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 penedetecta), 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 E). 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...
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 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).

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 allochthonous 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.

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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).