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Latitudinal variation in top-down and bottom-up control of a salt marsh food web

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Abstract. The shrub *Iva frutescens*, which occupies the terrestrial border of U.S. Atlantic Coast salt marshes, supports a food web that varies strongly across latitude. We tested whether latitudinal variation in plant quality (higher at high latitudes), consumption by omnivores (a crab, present only at low latitudes), consumption by mesopredators (ladybugs, present at all latitudes), or the life history stage of an herbivorous beetle could explain continental-scale field patterns of herbivore density. In a mesocosm experiment, crabs exerted strong top-down control on herbivorous beetles, ladybugs exerted strong top-down control on aphids, and both predators benefited plants through trophic cascades. Latitude of plant origin had no effect on consumers. Herbivorous beetle density was greater if mesocosms were stocked with beetle adults rather than larvae, and aphid densities were reduced in the “adult beetle” treatment. Treatment combinations representing high and low latitudes produced patterns of herbivore density similar to those in the field. We conclude that latitudinal variation in plant quality is less important than latitudinal variation in top consumers and competition in mediating food web structure. Climate may also play a strong role in structuring high-latitude salt marshes by limiting the number of herbivore generations per growing season and causing high overwintering mortality.

Key words: aphids; food web; *Iva frutescens*; latitude; multi-trophic interaction; omnivory; salt marsh; top-down, bottom-up control; trophic cascade; Uroleucon ambrosiae.

INTRODUCTION

Interest in latitudinal patterns dates from the beginning of ecology as a discipline. Early naturalists marveled at the diversity of the tropics and speculated that the nature of ecological interactions must change across latitude (Dobzhansky 1950). Experimental studies examining latitudinal variation in interactions have been few, but suggest that a variety of interactions, including plant–herbivore interactions (Coley and Aide 1991, Pennings et al. 2001), predation (Stachowicz and Hay 2000), and competition (James et al. 1997) are more intense at lower latitudes. There are two related problems with this conclusion. First, because simple trophic models do not allow the strengths of herbivory, predation, and competition to simultaneously increase at all trophic levels (Hairston et al. 1960), rigorously identifying the causal factors underlying latitudinal patterns requires a more sophisticated food web approach than has yet been applied in this context. Second, because competition, herbivory, and predation all may

interact, a proper understanding of latitudinal variation in any single process (e.g., herbivory) can only be obtained by understanding the broader trophic context. We are unaware of any studies that have attempted to experimentally investigate how the interactions among multiple trophic processes vary across latitude.

Salt marshes on the Atlantic Coast of the United States provide ideal systems for taking this next step. They support similar and simple communities across a range of latitude and climate from Florida through Maine (Pennings et al. 2001). We have a good understanding of how the importance of top-down and bottom-up factors changes at small spatial scales to affect ecological processes at a number of sites (Hacker and Bertness 1995, Denno et al. 2005). We also have an emerging understanding of latitudinal variation in herbivore population dynamics (Denno et al. 1996) and plant–herbivore interactions (Siska et al. 2002, Pennings et al. 2009) at large geographic scales. Here we report on experimental work examining latitudinal variation in top-down and bottom-up processes that control populations of herbivores associated with the high-marsh shrub *Iva frutescens*.

Within the *Iva* food web, plant quality is higher at high latitudes (Pennings et al. 2001), while top omnivores are present only at low latitudes (Pennings et al. 2009). Mesopredators (ladybugs and spiders) are present at all latitudes. We hypothesize that latitudinal variation

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in bottom-up (plant quality) and top-down (top omnivores) factors leads to different controls on herbivore density and food web structure across latitude. We further hypothesize that the effects of omnivores and mesopredators vary (1) with latitudinal variability in the quality of plants, and (2) among herbivore species due to differences in vulnerability to predation. We investigated latitudinal variation in top-down and bottom-up control using a combination of a mesocosm experiment and predation trials. This project, to the best of our knowledge, is the first to examine spatial variation in top-down and bottom-up control at a continental geographic scale.

METHODS

A full description of the *Iva frutescens* food web and how it varies across latitude is provided in Appendix A. To understand latitudinal variation in top-down and bottom-up controls on the abundance of herbivores (the aphid *Uroleucon ambrosiae* and the beetle *Ophraella notulata*), we conducted a full-factorial mesocosm experiment in an open-air greenhouse on Sapelo Island, Georgia, USA, varying plant origin (high- vs. low-latitude), herbivore stage (larval vs. adult *Ophraella notulata* beetles), and mesopredator (the ladybug *Hippodamia convergens*) and omnivore (the crab *Armases cinereum*) presence. All species are referred to generically hereafter. We collected *Iva* from five high-latitude sites and five low-latitude sites (Appendix B) and established mesocosms with two levels each of mesopredator (0 or 1) and omnivore density (0 or 1). Each mesocosm was stocked with 30 *Uroleucon* aphids and one of two ontogenetic stages of *Ophraella* beetles (3 adult or 5 larval *Ophraella*), with five replicates of each treatment combination. Initial arthropod densities were based on field data (Buck et al. 2003).

To initiate the mesocosm experiment, we measured the number of green and damaged leaves for each plant on 23 May 2008. We used a penetrometer (Chatillon scale model 516, Ametek, Largo, Florida, USA) to determine the initial toughness of leaves of extra plants, and three leaves each from these plants were lyophilized and analyzed for total nitrogen content at the University of Georgia Chemical Analysis Laboratory, Athens, Georgia, USA. Each plant was fitted with a mesh cage; on 26 May 2008 all herbivores were added to mesocosms, followed eight hours later by mesopredators (*Hippodamia*). Top omnivores (*Armases*) were introduced the following day.

After two weeks, we counted the number of *Uroleucon* and the number of damaged leaves in each mesocosm (other data were not taken in order to minimize disturbance). Mesocosms were broken down after ~3.5 weeks on 20 June 2008, because herbivores were reproducing rapidly in some treatments and were close to consuming entire plants. At the end of the experiment we counted herbivores; the number of damaged green, total green, and yellow leaves; estimated the percentage

of area of individual leaves damaged on three leaves from each plant, and calculated the relative growth rate (RGR) for plants and *Armases* (Appendix B). We measured the toughness of green leaves and lyophilized three green leaves from each plant for total nitrogen content. We standardized most response variables, with the exception of leaf toughness, percentage of damage per leaf and N content, by dividing by the initial number of green leaves. We used mixed-model nested ANOVAs to assess the effect of treatments for individual response variables where site was nested within latitude (random) and latitude, omnivore density, mesopredator density, and herbivore ontogenetic stage were fully crossed, fixed factors. We conducted planned contrasts (*t* tests) comparing the abundance of all *Ophraella*, adult *Ophraella*, and *Uroleucon* in subsets of our experimental treatments that most closely mimicked field conditions (e.g., high-latitude mesocosms without omnivores, started with larval *Ophraella* vs. low-latitude mesocosms with omnivores, started with adult *Ophraella*). No post hoc adjustment of significance levels was used for these tests, as these contrasts were designed to test a priori hypotheses (Quinn and Keough 2002). Means for all treatment combinations are provided in Appendix C.

To further understand our results, we conducted additional experiments and analyses (Appendix B). We conducted predation trials in the laboratory to assess which species from the *Iva* food web were most likely to feed on each other. We calculated the Relative interaction intensity (RII) of all predator combinations on each herbivore (Armas et al. 2004). Finally, we analyzed results of the mesocosm experiment using structural equation modeling (SEM) which allows a variable to be both influenced by other variables and cause variation in a dependent variable (Grace 2006).

RESULTS

High- vs. low-latitude food webs

In subsets of our experimental treatments that mimic field conditions at high and low latitudes (see *Methods*), no differences were apparent between the high- and low-latitude combinations after two weeks (proportion of total leaves with damage, $t_{1,8} = -1.35$, $P = 0.21$; *Uroleucon*, $t_{1,8} = -0.08$, $P = 0.94$). At the end of the experiment, however, leaves were more damaged in the low-latitude food web (percentage of damage, $t_{1,8} = -1.88$, $P = 0.048$; proportion of total leaves with damage, $t_{1,8} = -2.00$, $P = 0.04$). Aphid populations did not differ between northern and southern food webs ($t_{1,8} = -0.48$, $P = 0.32$). Densities of *Ophraella* beetles were greater on low-latitude plants ($t_{1,8} = -2.34$, $P = 0.024$). Why these patterns developed is revealed by considering all possible food web combinations.

All food web combinations

Initial responses.—After two weeks, plant damage (number of leaves damaged/initial number of green leaves) was greatest in high-latitude mesocosms initially

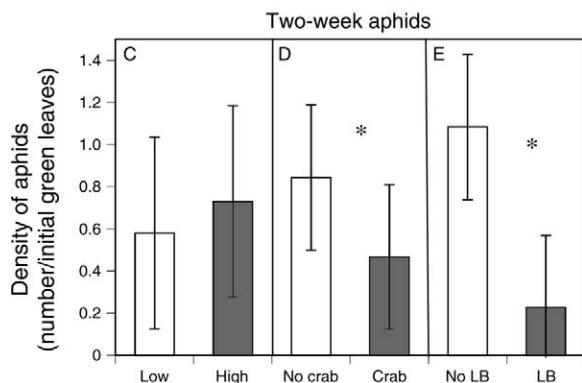
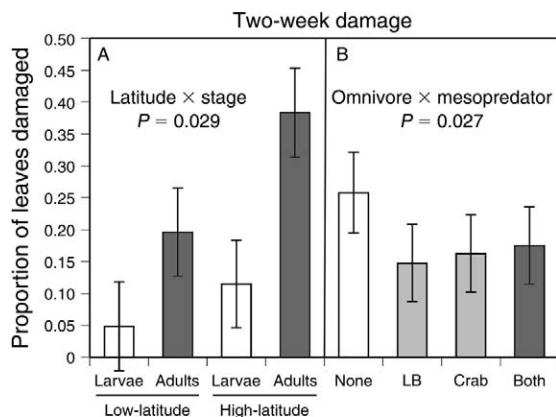


FIG. 1. Chewing damage to plants (the salt marsh shrub *Iva frutescens*) and aphid (*Uroleucon ambrosiae*) densities at two weeks in the mesocosm experiment. (A, B) Interaction of (A) latitude and herbivore stage of *Ophraella notulata* beetles and (B) omnivore (crab) and mesopredator (ladybug; LB) for plant damage. (C–E) Main effects of (C) latitude, (D) omnivore presence, and (E) mesopredator presence on aphid densities. Asterisks indicate significant differences in main effects. Data are back-transformed means and 95% confidence intervals.

stocked with adult *Ophraella* (latitude × resistant herbivore stage, $P = 0.029$; Fig. 1A; Appendix C: Table C1). Predators decreased the proportion of damaged leaves on plants (omnivore × mesopredator, $P = 0.03$; Fig. 1B). The abundance of *Uroleucon* did not differ between plants from high and low latitudes (Fig. 1C; Appendix C: Table C1), but was reduced by the presence of crabs ($P = 0.02$; Fig. 1D) or ladybugs ($P < 0.0001$; Fig. 1E).

Final plant responses.—We found several higher order interactions in the final plant responses (Appendix C). Leaf toughness was lowest in mesocosms stocked with both predators and adult beetles (omnivore × mesopredator × herbivore stage, $P = 0.02$). Latitude interacted with the presence of omnivores and mesopredators to affect the percentage of leaf area damaged (latitude × omnivore × mesopredator, $P = 0.036$), indicating that crabs decreased damage to low-latitude plants more effectively than on high-latitude plants (Fig. 2E). The RGR of plants was determined by the interaction of predator presence and the life history

stage of *Ophraella* beetles (omnivore × stage $P = 0.03$; mesopredator × stage, $P = 0.03$, Fig. 3A, B). Overall, the presence of each predator reduced the percentage of leaf area damaged on plants (mesopredator, $P = 0.019$; omnivore, $P < 0.0001$; Fig. 2E) and increased the RGR of plants (mesopredator, $P = 0.001$; omnivore, $P = 0.003$; Fig. 3B) relative to treatments without predators. Plants were most damaged (percentage of damage, $P < 0.0001$; Appendix C: Table C3) and grew the least (RGR green leaves, $P < 0.0001$; Fig. 3A) when mesocosms were initially stocked with adult vs. larval beetles.

Final herbivore responses.—*Uroleucon* aphids were strongly suppressed in mesocosms that had been stocked

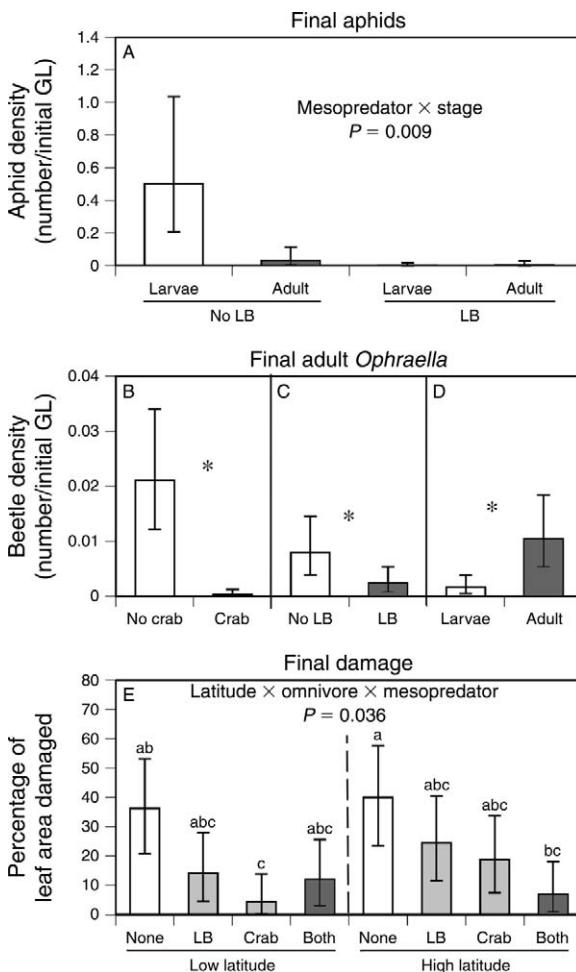


FIG. 2. Final herbivore densities and damage to plants. (A) Interaction of mesopredator presence and herbivore stage for the density of *Uroleucon* aphids per green leaf (GL). (B–D) Main effects of (B) omnivore presence, (C) mesopredator presence, and (D) herbivore stage on final densities of adult *Ophraella* beetles. (E) Interactive effects of latitude, omnivore presence, and mesopredator presence on final percentage of damaged leaves. Significant differences within interactions are shown by different lowercase letters (Tukey's hsd, $\alpha = 0.05$). Asterisks indicate significant differences in main effects ($P < 0.05$). Data are back-transformed means and 95% confidence intervals.

with ladybugs, or with adult *Ophraella* in the absence of ladybugs (mesopredator \times herbivore stage, $P = 0.009$; Fig. 2A). Overall ladybugs ($P < 0.0001$) but not crabs ($P = 0.93$) depressed the abundance of *Uroleucon*. Both crabs and ladybugs decreased the abundance of adult *Ophraella* (mesopredator, $P = 0.027$; omnivore, $P < 0.0001$; Fig. 2B, C). The abundance of *Ophraella* beetles was always greater when mesocosms were initially stocked with adult *Ophraella* vs. larvae ($P < 0.0001$; Fig. 2D).

The latitude of plant origin did not alter aphid (latitude, $P = 0.37$) or *Ophraella* (latitude, $P = 0.83$) densities across all food web combinations (Appendix C: Table C2). Aphid populations did not grow better on high-latitude plants either with or without predators (latitude \times omnivore \times mesopredator, $P = 0.24$). *Ophraella* population growth also did not differ by plant latitude (latitude \times omnivore \times mesopredator, $P = 0.38$), but latitude did affect the pattern of damage to plants (Fig. 2E).

Top consumers.—Only a few ladybugs survived to the end of the experiment; however, as reported above in *Final herbivore responses*, ladybugs survived long enough to have strong treatment effects. The RGR of *Armases* were similar across latitude ($F_{1,6.46} = 0.22$, $P = 0.66$) and between treatments with and without mesopredators ($F_{1,19.83} = 0.04$, $P = 0.85$) and with different herbivore stages ($F_{1,19.83} = 1.08$, $P = 0.31$).

Additional analyses

In predation trials with a larger suite of salt marsh predators, *Armases* ate roughly 10 times more *Uroleucon* than did *Hippodamia*; spiders ate almost no *Uroleucon*. Relative interaction intensity (RII) between predators and prey did not differ by latitude of plant origin. *Armases* showed the weakest RII against *Uroleucon*; ladybugs had the weakest RII against adult *Ophraella*. The results from SEM analysis generally supported results from ANOVAs: *Armases* had direct negative effects on *Ophraella* beetles and *Uroleucon* aphids; and *Uroleucon* were negatively affected by *Ophraella* and *Hippodamia* ladybugs. *Ophraella* beetles increased herbivore damage, decreased nitrogen content, and increased chlorophyll content of *Iva* plants. Details can be found in Appendix B.

DISCUSSION

Our mesocosm experiment indicated that the *Iva* food web is strongly structured by top-down control. Both crabs and ladybugs suppressed aphid populations at two weeks, and the ladybug effect continued to the end of the experiment. Consumer effects on beetles were not apparent at two weeks, but were strong at the end of the experiment, with crabs suppressing beetles more strongly than did ladybugs. Both crabs and ladybugs reduced beetle damage to plants and positively affected plant growth. These results were consistent with predation trials (Appendix B), which showed that both crabs and ladybugs could eat both beetles and aphids,

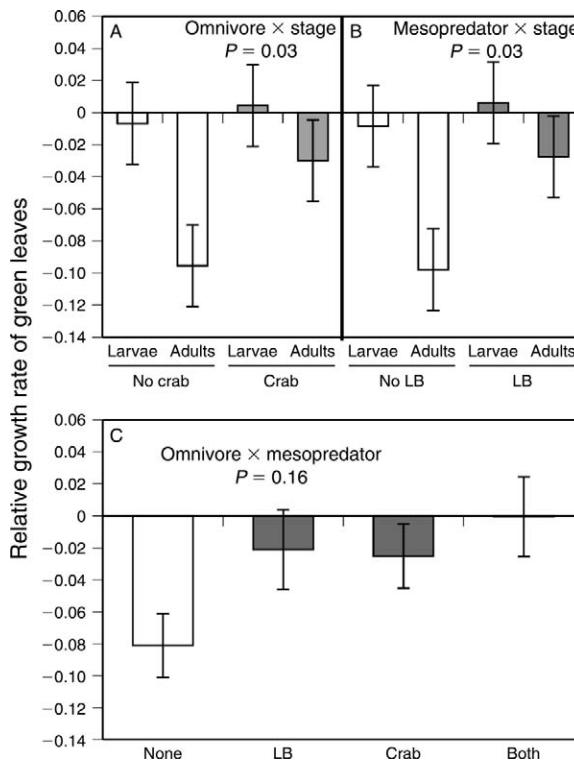


FIG. 3. Relative growth rate (RGR) of green leaves showing interactions of (A) omnivore and stage, (B) mesopredator and stage, and (C) omnivore and mesopredator. Data are back-transformed means and 95% confidence intervals.

and that crabs were more effective consumers of beetles than were ladybugs (Appendix B). The most likely reason that crabs did not strongly affect aphid densities late in the mesocosm experiment was that aphid densities were dropping at this time (compare Fig. 1C–E with Fig. 2A), due to (1) predation early in the experiment, (2) competition from *Ophraella*, and, (3) we speculate, increased plant resistance (see similar aphid dynamics in Ho and Pennings 2008).

Although *Armases* is omnivorous (Pennings et al. 2009), and has weak negative effects on *Iva* plants when no animal prey are available (Ho and Pennings 2008), *Armases* prefers to eat and grows best on a diet of animal prey when available (Buck et al. 2003, Ho and Pennings 2008). As a result, *Armases* functions as a top predator whenever animal prey are available, strongly suppresses many components of the food web, and has an indirect net positive effect on *Iva* plants (Ho and Pennings 2008).

In contrast to this strong top-down control, we found weak bottom-up control of herbivore populations. When given a choice, chewing herbivores prefer to feed on high- vs. low-latitude *Iva* plants (Pennings et al. 2001), and a diet of high-latitude *Iva* leaves decreases development time and increases larval growth rate of *Ophraella* (C. K. Ho and S. C. Pennings, unpublished manuscript). Nevertheless, latitudinal differences in plant quality did not strongly affect the outcome of

our mesocosm experiments. We saw one indication that latitudinal differences in plant quality affected *Ophraella* densities or feeding in that plant damage at two weeks was higher for high- vs. low-latitude plants; this effect was also documented at the end of the experiment in the SEM analysis (Appendix B). Overall, however, although high-latitude *Iva* plants are more nutritious and offer modest growth benefits, these benefits were mostly swamped in our experiment by much stronger consumer effects.

We saw no indication that latitudinal variation in plant quality mattered for aphid populations. The plant traits that affect palatability to chewing herbivores may not be relevant to sucking herbivores (Koricheva and Larsson 1998). We have not determined whether high-latitude *Iva* plants are preferred over low-latitude plants by aphids, but other performance studies also found, as we did here, that *Iva* plants from high latitudes do not support better population growth of aphids than *Iva* plants from low latitudes (C. K. Ho and S. C. Pennings, unpublished manuscript).

By feeding on more than one trophic level, omnivores can generate simultaneous and opposite direct and indirect effects on lower trophic levels. As a result, omnivores are expected to increase food web complexity and weaken trophic cascades (Polis and Strong 1996). Similarly, intra-guild predators, by suppressing other predators, may have opposite direct and indirect effects on lower trophic levels, and again might be expected to weaken trophic cascades (Finke and Denno 2004, but see Snyder et al. 2006). Our results were only partially consistent with these predictions. In the *Iva* food web, *Armases* is both an omnivore (consuming both herbivores and *Iva* leaves) and an intra-guild predator (consuming both ladybugs and herbivores). Nevertheless, *Armases* still had a strong, indirect positive effect on plants, reducing chewing damage and increasing plant growth rates. This general result occurred even with high-latitude plants, which are strongly preferred by *Armases* over low-latitude plants (Pennings et al. 2001). Moreover, other than one possible line of evidence for intra-guild interference (on low-latitude plants, chewing damage tended to be greatest when both predators were present; Appendix C), we found no evidence that *Armases* and ladybugs interfered with each other (no omnivore \times mesopredator interactions; Appendix C: Table C2). In general, because *Armases* strongly suppressed *Ophraella*, and *Hippodamia* was more successful at suppressing aphid populations, our results suggest that these consumers had complementary food web effects, and both had beneficial effects on plant growth (Fig. 3C).

The source and strength of herbivory depends on complex interactions between life history, colonization priority, and predation (Frechette et al. 2006). In our experiment, damage to *Iva* plants was greatest and growth rate of plants least when mesocosms were stocked with adult *Ophraella* beetles. Populations of *Ophraella* in these mesocosms were able to increase in

numbers almost immediately, because adults could lay multiple sets of eggs. In contrast, populations of *Ophraella* in mesocosms stocked with larvae could not increase in numbers until larvae grew, pupated, and emerged as adults. For this reason, we observed greater levels of chewing damage to leaves in treatment combinations stocked with adult beetles. Moreover, treatments stocked with adult beetles had lower final aphid numbers than treatments stocked with beetle larvae, likely as a result of competition, because predation trials confirmed that *Ophraella* do not directly eat *Uroleucon*.

Based on this discussion, we can now synthesize our results in the context of latitudinal controls on the *Iva* food web. Latitudinal variation in plant quality does not appear to have substantial effects on herbivore population dynamics. In contrast, top-down pressure may strongly limit herbivore populations, but in different ways at different latitudes. In particular, top-down control of aphid populations is likely strong at all latitudes because ladybugs are present at all latitudes, but might be more consistent at low latitudes because either crabs or ladybugs can suppress aphids. In contrast, beetle populations are less limited by ladybugs, but are suppressed at low latitudes by crabs.

Because crabs suppress beetles at low latitudes, one might expect that beetles would be more abundant at high latitudes; however, the opposite is true (Pennings et al. 2009). This points to a likely role of climate in limiting beetle populations at high latitudes. The harsh climate at high latitudes could limit beetle populations in two ways. First, because the growing season is shorter at high latitudes, and *Iva* plants senesce for the winter, high-latitude beetle populations have fewer generations each year, reducing potential growth rates. The importance of this was revealed by the strong effect of the beetle life history treatment on final beetle numbers. Second, harsh winter freezes at high latitudes may kill overwintering individuals, reducing beetle populations. Although we lack data on overwintering mortality for *Iva* beetles, severe winters are known to reduce overwinter survival in many coleoptera, including the ragweed beetle *Ophraella communa* (Watanabe and Hirai 2004), the Colorado potato beetle (Milner et al. 1992), and many other chrysomelid beetles. In general, herbivores are likely to be strongly limited at high latitudes by a short growing season and harsh winters. Finally, because beetles are more abundant at low vs. high latitudes, they are likely to compete more with aphids at low latitudes, increasing "side-to-side" control of the food web (Moon and Stiling 2002).

In summary, our results suggest that both predation and competition decrease for *Iva* herbivores at high latitudes. Plant quality is also better at high latitudes. Despite the many advantages to life at high latitudes, herbivore densities are lower at high than low latitudes, likely because a short growing season and harsh winters limit populations. These conclusions are based on

mesocosm experiments and inference, and need to be confirmed in the field, but they illustrate an important difficulty in understanding macro-ecological patterns. Because so many factors are likely to change geographically, geographic variation in any one process can be overwhelmed by variation in another. As a result, geographic changes in a given process must be evaluated in the context of other processes in order to draw robust conclusions: It is very easy to confuse geographic variation in the *intensity* of a process with geographic variation in its *importance* (Welden and Slauson 1986).

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APPENDIX A

Study system and species (*Ecological Archives* E092-023-A1).

APPENDIX B

Expanded methods and additional analyses (*Ecological Archives* E092-023-A2).

APPENDIX C

Details for analyses and full data table from mesocosm experiment (*Ecological Archives* E092-023-A3).