Oecologia (2006) 148: 593–601
DOI 10.1007/s00442-006-0407-2

PLANT ANIMAL INTERACTIONS

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Increased chemical resistance explains low herbivore colonization of introduced seaweed

Received: 20 October 2005 / Accepted: 21 February 2006 /

Abstract The success of introduced species is often attributed to release from co-evolved enemies in the new range and a subsequent decreased allocation to defense (EICA), but these hypotheses have rarely been evaluated for systems with low host-specificity of enemies. Here, we compare herbivore utilization of the brown seaweed, *Fucus evanescens*, and its coexisting competitors both in its native and new ranges, to test certain predictions derived from these hypotheses in a system dominated by generalist herbivores. While *F. evanescens* was shown to be a preferred host in its native range, invading populations supported a less diverse herbivore fauna and it was less preferred in laboratory choice experiments with important herbivores, when compared to co-occurring seaweeds. These results are consistent with the enemy release hypothesis, despite the fact that the herbivore communities in both regions were mainly composed of generalist species. However, in contrast to the prediction of EICA, analysis of anti-grazing compounds indicated a higher allocation to defense in introduced compared to native *F. evanescens*. The results suggest that the invader is subjected to less intense enemy control in the new range, but that this is due to an increased allocation to defense rather than release from specialized herbivores. This indicates that increased resistance to herbivory might be an important strategy for invasion success in systems dominated by generalist herbivores.

Keywords Biological invasion · Enemy release · *Fucus evanescens* · Herbivores · Phlorotannins

Communicated by Julia Koricheva

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Introduction

Biological invasions have become one of the most prominent elements of global change, altering biodiversity and function of natural ecosystems (Vitousek et al. 1996; Mack et al. 2000), and causing significant economic damage (Pimentel et al. 2000). To manage the increasing threat from introduced species, it is crucial to understand why particular species are able to proliferate and become widespread and abundant in their new ranges. One mechanism, which is often invoked to explain invasion success, is that proposed by the enemy release hypothesis (ERH) (e.g., Elton 1958; Keane and Crawley 2002). The ERH states that introduced species experience reduced negative impact of natural enemies such as herbivores and pathogens, since they are liberated from their coevolved enemies, and the native enemies in their new range fail to recognize them as adequate food or hosts. As a consequence, the invasive species will gain increased competitive capacity in comparison to indigenous competitors. As an extension of the ERH, Blossey and Nötzold (1995) formulated the so-called evolution of increased competitive ability hypothesis (EICA), which suggests that the release from natural enemies will select for invading genotypes that allocate resources to characters that increase competitive ability, rather than to costly chemical or structural defenses. The EICA and the ERH are not mutually exclusive models, rather they provide complementary mechanisms for an explanatory model that emphasize the importance of release from co-evolved enemies for the successful invasions of exotic species into new ranges.

Predictions derived from the ERH, and the corollary EICA, have mostly been tested for terrestrial plant–herbivore systems (see Keane and Crawley 2002; Coulatti et al. 2004, for reviews). The prediction that invading plant species should experience a significant enemy reduction has received support in several studies, especially in those focused on biogeographical comparisons, i.e., where native and introduced populations of the same species have been compared (Coulatti et al. 2004). Terrestrial herbivore communities are generally dominated by insect species with a high degree of host specificity (Strong et al. 1984) that can be predicted to be relatively slow to change their host range to include an introduced species. This contrasts strongly with marine seaweed communities, where most herbivore species are generalists that commonly exert an intense grazing pressure, having significant impact on the structure of marine communities and selecting for a range of defense strategies in seaweeds (Hay and Steinberg 1992). Recent refinement of the ERH and EICA has suggested that the effect of generalist feeders on exotics can be predicted to differ substantially from that of specialists (Müller-Schärer et al. 2004; Joshi and Vrieling 2005). Parker and Hay (2005) also showed that generalist freshwater herbivores actually preferred introduced to native plant species in choice experiments. However, despite the fact that marine algal–herbivore communities provide highly interesting complementary test systems for general theories about biological invasions, through their strong dominance of generalist enemies compared to terrestrial systems, little experimental work on these issues has been done in marine habitats. A few studies have investigated herbivore communities on introduced seaweeds (e.g., Trowbridge 1995; Bellan-Santini et al. 1996; Viejo 1999), but we know of no previous study that has explicitly tested the potential of the ERH or the EICA to predict the invasion success of introduced seaweeds.

In this study, we compare resistance to herbivory as well as chemical defense levels, relative to confamiliar competitors, in native and invasive populations of the brown seaweed *Fucus evanescens* L. *F. evanescens* is an arctic circumpolar species that has been introduced to southern Scandinavia and the British Isles during the 20th century (Hylmö 1933; Powell 1957; Wikström et al. 2002). We compared native populations of *F. evanescens* in Iceland with populations in recently invaded ranges on the Swedish west coast. The areas we compared are relatively similar in community structure, with one apparent difference in terms of herbivory, which is the presence of the generalist gastropod grazer *Littorina littorea* in Swedish, but not Icelandic, seaweed populations. Like other fucoid seaweeds *F. evanescens* contains relatively high concentrations of phlorotannins (Wikström and Pavia 2004), a class of polyphenolic metabolites that are unique to brown seaweeds (Ragan and Glombitza 1986). Phlorotannins have multiple primary and secondary functions (Amsler and Fairhead 2006), but their most well documented ecological role in fucoids is probably as inhibitors of grazing by littorinid snails (Pavia and Toth 2000), which are often a dominating group of mesoherbivores in the intertidal zone of the northern Atlantic (Little and Kitching 1996; Reid 1996).

We tested the hypothesis that invading populations of *F. evanescens* should experience a decreased herbivore pressure in their new ranges compared to its native region, by measuring the natural abundance and species compositions of herbivores in populations of *F. evanescens* and its most apparent confamiliar competitors, as well as the feeding preferences of the dominating herbivores in both regions. Formal comparisons of data were done among the competing seaweed species within each of the two regions. The outcome was then used to test the hypothesis that the relative difference in herbivore pressure should differ in the predicted way, i.e., that the herbivore pressure should be lower on *F. evanescens*, relative to its competitors, in its new region (Sweden) but not in its native region (Iceland). This approach can be seen as a combination of so-called biogeographical comparisons and community studies (see Coulatti et al. 2004), and it is arguably the only rigorous way to evaluate the potential for an arisen competitive advantage of an invader in its new region through enemy release mechanisms. Furthermore, in order to test the predictions of the EICA that invasive species/genotypes should benefit from enemy release through reduction in defenses, we measured the phlorotannin concentration of *F. evanescens*, as well as its confamiliar competitors, in both study areas.

Materials and methods

Study area

The study was performed in two regions: the archipelago south of Strömstad on the Swedish Skagerrak coast, and on the Reykjanes peninsula in south-western Iceland (hereafter Sweden and Iceland). In both regions, samples were collected from three different sites: Öddö-Likholmen (S1; 58°93′N, 11°13′E), Öddö-Styrsö (S2; 58°91′N, 11°12′E) and Saltö (S3; 58°87′N, 11°14′E) in Sweden, and Sandgerði (I1; 64°03′N, 22°43′W), Hvassahraun (I2; 64°01′N, 22°09′W) and Seltjarnarnes (I3; 64°10′N, 22°09′W) in Iceland. The distance between sites was 7–21 km in Sweden and 17–37 km in Iceland.

In both Sweden and Iceland, intertidal rocky shores are mainly occupied by a dense canopy of brown seaweeds of the Fucaceae family. In Sweden, the native fucoid flora consists of *Fucus vesiculosus* L., *F. serratus* L. and *Ascophyllum nodosum* (L.) Le Jol., of which *F. serratus* generally grows deeper than the other species. The same species also co-occur in south-western Iceland, together with *F. evanescens* which is native to this area. On the Swedish Skagerrak coast, *F. evanescens* was first recorded in 1924 (Hylmö 1933), but the exact date of introduction to the study area is not known. The donor area for the Swedish populations is not known, but since the species was probably introduced from living specimens transported by fishing vessels (Hylmö 1933), it is reasonable to assume that it invaded from adjacent native populations in either Iceland, the Faeroes or northernmost Norway.

Field study of herbivore abundance

The abundance of herbivores and number of herbivore species were investigated on *F. evanescens, F. vesiculosus* and *A. nodosum*, both in Sweden and Iceland. At each sampling site (S1–3 and I1–3), four plants of each species were collected by randomly placing four spots on the shore and collecting the closest specimen of >20 cm length of each of the three fucoid species at each spot. In Sweden, where the fucoids are growing submerged except for irregular periods of weather-driven low-water, the plants were collected by snorkeling, from a depth of 0.5 (± 0.2) m below the mean water level. The plants were enclosed in mesh bags (mesh size 300 μm), to catch all mobile animals, and carefully removed from the substratum. We tried to collect one single plant of each species, but some samples included a few intertwined fronds from the same species. In Iceland, plants were collected in the mid intertidal during low tide. One or a few adjacent fronds were collected in plastic bags, keeping algal biomass approximately similar between samples. The samples were brought to the laboratory and immediately frozen until sorted. After thawing, animals were rinsed off the plants through a 500-μm sieve and all animals larger than 3 mm were identified and counted. The feeding habit was determined from the literature for each species and only species reported as herbivores and omnivores were analyzed further. Seaweed biomass was measured after drying in 60°C to constant weight.

Phlorotannin analyses

For analysis of phorotannin concentrations, ten plants of each of the three fucoids (*F. evanescens*, *F. vesiculosus* and *A. nodosum*) were collected randomly at the same sites as above. The frond tips (10 cm length) were cut off, brought to the laboratory and immediately frozen and freeze-dried. Tissue samples for phlorotannin analyses were ground to a fine powder, placed in aqueous acetone and shaken under nitrogen in the dark at 4°C for 24 h. After extraction, the samples were centrifuged, evaporated in vacuo at less than 40°C to a small aqueous volume, filtered to remove precipitated lipophilic material, and diluted to a defined volume. Phlorotannins were quantified colorimetrically using the Folin-Ciocalteus method (Van Alstyne 1995). Phloroglucinol (1,3,5-trihydroxybenzene, art. 7069; Merck, Darmstadt, Germany) was used as a standard.

Feeding preference experiments

Feeding preference of three herbivore species, the isopod *Idotea granulosa* Rathke and the littorinid gastropods *Littorina obtusata* L. and *L. littorea* L., was tested in Sweden during June 2003. Two of these species (*I. granulosa* and *L. obtusata*) are also present in Iceland and were tested in separate experiments in Iceland during July 2003. The herbivore species were chosen because they are known to feed on fucoid seaweeds (Watson and Norton 1985, 1987; Pavia et al. 1999) and they were found in high abundance on the seaweeds in the field studies. In each experiment, the herbivore was presented with all possible pairs of *F. evanescens*, *F. vesiculosus* and *A. nodosum* collected in the same region.

Animals used in the experiments were collected from mixed stands of the fucoids 1–7 days before initiation of the experiments. The animals were collected from sites where all three fucoids were present, except for *I. granulosa* in Sweden which was collected from turfs of red algae. Prior to the experiment, the animals were kept in aquaria with through-flowing water (Sweden) or daily water exchange (Iceland) and fed with fronds of all species tested in the experiments. Algae were collected at two sites in each region (S2 and S3 in Sweden and I1 and I2 in Iceland) within 36 h prior to the start of the experiment. The fronds from the two sites within a region were mixed and kept immersed until the start of the experiments.

From each algal frond, two adjacent, similar-sized shoots (0.5 ± 0.1 g wet weight) without visible grazing damage were cut off. The wet weight of each shoot was determined after gently drying the fronds with soft paper. One shoot from each plant was presented to the grazer and the other one was used as control for autogenic changes during the course of the experiment. Shoots from different species were then paired, producing three species pairs (*F. evanescens* vs *F. vesiculosus*, *F. evanescens* vs *A. nodosum* and *F. vesiculosus* vs *A. nodosum*) that were replicated ten times, with corresponding controls without herbivores.

In Sweden, the experiments were set up outdoors in 200-ml bottles with through-flowing filtered seawater ($+10$°C, 31‰S) under ambient light (day length 18 h). In Iceland, the experiments were performed in the laboratory, in 365-ml bottles with daily change of water ($+10$°C, 32‰S) at 14 h photoperiod. In the *Littorina* experiments, five adult individuals (shell height: *L. obtusata* 12–15 mm, *L. littorea* 15–20 mm) were added to each bottle. In the *I. granulosa* experiments, 5–6 individuals (length 14–31 mm) were placed in each bottle, ensuring approximately the same size distribution in each bottle. The herbivores were allowed to graze for 3–4 days, after which the wet weight of the algae was measured as before.

Statistical analyses

Since the two regions differ in a number of environmental factors, we do not attempt to interpret the absolute within-species differences in herbivore community or phlorotannin concentration between the two regions, but restrict our analysis to within-region comparisons. The number of herbivore taxa, abundance of herbivores, and phlorotannin concentration in the seaweed species in each region was analyzed with 2-way ANOVAs with species as a fixed and site as a random factor. Homogeneity of variances was tested with Cochran's test and the data were transformed when required. When ANOVAs showed a significant effect of species, among-species differences were further explored with Tukey's post hoc test. Analysis of the preference experiments was done according to the method suggested by Peterson and Renaud (1989) for proper use of controls in feeding preference experiments. For each experimental bottle, the difference in weight change between the two seaweed species was calculated. Then the between-algae difference in containers with herbivores was compared with the difference in control bottles. In most comparisons, the variances were much higher in the herbivore treatment compared to the controls, violating the assumption of variance homogeneity necessary for parametric statistics. This is a problem inherent to the method, since the presence of grazers tends to increase the variance. To avoid the risk of excessive Type I error, the difference in between-algae differences was analyzed using sign test. Sign tests consider only the direction of difference between samples and thus tests the consistency of food preference instead of difference in the amount of seaweed tissue consumed.

Results

In Sweden, 21 taxa were found on the seaweed species, of which 14 were herbivores (Table 1). Corresponding numbers in Iceland were 13 taxa, of which 11 were herbivores. Both in Sweden and Iceland, the most abundant herbivores were *Littorina* spp., *I. granulosa* and amphipods (mainly *Gammarus* spp. in Sweden and *Hyale nilssoni* in Iceland). In Sweden, the herbivore community on the invading *F. evanescens* was clearly less taxon rich when compared to the native seaweed species; only 5 of the 14 herbivore taxa were found on *F. evanescens* while the number of taxa varied little between the native species (Fig. 1a). The average number of herbivore taxa per individual plant was also lower on *F. evanescens* compared to the other species (Table 2, Fig. 1a). In contrast, the herbivore community in Iceland was very similar between the seaweed species and there were no differences in average number of taxa on individual plants. The significant species × site interaction in Iceland was due to exceptionally low taxon richness on *A. nodosum* at one site. *L. obtusata* and *I. granulosa* were both absent from *F. evanescens* in Sweden but not in Iceland. The abundance of herbivores showed the same pattern as taxon richness, it was lower on *F. evanescens* compared to the native species in Sweden but did not differ between species in Iceland (Table 2, Fig. 1b).

The pattern of phlorotannin concentration also differed between the regions (Table 3, Fig. 2). In Sweden, *F. evanescens* had significantly higher phlorotannin concentration than *A. nodosum* at all sites and higher than *F. vesiculosus* at one of the sites. The opposite pattern was found in Iceland, where *F. evanescens* had lower phlorotannin concentration compared to *F. vesiculosus* and *A. nodosum* at all sites.

The feeding preference experiments showed that the preference pattern differed markedly between the Swedish and Icelandic grazers. In Sweden, the invader *F. evanescens* was less preferred than the native species in all comparisons (Fig. 3). Among the native fucoids there was no clear preference pattern, except that *L. littorea* showed less preference for *F. vesiculosus* when compared to *A. nodosum*. In Iceland, on the other hand, *F. evanescens* was preferred by both *L. obtusata* (compared to *F. vesiculosus* and *A. nododsum*) and *I. granulosa* (compared to *A. nodosum*).

Discussion

Lower enemy attack on introduced plant populations has previously only been documented from terrestrial systems. A number of biogeographical comparisons of native and introduced populations of a certain plant species suggest that introduced populations often experience a lower level of enemy attack (review in Coulatti et al. 2004). While such studies provide a good starting point to evaluate the enemy release hypothesis, simultaneous community studies that compare enemy effects between invaders and native, co-occurring species are required to show that the low enemy impact can potentially translate into a competitive advantage to the invader. Previous community studies of enemy effects on introduced and native species have only been performed in the new range of invaders (Coulatti et al. 2004, and references therein). By combining the 'biogeographical' and 'community' approaches, our study allow comparison of enemy attack on *F. evanescens* and its co-occurring competitors in both the new and native region.

As predicted by the enemy release hypothesis, the results of our study suggest that the introduced *F. evanescens* is less affected by herbivores in the new compared to the native range. While native *F. evanescens* was inhabited by a diverse herbivore community, similar to that of co-existing species, introduced populations hosted an impoverished fauna compared to the native competitors in Sweden. Similarly, all investigated herbivores showed low preference for *F. evanescens* in the

Table 1 List of mobile animal taxa found on seaweeds in Sweden and Iceland, their mean abundance per 100 g dry weight of *Fucus evanescens* (*Fe*), *F. serratus* (*Fs*), *F. vesiculosus* (*Fv*) and *Ascophyllum nodosum* (*An*), and their feeding habit

	Feeding habit	Sweden			Iceland		
		Fe	Fv	An	Fe	Fv	An
Gastropoda							
Ansates pellucida L.	H^{a}				0.1		
Littorina littorea L.	H^{a}	21.9	27.5	13.0			
L. obtusata L.	H^{a}		2.8	1.3	32.4	25.6	5.7
L. fabalis Turton	H^{a}	3.2	5.9	2.1	6.3	5.7	1.1
L. saxatilis Olivi	H^{a}				0.4	0.4	0.2
Lacuna vincta Montagu	H^{a}			0.1	0.1	0.3	
L. pallidula Da Costa	H^{a}				0.1		
Bittium reticulatum Da Costa	O^{a}			0.6			
Nucella lapillus L.	P					0.2	0.1
Isopoda							
Idotea granulosa Rathke	H^{a}		2.7	5.5	12.5	19.9	63.5
Jaera sp.	H^{a}		4.3	2.5	0.8	3.0	0.7
Amphipoda							
Hyale nilssoni Rathke	H^{a}		0.2		2.9	6.9	5.2
Gammarus sp.	H^{a}	1.2	12.6	13.1	0.3	0.8	0.7
Microdeutopus gryllotalpa Costa	D	0.5	0.4	0.3			
Corophium sp.	D		2.9	4.6			
Apherusa bispinosa Bate	D			0.1			
Calliopius laeviusculus Kroyer	O^{a}	0.7	10.7	9.1			
Jassa falcata Montagu	O^{a}		1.3	3.2			
Ericthonius sp.	O^{a}	0.8	3.8	2.4			
Stenothoidae	O^{a}		0.4	0.2			
Decapoda							
Carcinus maenas L.	P			0.4			
Palaemon elegans Rathke	P			0.1			
Insecta							
Chironomidae	H^{a}		6.7	5.2	11.4	26.0	3.7
Polychaeta							
Nereidae	P		0.2	0.2			
Oligochaeta	D^{b}				2.2	8.8	8.2
Asteroidea							
Asterias rubens L.	P		1.1	1.5			
Total no of herbivore taxa		5	12	13	11	9	8

Abundance data are means of 12 plants from three sites in each region

H Herbivore; *O* omnivore; *D* detritivore; *P* predator

[a] Species included in the statistical analyses

[b] Some taxa may consume microalgae

new range, while it was a preferred food choice in the native community. We only studied herbivory in one native and one introduced region of *F. evanescens*, but a number of studies in other native regions have shown that the species is often heavily grazed (e.g., Van Alstyne 1990; Worm and Chapman 1998) and is ranked high in the preference hierarchy for both periwinkles (Barker and Chapman 1990) and amphipods (Denton and Chapman 1991). Contrastingly, in the only previous study of herbivory on introduced *F. evanescens* (in western Baltic Sea), the herbivorous isopod, *Idotea baltica*, showed low preference for the invader compared to the co-occurring *F. vesiculosus* (Schaffelke et al. 1995). The fact that clear avoidance of *F. evanescens* is only seen in areas where the species has been introduced suggests that, in this particular species, introduced populations are generally less impacted by herbivores than populations in the area of origin.

Although our results seem to support the ERH, they are difficult to frame within the classical theory of enemy release, which predicts that low enemy impact is explained by the loss of specialized feeders or pathogens in the new range. The herbivore communities in both Sweden and Iceland were mainly composed of generalist feeders. Furthermore, the species composition of herbivores was similar across regions; almost 50% of the herbivores found in the samples were common to both regions. This reflects a general pattern in marine herbivore communities, which are dominated by generalists with widespread geographic distributions (Hay and Steinberg 1992). The herbivore species included in the preference experiments are all relatively general in their food choice, although *L. obtusata* feeds preferably on species of the Fucaceae family (Watson and Norton 1987; Reid 1996). Thus, *F. evanescens* escapes to some extent from attack by generalist herbivores in its new range, which is even more intriguing given that two of the tested herbivore species were also present in the native region and readily consumed the seaweed there.

Instead of release from specialized enemies, the results from the phlorotannin analyses suggest that the low herbivore preference for introduced *F. evanescens* is due to higher resistance to herbivory in invading compared to native populations. The comparison of phlorotannin concentrations between the fucoids showed that while native *F. evanescens* populations had considerably lower phlorotannin concentrations compared to the other species, populations in the new range had, instead, higher concentrations compared to *A. nodosum* and, in one site, to *F. vesiculosus*. We did not experimentally evaluate the

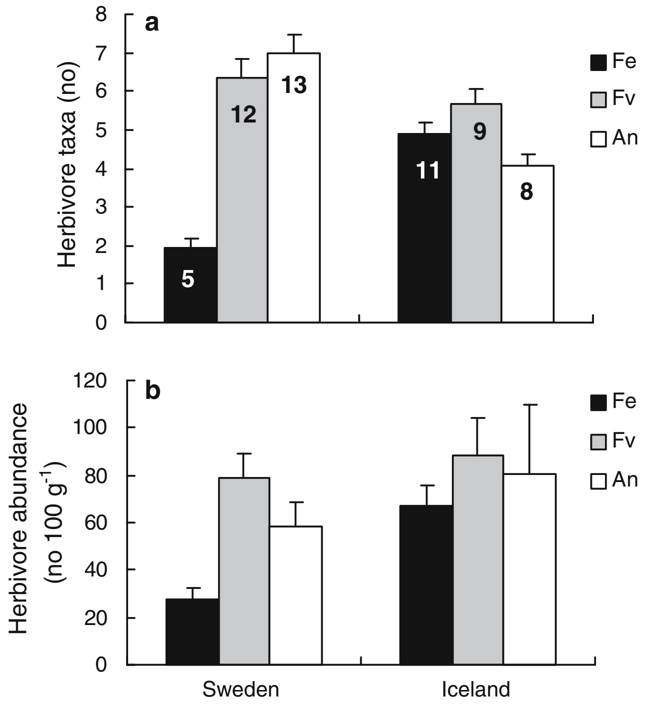

Fig. 1 Herbivore taxon richness on single plants (**a**) and herbivore abundance per 100 g dry weight (**b**) on *Fucus evanescens* (*Fe*), *F. vesiculosus* (*Fv*) and *Ascophyllum nodosum* (*An*) in Sweden and Iceland. *Error bars* show +SE ($n = 12$). *Numbers* within bars show the total number of herbivore taxa found on the species in that region

specific effect of phlorotannins for food choice in the investigated herbivores, but the importance of phlorotannins as anti-herbivore defense is suggested by several studies documenting a negative correlation between phlorotannin concentration and herbivore preference (e.g., Van Alstyne 1988; Yates and Peckol 1993; Pavia and Toth 2000), as well as performance (Toth et al. 2005). Furthermore, both *L. littorea* (Geiselman and McConnell 1981) and *L. obtusata* (Pavia and Toth 2000) have earlier been shown to be deterred specifically by high phlorotannin concentrations in feeding preference assays with food where the phlorotannin content was experimentally manipulated. Comparison of the results from the phlorotannin analyses and the assessments of grazing pressure in our study also showed that, in both Sweden and Iceland, the species with the highest phlorotannin concentrations tended to be least utilized by herbivores in the field and were avoided in the laboratory preference experiments.

The higher level of defense in introduced *F. evanescens* is opposite to the pattern predicted by the EICA, i.e., that enemy release allows introduced species to allocate less resources to defense (Blossey and Nötzold 1995). This may reflect a fundamental difference between systems depending on the importance of specialized enemies (Müller-Schärer et al. 2004). Both the ERH and the EICA logically rest on the assumption that resident enemies will have a greater impact on native competitors than on exotic invaders. As pointed out by Keane and Crawley (2002), there are no obvious logical reasons or strong empirical evidence to support the assumption that generalist enemies, which by definition are prone to host switching and/or diet mixing, should be better adapted to attack native species than to attack invading exotics. On the contrary, it could be argued that in regions where generalists dominate and exert a strong selection pressure, it is likely that native species have evolved effective defenses and/or tolerance against co-existing generalist enemies, and that potential invaders commonly will experience enemy accumulation rather than enemy release (Coulatti et al. 2004). Empirical evidence for selective attack of exotic plants comes from a recent preference study, including a diverse group of generalist herbivores from terrestrial and freshwater systems (Parker and Hay 2005), and numerous studies have shown that generalist consumers can limit the establishment and spread of exotic plants in a variety of systems (reviewed by Maron and Vilà 2001; Keane and Crawley 2002). Given this, generalist herbivores can be predicted to instead select for well-defended exotic species or genotypes.

We do not know the reason for the high defense level, relative to confamiliar competitors, in introduced compared to native populations of *F. evanescens*. Apart from

Table 2 Two-way ANOVA of the number of herbivore taxa and abundance of herbivores on different seaweed species (*Sp*; fixed) and sites (*Si*; random) in Sweden and Iceland

	df	Taxon richness						Abundance					
		Sweden			Iceland			Sweden			Iceland		
		MS	*F*	*P*	MS	*F*	*P*	MS	*F*	*P*	MS	*F*	*P*
Sp	2	91.583	54.950	**0.001**	6.083	2.147	0.233	39.575	8.003	**0.040**	7.188	1.347	0.357
Si	2	9.083	5.480	**0.010**	3.250	4.179	**0.026**	7.675	2.362	0.113	33.688	2.872	0.074
Sp × Si	4	1.667	1.006	0.422	2.833	3.643	**0.017**	4.945	1.522	0.224	5.336	0.455	0.768
Error	27	1.657			0.778			3.249			11.728		
Post hoc		Fe < Fv = An						Fe < Fv = An					

P-values in bold indicate significant effects ($P < 0.05$). Abundance data were square-root transformed to meet the assumption of variance homogeneity. Significant between-species differences according to Tukey's post hoc test ($\alpha = 0.05$) are given
Fe Fucus evanescens, *Fv F. vesiculosus*, *An Ascophyllum nodosum*

Table 3 Two-way ANOVA of the phlorotannin concentration in different seaweed species (fixed) and sites (random) in Sweden and Iceland

	df	Sweden			Iceland		
		MS	*F*	*P*	MS	*F*	*P*
Species (Sp)	2	59.473	12.390	**0.019**	94.650	14.985	**0.014**
Site (Si)	2	1.133	3.166	**0.047**	32.788	78.889	**0.000**
Sp × Si	4	4.800	13.417	**0.000**	6.316	15.197	**0.000**
Error	81	0.358			0.416		
Post hoc		Site 1: An < Fv < Fe Site 2 & 3: An < Fv = Fe			Site 1 & 2: Fe < Fv = An Site 3: Fe < An < Fv		

Data were square-root transformed to meet the assumption of variance homogeneity. *P*-values in bold indicate significant effects ($P < 0.05$). Significant between-species differences according to Tukey's post hoc test ($\alpha = 0.05$) are given

Fe Fucus evanescens, *Fv F. vesiculosus*, *An Ascophyllum nodosum*

their role as anti-herbivore defense, phlorotannins have been documented to have other functions in UV-protection (Pavia et al. 1997), fouling inhibition (Lau and Qian 1997; Wikström and Pavia 2004), and wound-healing processes (Lüder and Clayton 2004). Furthermore, phlorotannin content is a plastic trait that can be influenced by several external biotic and abiotic factors (Amsler and Fairhead 2006). Differences in external factors between Iceland and Sweden, for instance the lack of tide on the Swedish coast, could potentially drive differences in phlorotannin production, although this should most likely be reflected in native as well as exotic fucoid species. From our results, we cannot rule out that other factors than herbivory are involved in creating the observed pattern of phlorotannin concentrations, but we conclude that the pattern is concordant with the prediction that well-defended exotics are most likely to become successful invaders in systems where generalist consumers exert a significant selection pressure. Similarly, introduced populations of the highly invasive green alga, *Caulerpa taxifolia*, was shown to contain high levels of defensive secondary metabolites compared to native strains and to be avoided by important herbivores, which has been invoked to explain its large invasion success in the Mediterranean (Amade and Lemée 1998). A recent study of the noxious terrestrial weed, *Senecio jacobaea*, also showed that introduced

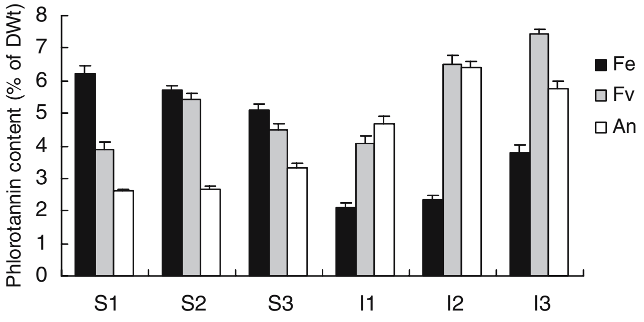

Fig. 2 Phlorotannin concentration (percent of dry weight) in plants of *Fucus evanescens* (*Fe*), *F. vesiculosus* (*Fv*) and *Ascophyllum nodosum* (*An*) in Sweden (*S1–3*) and Iceland (*I1–3*). *Error bars* show +SE ($n = 10$)

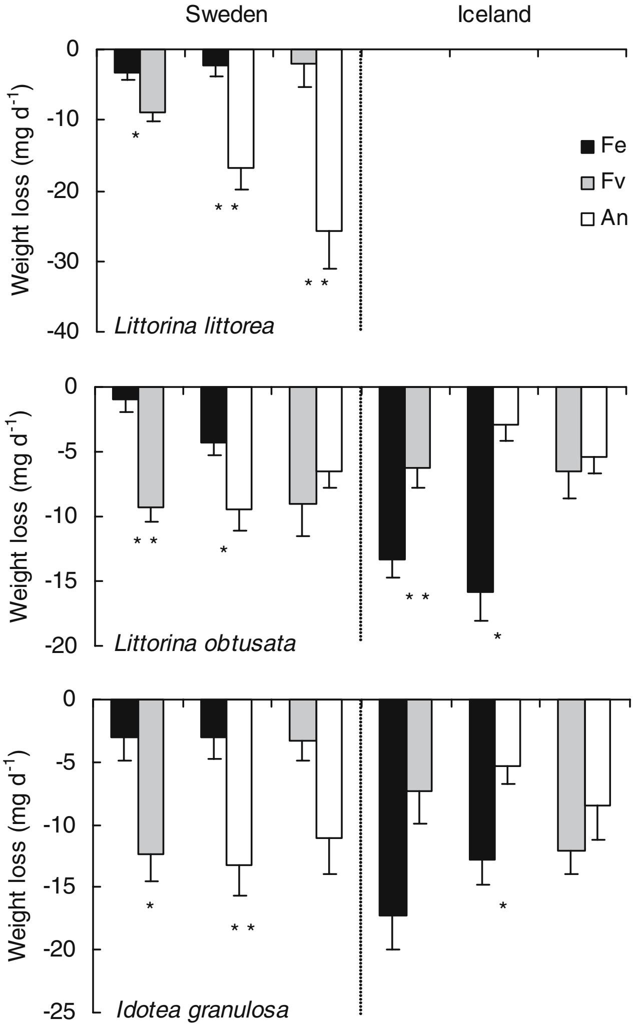

Fig. 3 Weight change (mg dry weight per day) of Swedish and Icelandic *Fucus evanescens* (*Fe*), *F. vesiculosus* (*Fv*) and *Ascophyllum nodosum* (*An*) in pair-wise choice experiments with *Littorina littorea*, *L. obtusata* and *Idotea granulosa* from the same geographical region. The value is obtained by subtracting weight change in the grazed fronds from that of the corresponding controls. Significant differences in between-alga difference between containers with and without herbivores according to sign test are indicated ($*P < 0.05$; $**P < 0.01$). *Error bars* show +SE ($n = 10$). Note the different scaling on the *y*-axes

populations have higher levels of so-called qualitative defenses against generalist herbivores than native populations (Joshi and Vrieling 2005), further supporting the hypothesis that generalists can select for increased resistance to herbivory in exotic plants. However, more tests of this hypothesis in different systems are clearly required in order to provide a general understanding of the impact of generalist herbivores on allocation to defense in plant invaders.

The effect of herbivores on introduced plant species has so far mostly been discussed in the context of specialist herbivores and the consequences of enemy release (e.g., Elton 1958; Keane and Crawley 2002; Coulatti et al. 2004). In contrast to many terrestrial examples of reduced enemy attack in the new range, our results indicate that the low herbivore preference for introduced *F. evanescens* cannot be explained by the loss of specialized feeders in the new range, but more likely by an increased resistance to herbivory, due to higher chemical defense levels. This stresses the importance of incorporating effects of generalist herbivores in explanatory models as well as empirical studies of the effects of natural enemies on introduced species. Given the large impact of generalist herbivores on community structure in many systems (see Parker and Hay 2005), a better understanding of their effect on exotic plant species is critical in predicting the fate and effects of plant invaders.

Acknowledgements We thank G. Cervin and M. Karlsson for help with phlorotannin analyses, O. Eriksson, J. Ehrlén and two anonymous reviewers for comments on the manuscript and the staff at Tjärnö Marine Biological Laboratory and Sandgerði Marine Centre for hospitality and practical assistance. MBS wish to thank Agnar Ingólfsson for his valuable support. Financial support was provided by the Swedish Environmental Protection Agency, the Swedish Research council through contracts 621-2002-289 and 621-2004-2658, the European Union through the European Regional Development Fund (Objective 2 West Sweden), the Icelandic Centre for Research (Rannís) and Stockholm Marine Research Centre. All experiments complied with the laws of Sweden and Iceland.

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