

Effects of non-native *Spartina patens* on plant and sediment organic matter carbon incorporation into the local invertebrate community

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Abstract The cycling of organic matter through food webs is a fundamental process that may be altered by the invasion of non-indigenous plants. We explored consequences of the invasion of non-indigenous *Spartina patens* to the composition of soil organic matter (SOM) and to detritivore and herbivore diets in the upper salt marsh within Corrubedo National Park, northwest Spain. We tested for the incorporation of *S. patens* carbon (C) into SOM and by detritivores and herbivores using stable isotope analysis, focusing primarily on detritivorous enchytraeid oligochaetes and herbivorous insects. Stable isotope results indicated that C derived from *S. patens* has been incorporated into SOM. Elevated densities of enchytraeids in stands of *S. patens*, and their incorporation of C derived from this plant, suggested that dense patches of *S. patens* may facilitate detritivore populations. In contrast, although insect herbivores used *S. patens* as habitat, there was little isotopic evidence for the widespread incorporation of *S. patens*-derived C by these consumers. The population and dietary response of enchytraeids to *S. patens* suggests that *S. patens* invasion could indirectly

influence soil processes and pathways mediated by detritivore activity (e.g., soil respiration rates, nutrient retention and transformation, energy flow). The loss of food resources to insect herbivores alters local food webs. However, insect herbivores may move and feed on native plants elsewhere. As a result, insect populations may be less immediately impacted than soil detritivore populations by *S. patens*. Our study suggests that the influences of *S. patens* invasion extend beyond the more obvious changes in native plant abundance, to include differing responses in the cycling of organic matter between detritivore and insect herbivore food web pathways.

Keywords Invasive *Spartina* · Detritus · Salt marsh · Food web · Sap-feeding · Insect · Oligochaete

Introduction

Invasions of exotic plants have been identified as significant threats to native biodiversity and ecosystem functioning world-wide (e.g., Hobbs and Huenneke 1992; Cronk and Fuller 1995; Vitousek et al. 1996; Mack et al. 2000; Simberloff 2005), and coastal wetland ecosystems are dramatically impacted by these invasions (Chambers et al. 1999; Talley and Levin 2001; Ayres et al. 2004; Gratton and Denno 2006). Among the more successful invaders of coastal wetlands are grasses of the genus *Spartina* (e.g., *Spartina alterniflora*, *S. anglica*, *S. densifolia*) that

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have been introduced and successfully spread over large geographical areas, in some cases hybridizing with native *Spartina* species (Callaway and Josselyn 1992; Castillo et al. 2000; Nieva et al. 2001; Ayres et al. 2004; Zhang et al. 2004; Nehring and Hesse 2008; Renny-Byfield et al. 2010).

The impact of *Spartina* invasions on low intertidal and non-vegetated mudflat habitat has received considerable attention recently (e.g., Dethier and Hacker 2005; Neira et al. 2005; Cheng et al. 2006; Levin et al. 2006; Wu et al. 2009). However, there remains a paucity of information on the ecological effects of *Spartina* invasions on the upper salt marsh-transition habitat although there is reason to believe that such effects may be appreciable. For example, non-indigenous *Spartina* have been inferred to out-compete native plants in the upper intertidal (summary in Daehler and Strong 1996; SanLeón et al. 1999), and shown to alter soil properties (Neira et al. 2006; Cheng et al. 2006), and benthic invertebrate community structure and trophic relationships in the lower intertidal (Neira et al. 2005; Levin et al. 2006; Chen et al. 2007).

Spartina patens (salt marsh hay, salt meadow cordgrass), native to the Atlantic and Gulf coasts of North America, is an invader of upper marsh habitat that has been introduced to the Pacific coasts of Canada (British Columbia) and the United States (Washington, Oregon, California), and to the Mediterranean (Callaway and Josselyn 1992; Frenkel and Boss 1988; Ayres et al. 2004). *S. patens* has also invaded the salt marshes of the northern Iberian Peninsula (e.g., Galicia, Spain) where it can be found in nearly monospecific stands in the upper high marsh (SanLeón et al. 1999).

The invasion history of *Spartina patens* on the Atlantic coast of Europe is ambiguous, but it has likely been present for many decades, perhaps originally introduced as packing material in shipping boxes and crates at ports in the Mediterranean in the nineteenth century and then spreading up the Iberian Peninsula (SanLeón et al. 1999 and references therein). In its native range, this plant is typically found above mean high water (MHW) (Blum 1968; Redfield 1972), a pattern related to a lower tolerance of anoxic soils in the lower intertidal (Bertness 1991).

Among the ecological functions of coastal wetlands that could be affected by the invasion of *Spartina patens* are the provision of habitat and

trophic support. Plants provide habitat via vertical and horizontal above and belowground structure and trophic support through the production of organic matter that is used by detritivores (e.g., leaf litter, roots, associated microbes) and by herbivores (plant sap, living leaves). Non-indigenous plants can differ from native species in rates of litter production, chemical composition, and palatability, attributes that may alter trophic structure and food web interactions through their effects on detrital (decomposer) and grazer (herbivore) pathways (Moore et al. 2004).

The upper marsh receives only occasional inundation, thus vascular plants rather than phytoplankton or benthic micro- and macroalgae most likely comprise the main source of primary production used by detritivores and herbivores in this habitat. The processing of organic matter by decomposers is considered the principle pathway of organic matter re-cycling (reviewed in Moore et al. 2004). Since *Spartina patens* occurs in thick monotypic stands (SanLeón et al. 1999; this study) that may accumulate litter at a faster rate than adjacent marsh vegetation (Frenkel and Boss 1988), we predicted that organic matter from this plant has altered the composition of SOM and the source of production used by soil detritivores in invaded habitat.

Some fraction of living plant production is also consumed by herbivores. A guild of herbivorous insects, primarily sap-feeding members of the Order Hemiptera is associated with living *Spartina patens* in its native habitat (Davis and Gray 1966; Raupp and Denno 1979; Denno 1980). These herbivores can attain high densities, tend to be plant host-specific, and support a food web that includes predaceous spiders and mirid bugs (Raupp and Denno 1979). However, less herbivory may occur on *S. patens* in invaded habitat if insect herbivores that would normally feed on this plant within its native range are absent. Little information is available on the use of non-indigenous *Spartina* by native insect herbivores (reviewed by Maron and Vilà 2001; but see Wu et al. 2009).

In this study, we explored the consequences of the *Spartina patens* invasion to the composition of soil organic matter (SOM) and to detritivore and herbivore diet at salt marsh sites in Corrubedo National Park, Galicia, northwest Spain. Specifically, we investigated the hypothesis that detritivores and insect herbivores vary in their use of *S. patens*, with organic matter from this source incorporated into marsh soil

and infaunal detritivores, but not herbivorous insects. We tested for the use of *S. patens* derived C by detritivores and herbivores using stable isotope analysis, focusing primarily on representative “indicator” taxa—detritivorous enchytraeid oligochaetes (Annelida) and herbivorous insects of the Orders Hemiptera (Homoptera) and Orthoptera. Enchytraeids are thought to influence biogeochemical cycling in sediments through their tunneling and feeding activities (van Vliet et al. 2004). Herbivorous insects can feed extensively on and adversely influence *S. patens* in its native habitat (Denno 1980).

Stable isotope analysis has been widely used to evaluate the contribution of C₃ versus C₄ plant-derived carbon to SOM (e.g., Boutton 1996; Cheng et al. 2006), and to the diets of soil detritivores (Martin et al. 1992; Briones and Schmidt 2004) and herbivorous arthropods (Fry et al. 1978; Petelle et al. 1979; Gratton and Denno 2006; Wu et al. 2009). Because isotopic differences between C₃ and C₄ plants are large (typically at least 10‰, reviewed in Fry 2006), we predicted that SOM in the *Spartina* zone would be ¹³C-enriched compared to SOM associated with native C₃ plants. The use of *Spartina*-derived C by detritivores and herbivores should also be evident by ¹³C-enriched signatures of these organisms sampled from patches of *S. patens* compared to those associated with the native C₃ plants.

Materials and methods

Study site

We conducted this study within the ~1 km² area tidal wetland of the Corrubedo National Park located in Galicia, NW Spain (42°34'20"N, 9°2'6"W; Fig. 1). *Spartina patens* is widely distributed in the upper high marsh within the Park (SanLeón et al. 1999). To test for the incorporation of *S. patens* detritus into the soil organic matter pool and use by detritivores and herbivores, we sampled three sites that differed in the cover of *S. patens* and two native plants (*Limonium dodartii* and *Juncus maritimus*). One site (A) possessed three distinct vegetation zones dominated by *L. dodartii*, *S. patens*, and *J. maritimus*, from higher to lower elevation, respectively. The second site (B), located approximately 150 m to the north of site A possessed well-delineated zones of *S. patens* and

J. maritimus, but lacked the *L. dodartii* zone. The last site (C), 80 m to the south of site A, possessed *L. dodartii* and *J. maritimus*, but lacked the *S. patens* zone.

Differences in the distribution and cover of these plant species was related, at least in part, to the elevation and topography of the marsh plain (unpublished data, Sánchez et al. 1996). The lower limit of *Juncus maritimus* corresponded approximately with mean high water (~+3 m relative to the most extreme low water spring tide, ELWS), whereas the lower limit of *Spartina patens* corresponded approximately with mean high water spring tides (~+3.5 m ELWS) (personal observation). Although *Limonium dodartii*, *S. patens*, and *J. maritimus* comprised collectively the highest cover of plants on the marsh plain, other species were present, including sparse cover of the native C₃ grass *Festuca rubra* subsp. *littoralis* at the upper elevations of site C, and the native C₃ plants *Sarcocornia perennis*, *L. vulgare*, *Halimione portulacoides*, and *Inula crithmoides* at lower elevations at all sites.

Vegetation characteristics and soil properties

We estimated the species composition and cover of vegetation at each site along transect lines that extended perpendicular to the water line in May 2008. Species and cover were recorded within a 50 × 50 cm quadrat spaced at 2 m intervals along the transect. At sites A and B, data were recorded from three transects located 3–5 m apart; one transect only was sampled at site C. The quadrat was divided into 100 squares and percent cover for a given species (or bare space) was estimated visually by counting the number of squares occupied by 50% or greater of that species. Relative change in elevation of the marsh plain was also measured at 2 m intervals at each site using a transit level.

The percentage of C and N in the SOM at all sites was determined at the same time that soil samples were analyzed for stable C and N isotopes (see below). We also sampled soil at sites A and B (see below) to determine grain size characteristics within the discrete vegetation zones. Soil samples were wet sieved on an analytical sieve shaker (Retsch AS-200) and categorized in terms of percentage composition of silt–clay (<63 μ) and sand (≥63 μ) (Wentworth 1922).

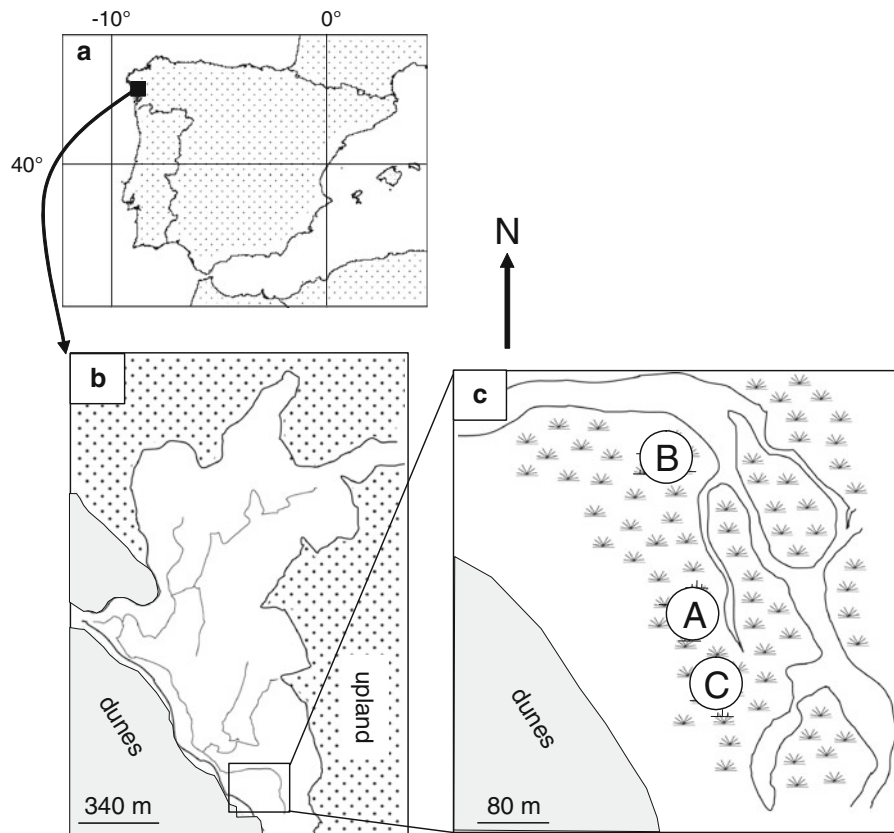


Fig. 1 Location of **a** Corrubedo National Park on the Iberian Peninsula, **b** the study area within the Corrubedo wetlands, and **c** the study sites

Sampling and processing of plants, soil and enchytraeids

To determine the isotope values of the dominant marsh plants, we collected samples on 21–28 May 2008 of *Limonium dodartii*, *L. vulgare*, and *Spartina patens*. We also collected samples of less abundant species, including *Sarcocornia perennis*, *Halimione portulacoides*, and *Festuca rubra* subsp. *littoralis*, and, from site B, samples of filamentous green algae that were sparsely distributed at the lower elevations of this site. Live leaf tissue was collected from several plants and composited to form one sample. At least three samples were collected of the dominant plant species (one from each site). Plant and algae samples were rinsed in de-ionized water, dried at 65°C for 24–48 h, and ground using a ball mill (Pulverisette 2, Fritsch) in preparation for isotope analysis.

To determine the isotopic composition of SOM, and the density and isotopic composition of enchytraeids,

soil cores were taken to a depth of 5 cm along one transect line within each site in May 2008. Samples were collected in 4 or 5 paired 7 cm diameter cores spaced equally within each of the *Limonium*, *Spartina*, and *Juncus* vegetation zones (if present, see above). Enchytraeid oligochaetes were separated from the soil using a modified wet funnel extraction (O'Connor 1955), counted, and freeze-dried in preparation for isotope analysis. The biomass of worms in individual core samples collected from the *Limonium* zone was not sufficient for isotope analysis. Consequently, all samples taken within this zone (sites A and C) were pooled for analysis ($n = 1$ from each site).

A subsample of soil from the core taken from 2 to 5 cm depth was dried, sieved through 1 mm mesh to remove root and other debris, and inspected under a dissecting microscope, where any obvious remaining root material was removed. The soil sample was then treated with 10% HCl to remove carbonates, re-dried, and ground using a mortar and pestle.

Sampling and processing of arthropods

To determine the relative abundance of herbivorous insect taxa and to sample insect herbivores and spiders for isotope analysis within each vegetation zone, we conducted net sweeps using a 50 cm diameter insect net while walking through the vegetation at each site (e.g., Denno 1977, 1980). Twenty to and fro net sweep samples were taken at mid-day along three longitudinal transects within each vegetation zone at each site such that the upper portion of the vegetation was hit by the net. These data provide a comparative “snapshot” of insect use of the three vegetation zones, but a more comprehensive sampling program, including vacuum sampling to better sample insects within the lower strata of vegetation, and temporal replication would be necessary to compare actual insect densities among zones.

Whenever possible, isotope analyses were performed on triplicate samples of insects or spiders collected in the net sweeps. Three individual plant-hoppers or leafhoppers were pooled to produce one sample for analysis. Individual grasshoppers and spiders were processed for analysis. Insect and spider samples were dried as above and gently crushed in a mortar and pestle prior to isotope analysis.

Isotope analyses

Isotope analyses of the soil, plant, and arthropod samples were conducted at the Servicios de Apoyo a Investigacion (SAI), University of A Coruña. Samples were analyzed using a ThermoFinnigan Flash EA 1112 elemental analyzer (Thermo Electron Corporation, Bremen, Germany) coupled with a Finnigan Delta Plus isotope ratio mass spectrometer (IRMS). Enchytraeid worms were analyzed at the Macaulay Land Use Research Institute (Craigiebuckler, Aberdeen, Scotland) using a Flash EA 1112 elemental analyzer coupled with a Delta Plus IRMS. Isotope values for carbon and nitrogen were calculated as: $\delta^X = (R_{\text{sample}} / R_{\text{standard}} - 1) \times 1,000$, where $X = \text{C}$ (carbon) or N (nitrogen) and $R = {}^{13}\text{C}/{}^{12}\text{C}$ for C and ${}^{15}\text{N}/{}^{14}\text{N}$ for N. Values are reported per mil (‰) relative to the PDB standard for C and atmospheric N_2 for N; analytical precision for C and N isotope values from both laboratories was $\pm 0.2\%$.

Data analysis

Analysis of covariance (ANCOVA) was used to test for significant differences in $\delta^{13}\text{C}$ and $\delta^{15}\text{N}$ values of SOM and enchytraeid oligochaetes, and enchytraeid densities among sites as a function of cover of *Spartina patens*. Site was treated as a categorical variable and cover of *S. patens* as a covariate. We evaluated the assumption of homogeneity of sample variances using Levine's (2003) test and $\log(x + 1)$ transformed data (enchytraeid densities) when this assumption was violated. Correlation and regression analysis was used to explore relationships between the isotope values of SOM and enchytraeids.

We made a coarse estimate of the contribution of $\text{C}_4\text{-C}$ (*Spartina patens*) to SOM in the *Spartina* vegetation zone using a two-source mixing model (method reviewed in Fry 2006; Cheng et al. 2006): $f = (\delta_{\text{SOM Mix}} - \delta_{\text{C}_3 \text{ SOM}}) / (\delta_{\text{Spartina}} - \delta_{\text{C}_3 \text{ SOM}})$, where f = the proportional contribution $\text{C}_4\text{-C}$ to SOM in the *Spartina* zone, $\delta_{\text{SOM Mix}} = \delta^{13}\text{C}$ value of SOM in *Spartina* zone, $\delta_{\text{C}_3 \text{ SOM}} = \delta^{13}\text{C}$ value of SOM in C_3 plant zones, and $\delta_{\text{Spartina}} = \delta^{13}\text{C}$ value of *Spartina patens*. Calculations of f and 95% confidence intervals around this value were made using Isoerror 1.04 (Phillips and Gregg 2001).

We made a similar assumption to that of Cheng et al. (2006) that the mean $\delta^{13}\text{C}$ value of SOM from the C_3 plant (in our case *Limonium*, *Juncus*) zones represented that of the SOM in the *Spartina* zone prior to invasion. This assumption was necessary because there is no “before” invasion data; however, it does not seem unreasonable since *Limonium* and *Juncus* overlap the elevational distribution of *S. patens* and were probably plant dominants in the *Spartina* zone prior to invasion. Among potential sources of error in estimates of the contribution of *Spartina* C to SOM are changes that may occur in the $\delta^{13}\text{C}$ value of plants during decomposition. These changes for the conspecific *Spartina alterniflora* have been reported to range from 0 during aerial decomposition (Ember et al. 1987; Currin et al. 1995) to ~ -1 – -2% for litter buried for over 1 year (Ember et al. 1987; Benner et al. 1987), with larger changes predicted to occur over time by modeling (Benner et al. 1987). *S. patens* occurs at higher tidal elevations than *S. alterniflora* and it is unknown to what extent these changes apply at our site. However, to explore the sensitivity of model output to variation in the value of *S. patens*, we

calculated the potential contribution of *Spartina* C to SOM under three scenarios that encompass reported or projected changes in this value during decomposition of *S. alterniflora*.

Results

Vegetation characteristics and soil properties

Spartina patens occurred in highest cover (to 95%) in a band of ~10 m in width above the zone dominated by *Juncus maritimus* at sites A and B, whereas it was absent from a similar elevation range at site C (between 0.0 and -0.2 m relative elevation, Fig. 2). *Limonium dodartii* occurred at the highest elevation in discontinuous patches that varied in width from ~7 to 10 m that were intermingled with bare space (to 48% cover at site A). This plant was absent at site B, where the upper elevation was covered with wrack consisting of dead vegetation (primarily *S. patens*). *J. maritimus* occurred in highest cover (to 95%) at lower elevations in a band that varied in width from ~10 m at site A to ~30 m at sites B and C. Other plants, notably *Halimione portulacoides* and *Sarcocornia perennis*, were present in a narrow band of a few meters in width below *J. maritimus* and adjacent to tidal creeks. The native *Spartina maritima*, which occurs at lower elevations within the Corrubedo wetlands, was not present in our study area.

Soil properties varied among vegetation zones with soil from the lower elevation *Juncus* zone containing a higher proportion of fine sediments (silt-clay), and having a higher organic C content than soil from the *Limonium* and *Spartina* zones (Table 1).

Distribution and densities of enchytraeid oligochaetes

Across all vegetation zones and sites, the density of enchytraeids was highly variable in individual samples, ranging from 259 to 55,873 m⁻². There was a significant site × *Spartina* interaction effect on mean enchytraeid densities ($P = 0.048$, $F_{1,30} = 4.244$, ANCOVA); therefore, densities among vegetation zones were compared within each site. The mean density of enchytraeids was significantly higher in the *Spartina* zone than other vegetation zones at site A ($P = 0.004$, $F_{2,12} = 8.838$). Mean enchytraeid

densities were not higher in the *Spartina* zone at site B ($P = 0.325$, $t = 1.049$, $df = 8$) where densities were highly variable among samples within this zone (range, 1,040–55,873 m⁻²) (Fig. 3). There was no difference in mean enchytraeid densities between the two vegetation zones (*Limonium*, *Juncus*) sampled at site C ($P = 0.279$, $t = 1.160$, $df = 8$). Overall, there was a trend of higher and more variable densities of enchytraeids in the *Spartina* than in the *Juncus* or *Limonium* zones (Fig. 3).

Insect herbivores

Flies (Diptera) and planthoppers and leafhoppers (Hemiptera) comprised >90% of insects captured in net sweeps within the *Spartina* ($n = 74$ insect specimens) and *Juncus* ($n = 155$) zones and 75% of insects captured within the *Limonium* zone ($n = 42$) (Fig. 4). The planthopper *Pentastiridius leporinus* (Hemiptera, Cixidae) was the most conspicuous herbivore comprising 55 and 25% of captured insects within the *Spartina* and *Juncus* zones, respectively. This is the first record of this species in Galicia, being reported previously from Aranjuez in central Spain and from Mallorca in the Balearic Archipelago, Mediterranean Sea (D. Aguín-Pombo, personal communication). A small percentage (1.4%) of insects captured in the *Spartina* and *Juncus* zones were grasshoppers (Orthoptera, Acrididae) and katydids (Orthoptera, Tettigoniidae); these taxa comprised a higher percentage (21%) of insects captured in the *Limonium* zone.

Isotopic composition of plants, soil organic matter and oligochaetes

As expected, mean $\delta^{13}\text{C}$ values of *Juncus maritimus* and *Limonium dodartii* (-26 to -25‰) were within the range expected for C₃ plants and distinct from the value for the C₄ grass, *Spartina patens* (-15.3‰; Table 2). The $\delta^{13}\text{C}$ value for filamentous green algae, which was present in low cover at site B, was intermediate between the values for C₃ and C₄ plants. $\delta^{15}\text{N}$ values were similar among *Juncus*, *Limonium*, and *Spartina* and filamentous green algae (-0.4–0.5‰; Table 2).

$\delta^{13}\text{C}$ values of SOM varied significantly with the cover of *Spartina patens* ($P < 0.003$, $F_{1,18} = 11.565$) and site ($P = 0.022$, $F_{2,18} = 4.776$, ANCOVA).

Fig. 2 Percent cover of the most abundant plant species, bare space, and filamentous green macroalgae as a function of distance along transect lines perpendicular to the water line at our study sites in Corrubedo wetlands. $n = 3$ transects (a, b), $n = 1$ (c). Mean values (a, b) ± 1 SD

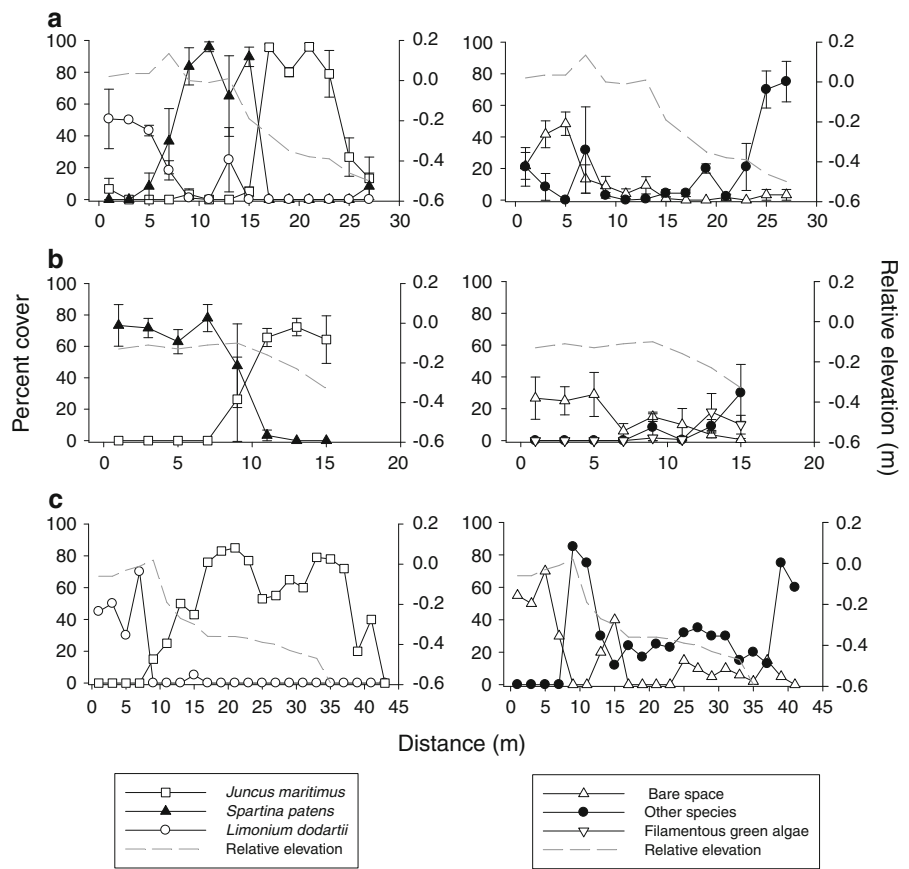


Table 1 Selected properties of soil sampled from the *Limonium*, *Spartina*, and *Juncus* vegetation zones

Site	Vegetation zone	% silt-clay (<63 μ)	% sand (≥ 63 to <4 μ)	SOM %C	SOM %N
A	<i>Limonium</i>	4.1 \pm 0.5	93.1 \pm 0.4	1.0 \pm 0.7	0.1 \pm 0.0
	<i>Spartina</i>	1.2 \pm 0.5	92.2 \pm 2.8	6.2 \pm 3.5	0.7 \pm 0.3
	<i>Juncus</i>	25.5 \pm 1.3	53.7 \pm 3.4	16.0 \pm 5.7	1.3 \pm 0.3
B	<i>Spartina</i>	1.9 \pm 0.8	90.1 \pm 4.8	2.2 \pm 1.0	0.3 \pm 0.1
	<i>Juncus</i>	27.8 \pm 19.4	59.5 \pm 9.0	4.2 \pm 3.5	0.3 \pm 0.3
C	<i>Limonium</i>	–	–	1.7 \pm 1.2	0.1 \pm 0.0
	<i>Juncus</i>	–	–	5.0 \pm 4.0	0.5 \pm 0.4

% C measurements made following treatment of soil samples with HCl. *Limonium* and *Spartina* zones absent from sites B and C, respectively. $x \pm 1$ SD, $n = 4$. –, no data

Overall, SOM samples from the *Spartina* zone were ^{13}C -enriched by 3.1‰ compared to SOM samples from the *Limonium* and *Juncus* zones (Table 3). There was a significant *Spartina* \times site interaction on SOM $\delta^{15}\text{N}$ values ($P = 0.039$, $F_{2,23} = 3.739$). However, the mean $\delta^{15}\text{N}$ value of SOM from the *Spartina* zone differed by only 0.5‰ from the mean value of SOM from the *Limonium* and *Juncus* zones (Table 3).

A similar pattern of ^{13}C -enrichment in the *Spartina* zone was evident in the $\delta^{13}\text{C}$ values of enchytraeid oligochaetes (Table 3). There was a significant effect of *Spartina* cover on enchytraeid $\delta^{13}\text{C}$ values (*Spartina*, $P < 0.001$, $F_{1,21} = 18.359$; site, $P = 0.961$, $F_{2,21} = 0.040$, ANCOVA). Across sites, $\delta^{13}\text{C}$ values of oligochaetes were highly correlated with the cover of *S. patens* ($P < 0.001$,

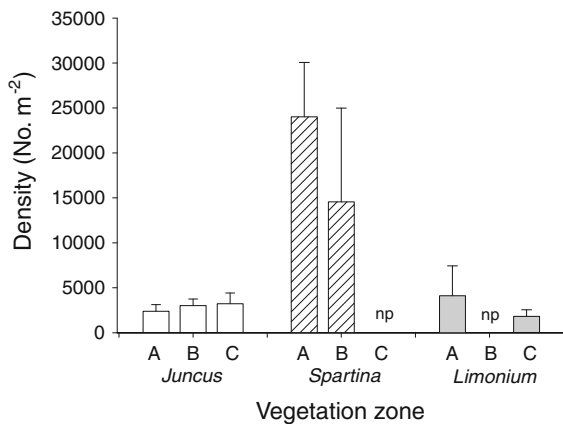


Fig. 3 Density of enchytraeid oligochaetes (m^{-2}) within zones of dominant vegetation (*Juncus maritimus*, *Spartina patens*, *Limonium dodartii*). np vegetation zone not present. Mean values ± 1 SD, $n = 5$

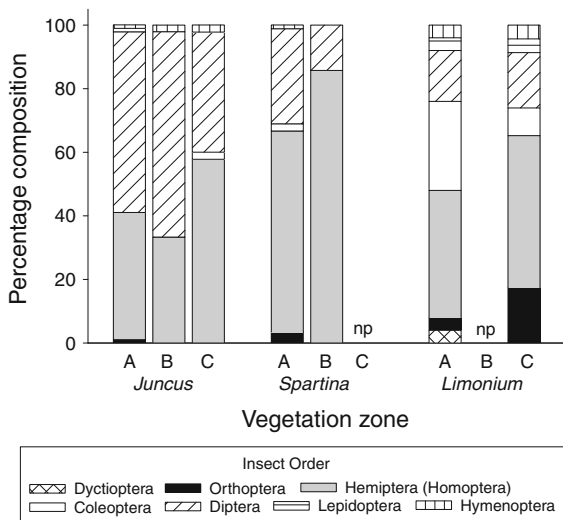


Fig. 4 Taxonomic composition of insects captured in net sweeps within vegetation zones dominated by *Juncus maritimus*, *Spartina patens*, and *Limonium dodartii*. Sample sizes provided in text. np vegetation zone not present

$r = 0.720$, $n = 25$). Overall, enchytraeid $\delta^{13}\text{C}$ values were 4‰ higher in the presence of *S. patens* ($-20.0 \pm 1.6\text{‰}$) than C_3 plants ($-24.0 \pm 0.2\text{‰}$) (Table 3). There was a significant *Spartina* \times site interaction on enchytraeid $\delta^{15}\text{N}$ values ($P = 0.039$, $F_{2,20} = 3.825$); however, mean $\delta^{15}\text{N}$ values differed by $<1\text{‰}$ between the *Spartina* and the *Limonium* and *Juncus* zones (Table 3).

There was a significant correlation between the $\delta^{13}\text{C}$ values of enchytraeids and SOM ($P < 0.001$,

Table 2 $\delta^{13}\text{C}$ and $\delta^{15}\text{N}$ values (‰) of salt marsh plant species in Corrubedo wetlands

Dominant plant species	$\delta^{13}\text{C}$ (‰)	$\delta^{15}\text{N}$ (‰)	n
<i>Limonium dodartii</i>	-25.7 ± 0.4	-0.4 ± 0.7	3
<i>Spartina patens</i>	-15.3 ± 1.2	-0.4 ± 0.8	3
<i>Juncus maritimus</i>	-26.2 ± 0.6	0.5 ± 0.9	6
Other plant species			
<i>Halimione portulcooides</i>	-25.8	3.6	2
<i>Limonium vulgare</i>	-26.2 ± 0.4	0.8 ± 0.4	3
<i>Inula crithmoides</i>	-28.6	-0.3	2
<i>Sarcocornia perennis</i>	-29.5 ± 3.4	1.1 ± 1.0	3
<i>Festuca rubra</i> subsp. littoralis	-28.0	-2.1	1
Alga			
Green macroalgae (filamentous)	-22.8 ± 0.9	-0.5 ± 0.6	5

$x \pm 1$ SD, $n =$ sample size

$r = 0.653$, $n = 22$: Fig. 5a). A weak negative, but significant correlation occurred between $\delta^{15}\text{N}$ values of enchytraeids and SOM ($P = 0.044$, $r = -0.444$, $n = 22$: Fig. 5b).

Results from mixing model calculations suggested that an average of from 35 to 63% of SOM at depths of 2–5 cm could be composed of C derived from *Spartina patens*, depending on the scenario of assumed change in $\delta^{13}\text{C}$ values during plant decomposition (Table 4). Decreasing the $\delta^{13}\text{C}$ value of *S. patens* increased the estimated contribution of this source. The significant correlation between $\delta^{13}\text{C}$ values of enchytraeid oligochaetes and of SOM across C_3 and C_4 plant zones (Fig. 5a), suggested that these detritivores were using some C derived from *S. patens*.

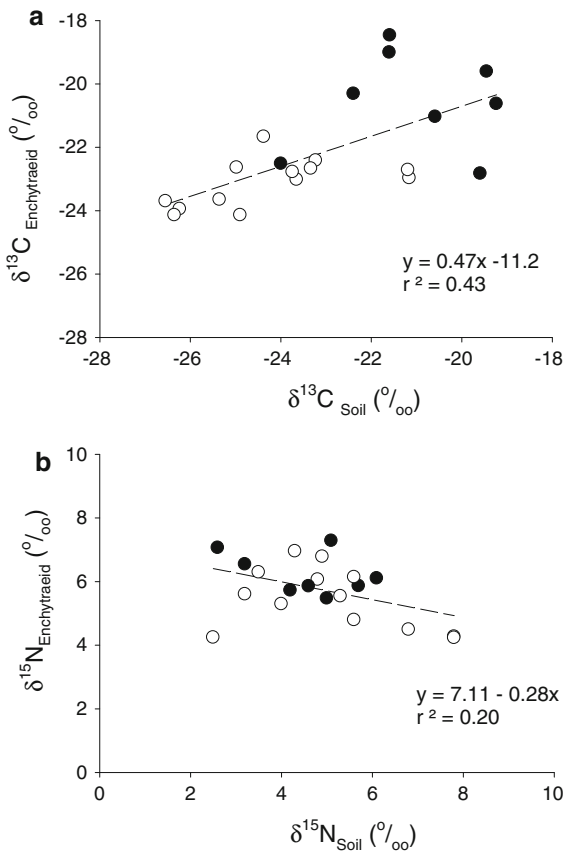
Isotopic composition of plants and arthropods

In general, $\delta^{13}\text{C}$ values of planthoppers and leafhoppers ($\sim -25\text{‰}$) revealed the use of C_3 as opposed to C_4 plants (Table 5; Fig. 6). There was one exception to this pattern. Planthoppers collected from the *Spartina* zone of site B were ^{13}C -enriched relative to specimens collected from the other sites. $\delta^{13}\text{C}$ values of the grasshoppers and katydids (-27 to -26‰) also indicated the principal use of C_3 plants. $\delta^{13}\text{C}$ values of spiders (-25 to -24‰) overlapped

Table 3 Mean $\delta^{13}\text{C}$ and $\delta^{15}\text{N}$ values (‰) of SOM and enchytraeid oligochaetes in vegetation zones dominated by either C_4 (*Spartina patens*) or C_3 (*Juncus maritimus*, *Limonium dodartii*) plants

Vegetation zone	Carbon		Nitrogen		<i>n</i>
	SOM	Enchytraeid	SOM	Enchytraeid	
<i>Spartina patens</i> (C_4)	-21.1 ± 1.7	-20.6 ± 1.6	5.1 ± 1.7	5.4 ± 1.0	8
<i>Juncus maritimus</i> , <i>Limonium dodartii</i> (C_3)	-24.2 ± 1.8	-23.1 ± 0.7	4.6 ± 1.2	6.2 ± 0.7	14

Mean values \pm 1 SD, *n* = number of samples

**Fig. 5** Relationship between **a** $\delta^{13}\text{C}$ values of SOM and enchytraeid oligochaetes and **b** $\delta^{15}\text{N}$ values of SOM and enchytraeid oligochaetes

values expected if these predators were consuming prey that were feeding primarily on C_3 plants (Fig. 6). Overall, $\delta^{15}\text{N}$ values of herbivores ranged from -1.5 to 4.4 ‰ with no significant differences in mean values among vegetation zones. Two species of spiders were ^{15}N -enriched by at least 2–3‰ relative to potential herbivore prey (Table 5; Fig. 6).

Discussion

The occurrence of the non-indigenous *Spartina patens* in nearly monospecific stands in the upper marsh suggests that this plant has had negative impacts on native plant populations (SanLeón et al. 1999; this study). Stable isotope analysis provided one approach to explore less obvious impacts of this plant invasion on the ecological functions of upper marsh habitat, including the alteration of organic matter sources, which may ultimately influence soil properties, detritivore and herbivore populations and trophic pathways (Levin et al. 2006; Whitcraft et al. 2008). Our results suggest that inputs from *S. patens* have altered the source composition of SOM in the upper marsh, but have not yet completely displaced organic matter derived from C_3 plants. This conclusion is based on the C isotope value of SOM in the *Spartina* zone, which was ^{13}C -enriched relative to that of SOM in zones dominated by C_3 vegetation.

Mixing model results provided a coarse estimate of the proportional contribution of *Spartina patens* C to SOM (mean values 35–63%). Although we are not aware of published data for *S. patens*, isotope values of *S. alterniflora* plant litter have been shown to decrease during decomposition in low marsh sediments. These changes (~ -1 to -2 ‰ after <2 years, Ember et al. 1987; Benner et al. 1987), with relatively larger changes projected over time by modeling (Benner et al. 1987), are the result of the selective use of ^{13}C -enriched compounds (e.g., cellulose) by microorganisms and the preservation of ^{13}C -depleted refractory C (e.g., lignin) (Ember et al. 1987; Benner et al. 1987). In contrast, little change in the $\delta^{13}\text{C}$ value of *S. alterniflora* occurred during aerial decomposition (Ember et al. 1987; Currin et al. 1995). Decreasing the values of the *S. patens* isotope end-member used in our mixing model to bracket

Table 4 Estimates of percentage contribution of *Spartina patens* (C₄) C to SOM in the *Spartina* zone

Scenario	Shift in $\delta^{13}\text{C}$ (‰) of <i>S. patens</i> source	Estimated percentage (%) contribution from <i>S. patens</i>
1	0	35 (17–52)
2	–2	45
3	–4	63

End-member $\delta^{13}\text{C}$ values ($x \pm 1$ SD) used in two source mixing model: $-15.3 \pm 1.2\text{‰}$ represent recent C inputs and $-24.2 \pm 1.8\text{‰}$ represent SOM values prior to invasion (Table 1). Estimate made under three scenarios: 1, no change in *Spartina* end-member values during decomposition, 2, change in values by -2‰ during decomposition, and 3, change in values by -4‰ during decomposition. 95% CI for Scenario 1 only in parenthesis

Table 5 $\delta^{13}\text{C}$ and $\delta^{15}\text{N}$ values (‰) of herbivorous insects and spiders sampled within vegetation zones dominated by *Spartina patens*, *Limonium dodartii*, or *Juncus maritimus* in Corrubedo wetlands

Vegetation zone	Taxon	Site	$\delta^{13}\text{C}$ (‰)	$\delta^{15}\text{N}$ (‰)	
<i>Limonium dodartii</i>	<i>Pentastiridius leporinus</i> (L.) (Hemiptera, Cixidae)	A	–25.5	–1.5 (2)	
		C	–24.6	–0.2 (1)	
	Hemiptera, Cicadellidae	C	–25.1	4.0 (2)	
		<i>Aiolopus strepens</i> (Orthoptera, Acrididae)	A	–26.2	2.8 (1)
			C	–26.0	0.2 (1)
<i>Spartina patens</i>	Arachnida, Araneomorphae	A	-24.2 ± 0.4	5.8 ± 0.8 (3)	
	<i>Pentastiridius leporinus</i>	A	-25.3 ± 1.4	-0.2 ± 0.4 (4)	
		B	-19.6 ± 0.8	1.3 ± 0.9 (3)	
	Hemiptera, Cicadellidae	A	–25.6	1.8 (1)	
		Orthoptera, Tettigoniidae	A	–26.9	4.4 (2)
	Arachnida, Araneomorphae	A	–23.5	7.5 (2)	
	<i>Juncus maritimus</i>	<i>Pentastiridius leporinus</i>	A	-24.3 ± 2.2	0.1 ± 0.5 (3)
A			–24.7	3.3 (1)	
B			-25.0 ± 0.9	1.2 ± 1.4 (3)	
<i>Aiolopus strepens</i>		C	-24.6 ± 0.4	3.2 ± 2.6 (3)	
		A	–27.4	1.3 (1)	
		Arachnida, Theraphosomorphae	A	–25.0	7.1 (1)
Arachnida, Araneomorphae	C	–24.0	1.5 (1)		

Mean values ± 1 SD when $n \geq 3$, sample size in parenthesis

values measured empirically or estimated from modeling for *S. alterniflora* increased the estimate of the proportional contribution of *S. patens* C to SOM. Inputs of other autochthonous (e.g., benthic algae) or allochthonous (e.g., phytoplankton) production that could also influence end-member values are probably minimal because of the high intertidal location, and thus only occasional inundation of our upper marsh sites.

One explanation for the apparent persistence of residual C₃ plant-derived compounds in SOM within the *Spartina patens* zone is that the rate of

incorporation of C₄–C into SOM is slow relative to the timescale of this invasion (several decades). Unfortunately, there appear to be few data that have examined the replacement rates of C₃–C by C₄–C in *Spartina*-invaded salt marshes. In a recent invasion of an established native *Scirpus marquerter* (a C₃ plant) plant community by *Spartina alterniflora* (Jiuduansha wetlands, China, Cheng et al. 2006), the contribution of *S. alterniflora* C to SOM in invaded areas after 7 years was estimated to reach a maximum of $\sim 10\%$ at a depth of 40 cm, a value lower than the values estimated in the decades-old invasion in our study.

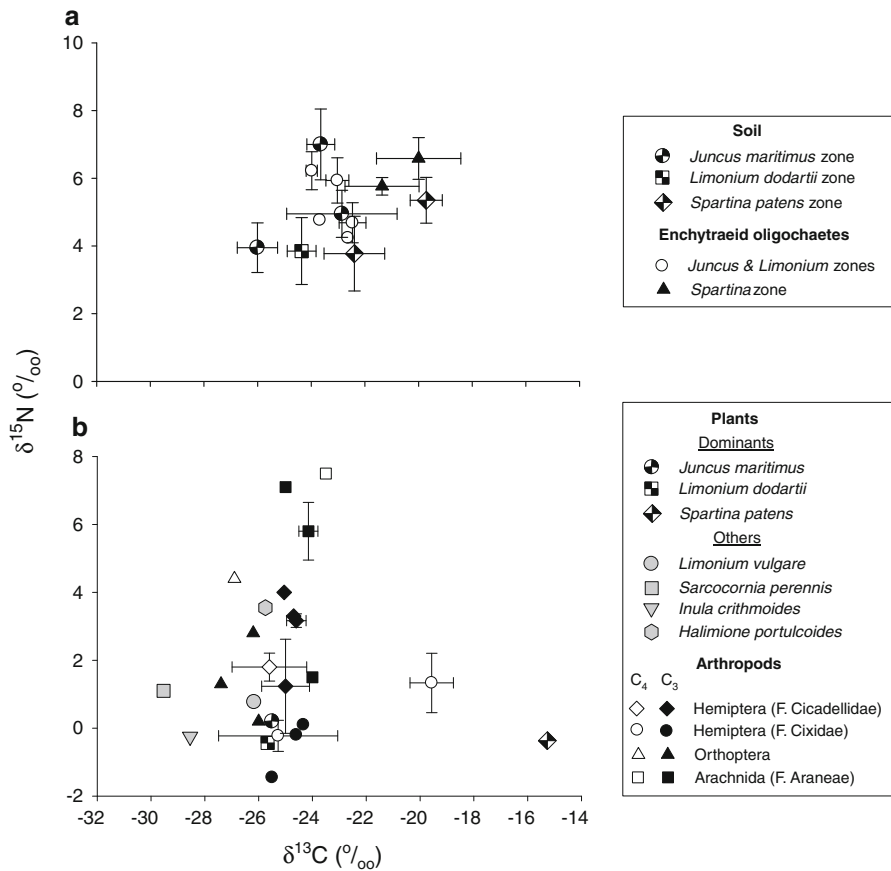


Fig. 6 Plot of $\delta^{15}\text{N}$ versus $\delta^{13}\text{C}$ for **a** SOM and enchytraeid oligochaetes sampled in zones of C₃ (*Limonium* and *Juncus*) and C₄ (*Spartina patens*) vegetation and **b** dominant plant species, herbivorous insect taxa, and spiders. Mean values \pm 1 SD when $n \geq 3$

Enchytraeid oligochaetes incorporated C derived from *Spartina patens*, but did not have isotope values that indicated the preferential use of this recent source. The average isotopic enrichment of enchytraeids at our sites relative to the SOM (+1.2‰ in the *Limonium* and *Juncus* zones, +0.5‰ in *Spartina* zone, Table 2) was similar to the expected trophic enrichment factor of $\sim +1\%$ (DeNiro and Epstein 1978). In this regard, our results agree with recent work in a terrestrial ecosystem, which indicated that enchytraeids were not preferentially incorporating the most recent C inputs (Briones and Ineson 2002). This conclusion is further supported by reports of similar C and N isotope values in enchytraeids and endogeic earthworms, which use C derived from older decomposing material (Scheu and Falca 2000; Schmidt et al. 2004). It is also possible, however, that the input rates of organic matter from *Spartina* may not be great enough to reflect the preferential use of this recent C

by enchytraeids. More data on the rates of contribution of C₄-C to the SOM and of incorporation by detritivores will help to clarify the timescale across which *S. patens* invasions influence the composition and turnover of SOM and its use by soil detritivore populations.

Mean enchytraeid densities were higher (3–5x) in association with *Spartina patens* compared to areas where native plants dominated, including a site (C) that lacked *S. patens* from apparently suitable elevations. In other geographical settings, invasions of *Spartina* into low marsh and mudflat habitat have altered the density, composition, diversity and trophic structure of infaunal communities (Neira et al. 2005; Levin et al. 2006). It is thus possible that *S. patens* has also altered aspects of the upper marsh habitat (e.g., soil organic C) in ways that enhance enchytraeid abundance. The trend of higher enchytraeid densities in the *Spartina* zone, compared with the

Limonium and *Juncus* zones, did not coincide with the elevational gradient in % silt–clay, mean grain size, or % organic C of SOM. However, enchytraeid densities could also be influenced by factors that co-vary with the cover of *S. patens* (e.g., inundation frequency, soil drainage, shade) not measured in this study.

The insects captured in net sweeps within the *Spartina patens* zone were dominated by herbivorous taxa, particularly the planthopper *Pentastiridius leporinus* (Hemiptera, Cixidae). *P. leporinus* is found in wetland-upland transition habitats in western Europe with *Phragmites australis* reported as a host plant in other areas (Nickel and Remane 2002). Interestingly, this insect is a vector of bacterial disease to sugar beets in southern France (Bressan et al. 2010). *P. leporinus* was not among those identified as insect herbivores occurring in patches of *S. patens* along the New Jersey (Atlantic) coast, USA, which were mostly flightless forms (Denno 1977, 1980). In this regard, our data supports the observation that insect herbivores that would normally feed on the introduced plant species within its native range may be absent in the invaded habitat (Ohmart and Edwards 1991; Bell 1997; Maron and Vilà 2001).

Most of the herbivorous insects associated with *Spartina patens* in its native habitat are host specific (Davis and Gray 1966; Denno 1977). However, there was no evidence that herbivorous insects at our study sites preferred *S. patens* over native C₃ plants or that *S. patens* was widely used as a source of food by these taxa, at least during a period of time prior to our sampling that would be reflected in the stable isotope values of these consumers. Indeed, insect herbivores captured within both C₃ (*Limonium*, *Juncus*) and C₄ (*Spartina*) vegetation zones had C isotope signatures reflecting the use of C₃ plants. The proposed use of mainly C₃ plants by insect herbivores is further supported by the ¹³C-depleted isotope values of potential predators (spiders) from the *Spartina* zone (site A). There was one exception to this general pattern; planthoppers from the *Spartina* zone at one site (B) had intermediate C isotope values that suggested some use *S. patens* by sap-feeders.

Our findings suggest that herbivore use of *Spartina patens* is not as extensive as that found in its native range, where this plant is fed on heavily by several hemipteran species (Davis and Gray 1966; Denno 1980). At our sites, it appears that mobile herbivores

transit the *Spartina* zone, but apparently are not feeding extensively on this plant. In contrast, Denno (1980) reported that during the summer, the population of sap-feeding insects on large patches (500–1,000 m²) of *S. patens* in a New Jersey coastal marsh was high and the effects of feeding and oviposition were evident by the deterioration of the grass over time. Our results also differ from those of Wu et al. (2009), which suggested that some native taxa, katydids (F. Tettigoniidae) and crickets (F. Gryllidae), preferred the exotic *Spartina* (*S. alterniflora*) over the native *Phragmites australis* in a salt marsh in the Yangtze River estuary (China). We conducted our sampling during late May, a time period likely to have a high abundance of both enchytraeids and insects, and high food resource use in the study region. However, data on temporal variability in enchytraeid and insect populations is needed to assess to what extent our results may apply to other times of the year.

In conclusion, the elevated abundance of enchytraeids in association with *Spartina patens* and their use of C derived from this plant suggest that dense patches of *S. patens* may facilitate detritivore populations, and thus could indirectly influence soil attributes and processes that are mediated by detritivore activity, such as soil respiration rates, nutrient retention and transformation, energy flow, and habitat architecture (Moore et al. 2004). In contrast, although insect herbivores used *S. patens* as habitat, there was little isotopic evidence for the widespread incorporation of *S. patens*-derived C by these consumers. The loss of food resources to insect herbivores alters local food webs, but insect herbivores may move and feed on native plants outside of the *Spartina* zone. As a result, insect populations may be less immediately impacted than soil detritivore populations by the shift from native plants to *S. patens* in the upper marsh.

The distribution of *Spartina patens* is expanding in northern Spain (Campos et al. 2004) and this species is recognized as undesirable in this region and elsewhere (Frenkel and Boss 1988; Ayres et al. 2004); however, few studies have explored potential consequences of *S. patens* invasion on salt marsh functioning. Our study suggests that the impacts of *S. patens* invasion may extend beyond the more obvious changes in native plant abundance, to include differing responses in the cycling of organic matter between detritivore and insect herbivore food web pathways.

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