Latitudinal variation in plant–herbivore interactions in European salt marshes

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Ecological interactions often vary geographically. Work in salt marshes on the Atlantic Coast of the United States has documented community-wide latitudinal gradients in plant palatability and plant traits that may be driven in part by greater herbivore pressure at low latitudes. To determine if similar patterns exist elsewhere, we studied six taxa of saltmarsh plants (Atriplex, Juncus, Limonium, Salicornia, Spartina and Suaeda) at European sites at high (Germany and the Netherlands) and low (Portugal and Spain) latitudes. We conducted feeding assays using both native and non-native consumers, and documented patterns of herbivore damage in the field. As in the United States, high-latitude plants tended to be more palatable than low-latitude plants when offered to consumers in paired feeding assays in the laboratory, although assays with grasshopper consumers were less consistent than those with crab consumers, and plants in the field at low-latitude sites tended to experience greater levels of herbivore pressure than plants at high-latitude sites. Similarly, high-latitude leaf litter was more palatable than litter from low-latitude plants when offered to consumers in paired feeding assays in the laboratory. Latitudinal gradients in plant palatability and herbivore pressure may be a general phenomenon, and may contribute to latitudinal gradients in decomposition processes.

Species often have large geographic ranges, but interactions among species occur locally (Menge 2003). At any given site, local abiotic conditions and community composition mediate interactions between organisms, creating different selective pressures than those experienced by conspecifics at other sites (Dunson and Travis 1991, Sokta and Hay 2002, Toju and Sota 2006). As a result of local differences in both ecological context and local adaptation, the nature of interactions between species may vary geographically (Thompson 1988, Travis 1996, Callaway et al. 2002, Sokta et al. 2003). If so, an understanding of the nature of this geographic variation will be an essential component of any general theory of species interactions (Thompson 1994, 2005).

One simple way that interactions among species might vary geographically is as a monotonic gradient across latitude. Ecologists have long speculated that competition, predation and herbivory might all increase in intensity from high to low latitudes (Dobzhansky 1950, MacArthur 1972, Pennings and Silliman 2005). A variety of evidence supports these assertions (Vermeij 1978, Coley and Aide 1991, Stachowicz and Hay 2000), but rigorous studies are difficult, especially for plant–herbivore interactions, because taxonomic turnover and large geographic distances create obstacles to good experimental design (Pennings et al. 2001). A number of studies support the hypothesis that plant–herbivore interactions are...
more intense at lower latitudes (Coley and Aide 1991, Bolser and Hay 1996), but exceptions exist (Bryant et al. 1994), and many early studies suffered from limitations in design (reviewed by Pennings et al. 2001).

One of the most comprehensive studies of latitudinal variation in plant–herbivore interactions comes from coastal salt marshes on the Atlantic Coast of the United States, where similar plant communities extend from central Florida through Maine. For ten species of plants (the bulk of the plant community), individuals from low latitudes were less palatable to 13 species of herbivores than were conspecifics from high latitudes (Pennings et al. 2001). Differences in palatability were constitutive rather than induced (Salgado and Pennings 2005), and were linked to differences in plant nitrogen content, toughness, and chemical defenses (Siska et al. 2002). Herbivore pressure was greater at low latitudes (Pennings and Silliman 2005), and likely contributed to the different selective environments that produced plants with different traits at low versus high latitudes. It is likely that other factors in addition to herbivore pressure contribute to selecting for differences in plant traits that affect herbivory at low versus high latitudes, but these have not yet been studied.

Because the characteristics of leaf litter reflect the characteristics of the leaves that produce the litter (Grime et al. 1996, Cornelissen et al. 2004), it is likely that less palatable leaves will produce less palatable litter. If so, we might expect to see the same latitudinal gradients in litter–detritivore interactions that we see in plant–herbivore interactions. Because detritivores play a basic role in mediating decomposition in many systems, a latitudinal gradient in litter palatability might lead to important differences in mechanisms of nutrient cycling between high- and low-latitude systems. This hypothesis, however, has not been tested to date.

Although salt marsh studies from the Atlantic Coast of the US support the theory that plant–herbivore interactions are more intense at low versus high latitudes, one could argue that this body of work represents only a single geographic gradient, and thus could be an artifact of some unique feature of the US Atlantic Coast. To be confident that this is a general result, one would like to replicate these results across latitudinal gradients elsewhere in the world. Here, we test the hypotheses that latitudinal gradients in 1) plant palatability, 2) litter palatability and 3) herbivore pressure also occur in European salt marshes. Our results suggest that latitudinal gradients in plant–herbivore interactions are a general phenomenon, and suggest that these gradients may also affect decomposition processes.

Methods

Latitudinal comparisons of plant palatability

To compare the palatability of high- and low-latitude leaves and leaf litter, we collected plant material from three sites in Germany and two sites in Portugal (Appendix 1). German sites represented both the Baltic and North Sea coasts. None of the sites had been subject to intensive livestock grazing in recent years, although some had been grazed in the past. We collected six taxa of plants in both geographic regions. In one case (Suaeda maritima) conspecifics were collected from the two geographic regions, in four cases, congeners; and in one case (Salicornia, Sarcocornia, Arthrocnemum) a trio of morphologically-similar and closely-related genera (which are united in one genus in some taxonomic treatments). Thus, although these comparisons did not necessarily involve “identical” species at both latitudes, they did represent six independent comparisons in which phylogeny was controlled.

Collections were made in the first two weeks of August, 2001, except for Atriplex hastata from Germany, which was collected in the second week of September, 2001. Live leaves were healthy and green; leaf litter was either standing-dead or fallen-dead, as appropriate for the species. For every species, material from each site represented multiple individual plants. Plant material was pooled, lyophilized and ground to a fine powder.

The palatability of pairs of plants from the two geographic regions was compared in two-choice feeding assays using a detritivore from German salt marshes (the isopod Porcellio scaber, n = 7 assays), and an omnivore from American salt marshes (the grapsid crab Armases cinereus, n = 15 assays). We will refer to both species generically hereafter. Previous studies concluded that latitudinal differences in palatability were perceived similarly by a wide variety of consumers, with no indication of bias for or against “local” plants (Pennings et al. 2001); therefore, we selected these consumers for tractability in the laboratory. Porcellio is common among stranded litter at the upper fringe of German salt marshes (Pfauder and Zimmer 2005). Armases is a semi-terrestrial crab that is common at the upper fringe of salt marshes along the southeastern coast of the United States (Abele 1992). We used it as an assay organism because it is an omnivore that will readily eat both leaves and litter of a variety of salt marsh plants (Pennings et al. 1998, 2001, Siska et al. 2002, Buck et al. 2003) and because it was naïve with respect to most of the plants studied. Only 2 of 12 taxa, Salicornia europaea and Suaeda maritima, occur in the southeastern United States, where they are both quite rare (Pennings, pers. obs.). We therefore expected


*Armases* not to favor plants from either geographic region on the basis of familiarity or novelty. We conducted four additional assays with herbivorous grasshoppers (*Parasoya clavuliger, Orchelimum fidici-
nium, Orphulella pelidna*) from the southeastern coast of the United States, limiting these assays to plant taxa that the grasshoppers would readily consume. Grass-
hoppers were naive with respect to all tested plant species. Sites were haphazardly paired for feeding comparisons. When possible, we replicated compar-
sions using more than one site from each geographic region to ensure that results were not site-dependent.

### Feeding assays with *Porcellio*

Ground plant material was incorporated into an artificial diet. Agar (0.8 g) was dissolved in boiling water (20 ml). As the agar cooled, plant powder (4 g) was thoroughly stirred into the mixture. The diet was poured into the lid of a petri plate (9 cm diameter) and the inverted bottom of the petri plate was pressed into the lid in order to flatten the diet to a consistent thickness. After the diet cooled, we cut it into pieces for use in feeding trials. To determine the wet:dry ratio of the final mixture, four large pieces of the diet were removed, weighed, dried (50°C, 24 h) and weighed again.

Groups of five *Porcellio* were housed in petri dishes (9 cm diameter). We lined the lid of each petri dish with a piece of wet filter paper in order to maintain humid conditions. Each group of isopods was offered a choice between a high- and a low-latitude diet. Individual replicates (n = 15) were stopped when at least ½ of one of the diets had been consumed, or after 4 d. Autogenic controls (n = 5–10), which were treated identically except that they lacked isopods, were stopped in parallel with experimental replicates. Diets were weighed at the beginning of the experiment, and their dry mass calculated based on the wet:dry ratio of the diet. After the replicate was stopped, remaining diets were dried and re-weighed to calculate the dry mass consumed. The difference in mass change of the autogenic controls was compared with the difference in mass change of the corresponding experimental diets using a paired t-test (Peterson and Renaud 1989). For clarity, only mass change of diets exposed to isopods is shown in figures.

### Feeding assays with *Armases*

Assays with *Armases* were similar and followed Siska et al. (2002). Briefly, ground plant material in an agar diet was poured into a template resting on a screen with 1 mm² openings. Assays were stopped when substantial feeding on at least one diet had occurred, or after 3 d. Consumption was measured as mm² of screen exposed by feeding, and was compared between regions using a paired t-test.

### Geographic survey of herbivore damage

To determine if herbivore pressure could be selecting for geographic patterns of palatability, we measured damage to leaves by chewing herbivores on plants in 10 high- (Germany, The Netherlands) and 10 low-latitude (Portugal, Spain) sites (Appendix 2). At each site, we sampled 6–8 individuals of each species. Damage was estimated by visual estimates of missing leaf area (*Atriplex, Juncus, Limonium, Spartina*, 2–3 leaves/ plant, averaged to yield a single value/plant) or by counting the percentage of damaged segments out of 100 (*Salicornia/Sarcocornia/Arthrocnemum*) or the percentage of damaged leaves out of 100 (*Suaeda*). For statistical purposes, values from multiple leaves/plant were averaged to yield a single value/plant. Multiple plants within a site were then averaged to yield a single site mean for each variable at each site. Geographic comparisons used sites as replicates.

### Results

Using the conventional cutoff of p < 0.05 to indicate statistical significance, one would expect 1.3 assays out of 26 to be “significant” by chance alone. Twenty out of 26 of our feeding assays were significant, making it very unlikely that our results were due to chance.

Given a choice between reconstituted leaves from high- and low-latitude sites, *Armases* tended to eat more of the high-latitude diet in 9 out of 10 cases; 8 of these comparisons were statistically significant (Fig. 1). In the tenth case (*Limonium*), *Armases* preferred the low-latitude diet. Grasshoppers significantly preferred the high-latitude diet in one case (*Atriplex*), showing the same preferences for this taxa as did *Armases*. Grasshoppers preferred the low-latitude diet in three cases (*Spartina*, 2 of 3 assays significant), showing opposite feeding preferences for this taxa as did *Armases*.

Given a choice between reconstituted leaf litter from high- and low-latitude sites, *Porcellio* tended to eat more of the high-latitude diet in 6 of 7 cases; 4 of these comparisons were statistically significant (Fig. 2). In the seventh case (*Atriplex*), consumption of high- and low-latitude diets was similar. *Armases* ate more of the high-than the low-latitude leaf litter diet in 5 out of 5 cases.

Geographic surveys generally supported the hypoth-
thesis that damage from chewing herbivores was greater at low than high latitudes (Fig. 3). *Limonium, Salicornia* and *Suaeda* all had more herbivore damage at low-versus high-latitude sites. *Juncus* and *Spartina* had very
little damage in either geographic region. In the case of *Atriplex*, low-latitude individuals of *A. hastata* tended to display more damage than high-latitude individuals of *A. hastata*; however, this comparison was not statistically significant because we only located *A. hastata* at 3 low-latitude sites. Low-latitude individuals of *A. portulacoides* had less damage than high-latitude *A. hastata*. 

![Graph showing consumption of reconstituted high vs low latitude leaves in paired feeding trials](image)

**Fig. 1.** Consumption of reconstituted high vs low latitude leaves in paired feeding trials. Data are means ± 1 SE; sample sizes, consumer species, plant species, and collection sites are indicated below paired bars. Consumers: A, Armases; P, Parorya; Of, Orchelimum; Op, Orphulella. Plants: A, *Atriplex hastata* (N) vs *A. portulacoides* (S); J, *Juncus gerardi* (N) vs *J. maritima* (S); L, *Limonium vulgare* (N) vs *L. algarvensis* (S); Sa, *Salicorina europaea* (N) vs *Sarcocornia* spp. (S); Sp, *Spartina anglica* (N) vs M, *S. maritima*, or D, *S. densiflora* (S); Su, *Suaeda maritima* (N vs S). Sites: B, Bottsand, Germany; W, Westerhever, Germany; S, Schöburg, Germany; I, Bias, Portugal; F, Faro, Portugal. See Appendix 1 for additional information on sites.

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![Graph showing consumption of reconstituted high vs low latitude leaf litter in paired feeding trials](image)

**Fig. 2.** Consumption of reconstituted high vs low latitude leaf litter in paired feeding trials. Data are means ± 1 SE; sample sizes, consumer species, plant species, and collection sites are indicated below paired bars. Consumers: A, Armases; C, Porcellio. Plants: A, *Atriplex hastata* (N) vs *A. portulacoides* (S); L, *Limonium vulgare* (N) vs *L. algarvensis* (S); Sp, *Spartina anglica* (N) vs M, *S. maritima*, or D, *S. densiflora* (S). Site abbreviations as in Fig. 1. See Appendix 1 for additional information on sites.
Results for leaf litter showed a striking preference for high-latitude material. Both the detritivore Porcellio and the omnivore Armases preferred to eat litter of high- versus low-latitude leaves (4 of 7 and 5 of 5 comparisons, respectively). In no case was the litter of low-latitude leaves significantly preferred. Because much of the physical structure and some of the secondary chemistry of leaves is retained in leaf litter, it is not surprising that leaves of unpalatable plants might produce unpalatable litter (Grime et al. 1996, Cornelissen et al. 2004). Thus, any factor that selects for geographic differences in leaf palatability to herbivores is likely to also create differences in litter-detritivore interactions across geographic scales. If so, this might also affect geographic variation in ecosystem processes, with litter being more recalcitrant to decomposition at low versus high latitudes.

Because of logistic constraints, we worked with ground, freeze-dried plant material rather than unmanipulated leaves or litter. Our previous work suggested that processing plant material tends to reduce geographic differences (Siska et al. 2002), likely because differences in toughness are reduced when plant material is ground, and secondary chemicals may volatilize or degrade with processing. We speculate, therefore, that our results are likely to be conservative, and hypothesize that geographic differences in palatability of fresh leaves and litter are probably greater than suggested here.

In studies on the Atlantic Coast of the US, latitudinal differences in plant palatability were linked to latitudinal differences in leaf toughness, nitrogen content and chemical defenses (Siska et al. 2002). We did not address these mechanisms in the present study; however, preliminary data (not shown) suggested that some taxa differed geographically in nitrogen content and toughness. Thus, these leaf traits and others may have played proximate roles in creating geographic differences in palatability in European marshes.

Geographic surveys of leaf damage generally supported the hypothesis that herbivore pressure was greater at low latitudes, and thus, that herbivore pressure might be one factor selecting for lower palatability at low latitudes. Latitudinal patterns in
herbivore damage were striking for three taxa (Limonium, Salicornia/Sarcocornia/Arthrocnemum and Suaeda), all of which had markedly higher levels of herbivore damage at low- versus high-latitude sites. Results for Atriplex were less clear: A. hastata tended to have higher levels of herbivory at low-latitude sites (although this pattern was not statistically significant because A. hastata was found at only 3 of our low-latitude sites), but the most common low-latitude species of Atriplex, A. portulacoides, had less herbivore damage than high-latitude A. hastata. Little herbivore damage was observed on Juncus and Spartina species on the dates we surveyed the sites. Because we sampled herbivore damage on only one date at each site, it is possible that patterns might have varied seasonally. Nevertheless, the most common result was that herbivore damage was greater at low latitudes, as we have also found on the Atlantic Coast of the US (Pennings and Silliman 2005, Pennings, unpubl.).

We did not address the reasons leading to higher herbivore pressure at low versus high latitudes in this study, but biologists have long speculated that higher arthropod populations are facilitated by milder climates at low latitudes (Dobzhansky 1950). High levels of herbivore damage might select for increased plant defenses, and thus be one selective factor leading to reduced plant palatability at low latitudes. It is likely that other factors are also important, and these may interact with herbivore pressure in complicated ways to affect plant palatability. As one example, the longer growing season at low latitudes might require tougher leaves (in order to extend leaf life-span), and increased leaf toughness might reduce palatability to herbivores. These alternative hypotheses deserve attention, because they bear on whether the latitudinal gradient in herbivory and plant defenses is a reciprocal coevolutionary process or simply a consequence of parallel evolutionary responses by plants and herbivores to climate or other external drivers.

One potential caveat regarding our results is that, because the marsh plant flora differed between northern and southern Europe, we were not able to make many intraspecific comparisons. The only well-replicated intraspecific comparison that we were able to make was between high- and low-latitude individuals of Suaeda maritima, and this comparison showed a strong latitudinal pattern in palatability and herbivore damage. We also compared high- and low-latitude populations of Atriplex hastata, but this comparison was hampered by low replication at low latitudes, where A. hastata was rare. All other comparisons involved congenerics (five taxa) or closely related genera (Salicornia vs Sarcocornia and Arthrocnemum). By comparing closely-related species, we minimized possible effects of phylogenetic constraints on our results. Nevertheless, it is possible that some of the variability in our results, compared to results from the Atlantic Coast of the US (Pennings et al. 2001, Siska et al. 2002), was due to fundamental differences among species that were unrelated to herbivory.

These results are probably not unique to salt marsh habitats. Studies in forests have found more herbivore damage and higher expression of plant defensive compounds at low versus high latitudes (Coley and Aide 1991, Coley and Barone 1996), and studies of seaweeds have found that low-latitude plants are less palatable to herbivores than high-latitude plants (Bolser and Hay 1996). Geographic differences in plant and seaweed defenses appear to select for geographic differences in herbivore “offense” (Cronin et al. 1997, Toju and Sota 2006) and feeding behavior (Sotka and Hay 2002, Sotka et al. 2003). Although contrary patterns may exist at very high latitudes (Bryant et al. 1994), studies in temperate and tropical latitudes appear to support the speculation of early naturalists (Dobzhansky 1950) that biological interactions are more intense at low latitudes, creating geographic differences in selection patterns on both plants and herbivores that must be understood as part of any general ecological or evolutionary theory (Thompson 1994, 2005).

In summary, our results support the hypothesis that plant–herbivore interactions are more intense at low versus high latitudes in European salt marshes: herbivore damage is more extensive at low versus high latitudes, and (perhaps in response) low-latitude plants are less palatable than high-latitude plants. Despite a less-extensive data set and a less-powerful methodology (i.e. freeze-dried plant material), our results were consistent with the latitudinal patterns found in US salt marshes. In addition, our results indicated that geographic differences in the palatability of leaves are likely to be paralleled by differences in the palatability of leaf litter. As a result, factors that create geographic patterns in leaf palatability may not only affect plant-herbivore interactions, but also litter–detritivore interactions and ecosystem processes such as nutrient cycling.

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References


Appendices can be found at www.oikos.ekol.lu.se as Appendix O15591