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Utilization of invasive tamarisk by salt marsh consumers

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Abstract Plant invasions of coastal wetlands are rapidly changing the structure and function of these systems globally. Alteration of litter dynamics represents one of the fundamental impacts of an invasive plant on salt marsh ecosystems. Tamarisk species (*Tamarix* spp.), which extensively invade terrestrial and riparian habitats, have been demonstrated to enter food webs in these ecosystems. However, the trophic impacts of the relatively new invasion of tamarisk into marine ecosystem have not been assessed. We evaluated the trophic consequences of invasion by tamarisk for detrital food chains in the Tijuana River National Estuarine Research Reserve salt marsh using litter dynamics techniques and stable isotope enrichment experiments. The observations of a short residence time for tamarisk combined with relatively low C:N values indicate that tamarisk is a relatively available and labile food source. With an isotopic (^{15}N) enrichment of tamarisk, we demonstrated that numerous macroinvertebrate taxonomic and trophic groups, both within and on the sediment, utilized ^{15}N derived from labeled tamarisk detritus. Infaunal invertebrate species that took up no or limited ^{15}N from labeled tamarisk (*A. californica*, enchytraeid oligochaetes, coleoptera larvae) occurred in lower abundance in the tamarisk-invaded environment. In contrast, species that utilized significant ^{15}N from the labeled tamarisk, such as psychodid insects, an exotic amphipod, and an oniscid isopod, either did not change or occurred in higher abundance. Our research supports the hypothesis that invasive species can alter the trophic structure of an environment through addition of detritus and can also potentially impact higher trophic levels by shifting dominance within the invertebrate community to species not widely consumed.

Keywords Isotope enrichment · Salt cedar · Exotic species · Trophic · *Tamarix*

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Introduction

Invasion by exotic vascular plants in coastal wetlands is increasing globally, with dramatic consequences that include local extinctions of native species, genetic modifications, species displacements, and habitat degradation (Chapin et al. 1997; Grosholz 2002). Ecosystem-altering plants are found invading coastal wetlands around the world; examples include *Phragmites australis* (common reed) (Talley and Levin 2001; Rooth et al. 2003; Chambers et al. 2003), *Spartina* spp. (cordgrass) (Ayres et al. 2003; Neira et al. 2005), *Arundo donax* (Herrera and Dudley 2003), *Zostera japonica* (Japanese eelgrass) (Posey 1988), and now *Tamarix* spp. (Whitcraft et al. 2007). Only recently, however, have trophic modifications by invasive

plants in wetlands been recognized as important mechanisms underlying ecosystem change (Vitousek et al. 1996; Wardle et al. 2004; Levin et al. 2006). Knowing the trophic effects of an invasion will advance our understanding of the mechanisms behind observed invasion impact, allowing for prediction of potential future ecosystem changes.

The consequences of plant invasions often are focused on one trophic level through changes in the abundance, composition, and diversity of sediment microbial or animal communities (Wardle et al. 2004; Levin and Talley 2000). Invasive plant species can modify the quantity and quality of detritus, which is often the main energy source in wetlands (Moore et al. 2004). Yet, the importance of the detrital pathway as the driving force behind observed plant influence is often omitted from the study of plant invasion consequences (Kennedy and Hobbie 2004; Levin et al. 2006).

One example of an ecosystem-altering woody plant is *Tamarix* spp., salt cedar or tamarisk, a group containing 54 species and several hybrids. Native to Eurasia, tamarisk was introduced into North America for horticulture, erosion control, and shade in the early 1800s (Di Tomaso 1998). At least seven species have become established in the United States (Baum 1978). Tamarisk, considered one of most serious invaders in the United States (Morisette et al. 2006; Stein and Flack 1996), has become established over 0.6 million hectares of floodplains, riparian areas, and freshwater wetlands in the western United States (Zavaleta 2000), making it the third most frequently occurring woody plant in riparian areas of the United States (Friedman et al. 2005).

Despite widespread invasion of coastal wetlands by plants, most of the salt marshes of southern California have been, until recently, relatively free of habitat-altering invasive plants. An exception is invasion of tamarisk into the Tijuana River National Estuarine Research Reserve (TR NERR) where the intertidal, pickleweed (*Sarcocornia pacifica*) marsh now supports dense stands of these salt-tolerant trees (Whitcraft et al. 2007). The trees invading the TR NERR low salt marsh habitat are primarily a hybrid, *T. ramosissima* × *T. gallica*, which converts the salt marsh from a succulent-dominated canopy of less than 1 m height to a landscape dominated by stands of woody trees that can grow to over 3 m tall (Whitcraft et al. 2007). Information about the effects of tamarisk invasion in North America comes primarily from low salinity, woody plant-dominated riparian systems. Tamarisk is a novel invader in the succulent-dominated salt marsh ecosystem, making salt marsh-specific studies crucial to effective management. Anecdotal reports and an unpublished survey of tamarisk occurrence in salt marshes exist in southern California (Crooks et al., unpublished), but the extent of this outside of southern California is unknown.

Numerous studies have linked litter decomposition rates to invertebrate feeding preferences and thus litter quality (i.e., Webster and Benfield 1986; Kennedy and Hobbie 2004). In freshwater riparian areas, tamarisk litter can decompose faster than native litter, potentially causing decreases in macroinvertebrate richness and abundance and an alteration in macroinvertebrate community structure (Bailey et al. 2001; Kennedy and Hobbie 2004, but see Ellis et al. 1998). We, therefore, can predict that the community change from pickleweed to tamarisk in the salt marsh environment will affect the litter dynamics of the system, potentially translating into community-level food web effects through the alteration of detrital pathways (e.g., Stevens 2000; Crooks 2002).

Our overall research objective was to delineate the effect of tamarisk invasion on the salt marsh detrital pathway. We used litter quantity and quality measures, quantitative benthic macroinvertebrate community structure analysis, and natural and enrichment stable isotope experiments to address several general questions. (1) Is tamarisk available to benthic macroinvertebrates as a detrital food source? (2) Which species and trophic groups derive nitrogen from experimentally enriched tamarisk detritus? (3) Does tamarisk detritus utilization by benthic macroinvertebrates differ by depth in the sediment and/or between adjacent invaded and native habitats? and (4) How does tamarisk affect overall trophic structure of the salt marsh ecosystem?

Materials and methods

Site description

Tijuana River National Estuarine Research Reserve (TR NERR), a 2,500-acre (c. 1,000-ha) reserve, is situated near Imperial Beach, in San Diego County, CA, USA, on the US–Mexican border. The estuary is located at the mouth of the Tijuana River watershed, with over two-thirds of the 4,420 km^2 watershed lying within Mexico (Zedler et al. 1992). Extensive tamarisk stands (percent cover >75%) exists along main tributaries, channels, and upland transition zones within TR NERR. Areas of tamarisk presence with percent cover <10% exist in low, middle, and high marsh habitats of the reserve (Whitcraft et al. 2007). Our study considers tamarisk in the low intertidal salt marsh habitat, which represents approximately 20% aerial cover within the reserve (Zedler et al. 1992). The study area, immediately adjacent to the main channel of the Tijuana River in the USA, contains tamarisk-present habitat (TAM) (defined to be an area with 90–100% tamarisk canopy cover) and tamarisk-absent habitat (SP). The SP contains no tamarisk and is dominated by *Sarcocornia pacifica* (formerly *S. virginica*)

and *Jaumea carnosa*; percent cover of *S. pacifica* in TAM blocks was significantly less than in SP blocks (TAM = 28 ± 10%, SP = 91 ± 15%; *t* test, $t_3 = -3.51$, $P = 0.039$) while percent open space was greater in TAM blocks (TAM = 58 ± 38%, SP = 0 ± 0%; *t* test, $t_3 = 3.05$, $P = 0.051$).

Litter dynamics

To determine the fate of tamarisk detritus in summer, we evaluated rates of litter fall, fallen litter standing stock, and leaf degradation/utilization rates in tamarisk stands in TR NERR using the methods outlined by Twilley et al. (1997) and Kennedy and Hobbie (2004). We collected all litter parameters (litter fall, standing crop, decomposition rates) in selected areas along this transect. Five sampling locations were chosen at random distances along a 50-m transect.

To measure litter fall, we secured one basket (0.25 m^2) under the drip line of 10 tamarisk trees (1 basket per tree) for 7 days in August/September 2005 and for 7 days in August 2006. Litter standing crop was measured by collecting litter from 0.25 m^2 quadrats on the ground below the tamarisk tree. Each quadrat was randomly placed 1 m from one of the corners of a litter basket. Material from the baskets and quadrats was collected, separated into leaves, reproductive structures (flower, fruit), wood, and miscellaneous (included small pieces of tamarisk debris), dried at 60°C to a constant weight (2–3 days) and weighed to the nearest 0.1 g.

We measured the loss of dry mass from fiberglass mesh bags as a proxy for tamarisk leaf degradation rates (Twilley et al. 1997; Kennedy and Hobbie 2004). This degradation is the sum of several processes: consumption of plant material by organisms (<1 mm), bacterial decomposition, and physical degrading of the plant material. In summer 2005 and 2006, 4 g (wet weight) of air-dried fresh tamarisk leaves were placed in litterbags (20 × 20 cm, mesh 1 mm) constructed of window screening. At each vertical litter basket in 2005 and 2006, 2 mesh bags were placed 0.5 m apart on the sediment surface 1 m from each of the baskets and were collected after 3 weeks. The plant material was rinsed in Milli-Q, dried at 60°C to a constant weight (2–3 days), and weighed to the nearest 0.10 g. Fresh tamarisk leaves (4–5 g) were dried to a constant weight at 60°C to obtain an average conversion factor of wet leaf weight to dry weight (46 ± 2% SE weight loss).

Leaf turnover calculations

Decay constants were calculated for each litterbag assuming a simple negative exponential decay (k) (Olson 1963):

$$\ln M_t/M_0 = -kt$$

where M_t is the litter mass at time t and M_0 is the initial litter mass. Leaf turnover based on leaf degradation experiments removes the influence of tidal export and consumption via large macrobenthos (>1 mm). K_d estimates were compared between sites based on 3 weeks of data.

Leaf turnover rates, including degradation, burial, and outwelling, were estimated based on leaf fall estimates and litter standing crop. Leaf turnover rates were estimated using the following equation:

$$K_t = L_f/L_{sc}$$

where K_t is the turnover coefficient, L_f is the leaf litter fall in g m^{-2} day^{-1}, and L_{sc} is the leaf standing stock in g m^{-2}. This equation assumes a steady state where leaf litter production equals leaf litter losses (Twilley et al. 1997). K_t values were daily averages for 3 weeks of data.

Litter quality

C:N ratios of plants have been utilized as measures of litter quality (Sterner and Elser 2002; Pennings et al. 1998). To measure C and N content, fresh leaf material from non-senescent tamarisk and several native plants (*S. pacifica, Juncus acutus*, *J. cornosa*) in each block ($n = 4$) was collected from the study site, rinsed with Milli-Q® water, placed in pre-combusted vials or tin boats, dried at 65°C, and kept in a desiccator until analysis. In addition, particulate organic matter (POM), sediment organic matter (SOM), and benthic microalgae were collected from each block ($n = 4$) and processed as discussed below. These samples were analyzed for C:N content using an elemental analyzer (PDZ Europa ANCA-GS, Northwich, UK).

Benthic community structure

In September 2004, paired sediment cores (18.1 cm^2 surface area, 2 cm deep) were collected in patches with hybrid tamarisk present (TAM) and in adjacent *S. pacifica* habitat where tamarisk was absent (SP) for quantitative analyses of macrofaunal density. Four blocks (1 m^2), located 10 m apart within an area of similar elevation, soil type and drainage, containing TAM and SP habitats were sampled to obtain a total of eight cores.

We selected a 4.8-cm-diameter core, consistent with published literature, to target macrofauna typically in the 1- to 2-mm size range, recognizing that this is likely to exclude megafauna, such as large clams or crabs (i.e., Levin et al. 1998; Talley and Levin 1999; Levin and Currin 2005). Cores were preserved (unsieved) in 8% buffered formalin with Rose Bengal. For macrofaunal quantification, the core

sediments were washed through a 0.3-mm mesh. The animals retained were sorted under a dissecting microscope (Wild M5A) at 12× magnification, identified to the lowest taxonomic level possible, counted, and stored in 70% ethanol. Most insects collected were larvae; identifications of these were at the family level only. For other organisms, identifications were to species level, although putative names were used in some cases.

Natural abundance stable isotope analysis

Stable isotope analyses were used to assess whether signatures of the primary producers change with altered plant cover and which consumer species rely on tamarisk as a food source. During September 2004, the TAM and SP habitats of the four blocks previously sampled for macrofauna were sampled for POM, SOM, microalgae, plants, and macrofauna to determine natural abundance isotopic signatures ($\delta^{13}C$, $\delta^{15}N$) of food web components. Collection and processing methods were similar to those described in Moseman et al. (2004) and Levin et al. (2006). At low tide, POM was obtained by filtering 2 L of tidal creek water from the nearest tidal creek onto Whatman GFF filters. SOM was sampled by collecting surface sediment (upper 2 cm), drying and homogenizing sediments. Microalgae were collected using density centrifugation with ludox (colloidal silica), providing a pure algal sample (devoid of sediment) (Blanchard et al. 1988). Multiple leaves were gathered from each plant species within the sampling area, washed in Milli-Q® water, dried at 65°C, and then ground with mortar and pestle. Sub-samples of ground leaves were placed in pre-combusted vials or tin boats, and kept in a desiccator until analysis. A non-quantitative scoop of the surface sediment (0–2 cm) was collected for macrofaunal invertebrates. Subsequently, in the laboratory, these sediments were sieved on a 0.3-mm mesh to retain macroinvertebrates that were identified to species under a dissecting microscope at 12× magnification. All animals were kept alive in seawater and allowed to evacuate guts for 12 h (Levin et al. 2006). Animal material was then washed in Milli-Q® water, placed in pre-combusted vials or tin boats, dried at 65°C, and kept in a desiccator until analysis. Larger organisms were removed from the shell or carapace, dried at 65°C, and then ground with a mortar and pestle. All samples were treated with Pt Cl_2 to remove inorganic carbon (Fry and Wainwright 1991).

Isotopic composition was analyzed by a PDZ Europa (Crewe, UK) 20–20 mass spectrometer connected to an elemental analyzer. Stable isotope abundance is expressed in parts per thousand in a ratio of heavy to light isotope content (^{15}N:^{14}N or ^{13}C:^{12}C) relative to a standard. Working standards, sucrose, and ammonium sulfate, were $\delta^{13}C = -23.83‰$ versus Vienna Pee Dee Belemnite Standard or $\delta\ ^{15}N = +1.33‰$ versus air N_2. Typical sample precision is better than 0.1‰.

Isotope labeling and enrichment experiments

In order to trace plant-derived nutrients through food webs using stable isotopes, it is necessary for the invader to have an isotopic signature distinct from native food sources. If potential food sources have overlapping signatures, alternative approaches must be utilized to distinguish the invader. One effective alternative is isotopic labeling of the invasive plant with ^{15}N to track the labeled material into consumer tissues (i.e., Herman et al. 2000; Carman and Fry 2002; Neira et al. 2005; van Oevelen et al. 2006, Levin et al. 2006). In this study, we apply the ^{15}N enrichment approach due to the overlap of tamarisk isotope natural abundance values ($\delta^{13}C$, $\delta^{15}N$) with an important native food (benthic microalgae) (see Results).

In situ labeling

Four *T. ramosissima* × *T. gallica* hybrid trees that were functionally representative of but geographically isolated from the study site (in TR NERR) were labeled with ^{15}N by enclosing plants in situ in 4 plastic pots with the bottoms cut out during June 2004. Sediments surrounding the tamarisk plants were injected daily with 250 ml of 6 mmol/l ammonium sulfate (98 atom % $^{15}NH_4$) per pot for a 3-day period (method modified from White and Howes 1994 and Levin et al. 2006). Plants (all parts) were harvested 12 weeks after injections (September 2004), chopped into 5 mm pieces, and deployed 1 day later.

Deployments and collections

Based on the observation that tamarisk leaves often appeared both on the sediment surface and as belowground biomass in sediment samples, labeled tamarisk was introduced in two modes to the four paired blocks discussed above: either buried in litter bags (with 2 bags per plot) or spread uniformly onto the sediment surface (in three circular 90-cm^2 areas per plot). Nylon litter bags (2.6 × 1.2 cm, 5 mm mesh) were filled with 7 g of either leaf, root, or stem material and were deployed at a depth of 1–2 cm below the sediment surface in each quadrat. To test for differences in macroinvertebrate assimilation of ^{15}N among different plant parts, we buried three 5-mm mesh bags of detritus (1 bag of leaves, 1 bag of roots, and 1 bag of stems) in each habitat and collected the bags 90 days later (labeled "plants" in Electronic supplementary material S1). We buried 2 bags of leaf detritus per plot per habitat (for a total of 16 bags) (Electronic supplementary

material S1). We collected 1 set of bags (1 from TAM, 1 from SP) from each block 14 and 90 days later, washed the bags, sieved the overlying sediment, and sorted the associated macroinvertebrates under a dissecting microscope.

In addition, to test for N-leaching and uptake by bacteria and algae, ^{15}N-labeled tamarisk leaves were deployed in Nitex® mesh (61 μm) bags (1 per habitat per block) (labeled "leach" in Electronic supplementary material S1). We collected two bags (1 from TAM plot, 1 from SP plot) from each block 90 days later, washed the bags, sieved the overlying sediment, and sorted the associated macroinvertebrates under a dissecting microscope.

^{15}N-labeled tamarisk leaves were also cut into 5 mm pieces and placed in the field as loose, surface detritus. This plant material was spread uniformly on the surface in six circles (90 cm^2 diameter) per habitat, pressed 1 mm into sediment with forceps, and marked at the center with red wire so that the exact location could be sampled later (as in Levin et al. 2006) (Electronic supplementary material S1). These surface detritus areas were sampled by scooping the surface sediment (0–2 cm) from within the circles at 0, and 1, 4, 14, 90, and 270 days after deployment.

Immediately after deployment of litter bags and detritus on the sediment surface, we collected samples of infauna (>0.3 mm), microalgae, POM, and SOM to determine time 0 point (T0) values for δ^{13}C and δ^{15}N isotope signatures. These provided background values and allowed us to check for labeling artifacts. Microalgae were subsequently collected 1, 4, 14, 90, and 270 days after deployment for stable isotope analysis and treated as described above for the natural abundance stable isotope samples.

Statistical analysis

All univariate tests were conducted with JMP 5.1 statistical software (SAS Institute, NC, USA). Data were tested for normality, and $\log_{10}$ transformed as needed prior to analysis. Benthic community composition data (density, diversity parameters) were compared using randomized complete block ANOVAs. If normality could not be obtained through transformations, Wilcoxon non-parametric ANOVAs (statistics shown as χ^2) were conducted. Multivariate analyses (ANOSIM, SIMPER) were conducted on macrofaunal count data (fourth root transformed) using Primer 5 (Plymouth Marine Laboratory) (Clarke 1993; Clarke and Warwick 1994). Analyses are based on Bray–Curtis similarity indices (Clarke 1993). Pairwise comparisons of overall community similarity were made using Analysis of Similarity, ANOSIM.

Macroinvertebrates collected in isotope experiments were divided into feeding groups based on natural abundance isotope data generated for this project and on literature designations to make comparisons of tamarisk utilization among food preference type (detritivores, microalgal feeders, and mixed-diet feeders) (Table 2). Because comparisons among trophic groups involved multiple species per group, we used mean isotopic signatures of feeding groups (discussed above) within blocks as replicates for tracer uptake comparisons of subsurface versus surface and of tamarisk versus natural habitats in one-way ANOVAs with a posteriori Tukey's HSD tests. We tested differences in uptake of label separately for each time point (1, 4, 14, 90, 270) and for each habitat (TAM, SP) among feeding groups, among food preference groups, and among species. A paired approach was required because of the inherent initial differences in species values. In figures and text, one standard error about mean is presented for all data unless otherwise noted.

To estimate the fraction of tamarisk and other food sources in the infaunal diets, we applied a single isotope, two-source mixing model (Fry and Sherr 1984) for δ^{15}N in which labeled tamarisk detritus was treated as one food source and native food sources ("other" represents grouped food sources with similar values—microalgae, POM and SOM) from the appropriate time period (T1, T4 etc.) were treated as a second food source, using the formula:

$$\%\,\text{tamarisk} - \text{derived}\,\text{N} = [(\delta^{15}\text{N}_{\text{infauna}} - \delta^{15}\text{N}_{\text{other}})/ (\delta^{15}\text{N}_{\text{labeled tam}} - \delta^{15}\text{N}_{\text{other}})] \times 100$$

Using this approach, we calculated the percentage of N in infaunal tissues that was derived from the labeled tamarisk detritus. A trophic level shift of 2.2‰ for δ^{15}N was applied (McCutchan et al. 2003). We applied one trophic level shift to most species (grazers or deposit feeders); known carnivores were analyzed with a two-level shift. For N-enrichment experiment, we calculated change in δ^{15}N by subtracting the values for background animals in non-enriched sediment from values of animals exposed to ^{15}N-enriched tamarisk.

Results

Litter dynamics

Values for standing stock, leaf residence times and leaf degradation did not differ between years (Wilcoxon, $P > 0.05$) so results for these parameters are discussed together. A significantly greater amount of tamarisk litter fall was recorded in 2005 than in 2006 thus these results are summarized by year ($\chi^2_1 = 4.21$, $P = 0.040$). Average tamarisk load to the system (dry weight) was 1.47 ± 0.45 g day^{-1} 0.25 m^{-2} in 2005 and 1.01 ± 0.47 g day^{-1} 0.25 m^{-2} in 2006 for leaf-specific litter supply and 2.17 ± 0.47 g day^{-1} 0.25 m^{-2} in 2005 and 1.23 + 0.50 g

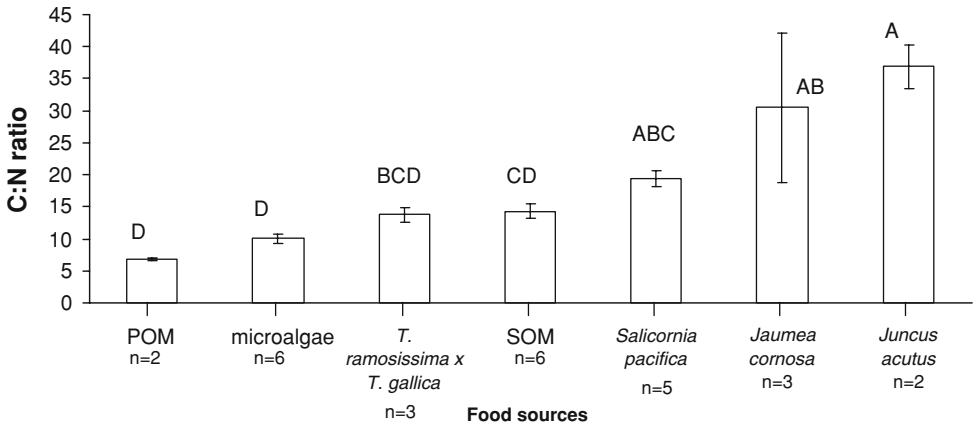

Fig. 1 Differences among C:N ratios (mean ± SE) of unlabeled invasive tamarisk (*T. ramosissima* × *T. gallica*) and natural food sources in the Tijuana River National Estuarine Research Reserve (TRNERR) salt marsh (ANOVA, $F_{7,18} = 11.53$, $P < 0.0001$). *Letters* indicate a posteriori differences among treatments ($P < 0.05$). *POM* particulate organic matter, *SOM* sediment organic matter

day^{-1} 0.25 m^{-2} in 2006 for total detrital tamarisk litter supply. The averaged standing stock values of tamarisk leaf tissue and total tamarisk material (dry weight) on the sediment surface were 2.05 ± 1.06 g 0.25 m^{-2} and 43.49 ± 21.96 g 0.25 m^{-2}, respectively. Decomposition experiments revealed a K_t for tamarisk leaves of 0.03 ± 0.008 (from a single-rate decay model), a 0.7-day residence time. Leaf residence times based on K_t was estimated to be 29 days.

Litter quality

T. ramosissima × *T. gallica* leaf detritus had a significantly lower C:N ratio than *Juncus acutus*, and C:N ratios were not significantly different than other native food sources (Fig. 1).

Benthic community structure

Although there were no overall differences in total density or diversity relative to the SP blocks, TAM blocks exhibited an altered macrofaunal community composition based on assemblage data (ANOSIM, TAM ≠ SP, $P = 0.003$) with 70% dis-similarity between TAM and SP blocks (SIMPER) (Fig. 2). These composition changes in TAM plots involved significantly fewer gastropods (*Assiminea californica*), enchytraeid oligochaetes, Coleoptera larvae, and greater numbers of Oniscidae isopods (*Littorophiloscia richardsonae*) (Fig. 2, Appendix 1 of Electronic supplementary material). When macrofauna were grouped by feeding mode (Table 2), we observed a significant decline in density of microalgal feeders in the TAM blocks versus SP blocks (TAM = 4.3 ± 0.9, SP = 3.25 ± 1.3, $t_3 = -3.3$, $P = 0.047$).

Natural abundance stable isotope analysis

δ^{13}C and δ^{15}N analyses of food sources and consumers demonstrated isotopic differences as a function of habitat

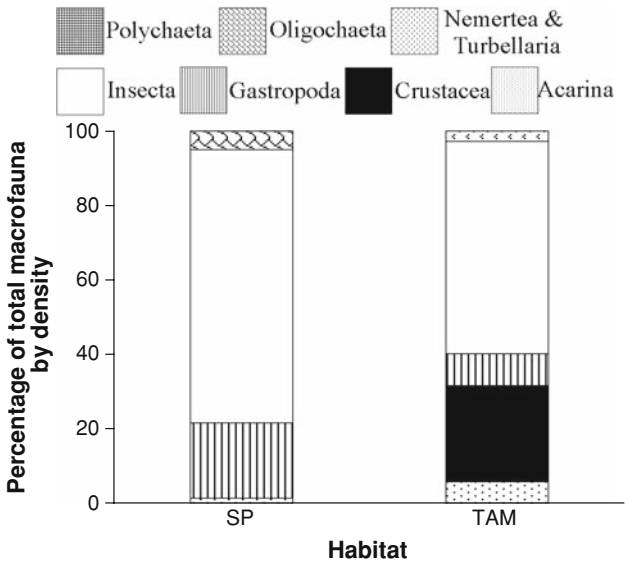

Fig. 2 Macrofaunal (>0.3 mm) community composition based on density data in tamarisk-absent (*TAM*) and tamarisk-present (*SP*) habitats in September 2004

(SP vs TAM). The SP habitat microalgae and SOM exhibited significantly lighter δ^{13}C than the microalgae and SOM from TAM habitat (microalgae, $F_{1,13} = 7.48$, $P = 0.017$; SOM, $F_{1,12} = 12.11$, $P = 0.005$) (Fig. 3, Appendix 2 of Electronic supplementary material). In addition, two of the potential food sources (tamarisk and microalgae) had overlapping δ^{13}C signatures within the tamarisk habitat, leading to our use of a ^{15}N isotopic enrichment experiment to track tamarisk within the marsh food web (Fig. 3). *S. pacifica* and *J. cornosa* had overlapping δ^{13}C signatures that were distinct from the *Juncus* sp. signature; all three were distinguishable from tamarisk and microalgae δ^{13}C values.

Isotope enrichment experiment

At the start of the detritus fate experiment, labeled tamarisk detritus had a mean δ^{15}N signature of 394, 225, and 234‰

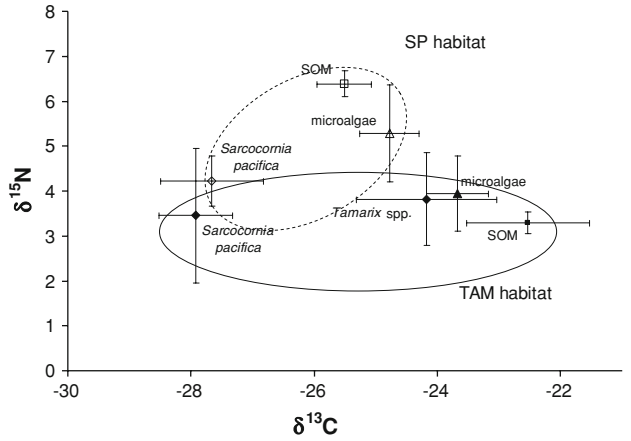

Fig. 3 Dual isotope blocks of natural abundance $\delta^{13}C$ and $\delta^{15}N$ signatures (mean ± 1 SE) among primary food sources in both TAM and SP habitats. The *circles* are shown to group signatures from each habitat (TAM, SP) and do not indicate significance, and *open symbols* indicate food sources from SP habitat while *closed symbols* indicate food sources from TAM habitat

(equivalent to 10,214, 5,790, and 6,025% enrichment compared to ambient levels) for leaves, stems and roots, respectively. Several macroinvertebrate species acquired substantial quantities of ^{15}N equally from leaves, stems, and roots; there were no significant differences in the mean isotopic signatures of species feeding on different plant parts (animals in leaf treatment = 35.8‰ ± 9.9, animals in stem treatment = 32.8‰ ± 13.1, animals in root treatment = 58.3‰ ± 21.4, $F_{1,10} = 2.12$, $P = 0.673$). The maximum δ ^{15}N value for microalgae (34‰) was observed at 14 days and indicated up to 554% enrichment from background values. This elevated ^{15}N was observed in microalgae within 24 h, potentially reflecting leaching from the labeled tamarisk detritus, but the signals were an order of magnitude lower than that of the labeled detritus (Appendix 3 of Electronic supplementary material). These elevated microalgae δ ^{15}N values were incorporated into subsequent mixing model calculations. In addition, a comparison of $\delta^{15}N$ signatures of invertebrates from leaching bag treatments with $\delta^{15}N$ signatures of invertebrates from normal litter bag treatments revealed that uptake of ^{15}N by animals exposed to N leached through 61-μm mesh was significantly less than uptake of ^{15}N by animals exposed to N detritus directly in either surface or subsurface treatments (ANOVA, $F_{1,11} = 7.46$, $P = 0.020$) (Appendices 2, 3 of Electronic supplementary material).

Species of several major taxa (Acarina, Insecta, Mollusca, Crustacea, Oligochaeta, Polychaeta, and Turbellaria) in TAM and SP habitats incorporated substantial amounts of $\delta^{15}N$ label after 4 days, such that at least 0.5% of their N was estimated from a two-source mixing model to have been derived from labeled tamarisk detritus (Table 1). Averaged within feeding groups, utilization percentage did not differ among animals in TAM and SP marsh habitats (ANOVA, $P > 0.05$ for all feeding groups except microalgal grazers at T270, $F_{1,5} = 12.02$, $P = 0.018$). For most taxa, utilization of tamarisk-derived N peaked at 14 days and declined after 90 and 270 days. Major taxonomic groups did not differ in percent utilization (ANOVA, $F_{1,5} = 0.50$, $P = 0.809$). Psychodidae insects and *Grandidierella japonica* (Crustacea) incorporated the most ^{15}N label after 14 and 90 days, respectively, such that >50% of their N was estimated to have been derived from labeled tamarisk detritus (Table 1). The majority of other species had intermediate levels of uptake: Staphylinidae (both adults and larvae) and Stratiomyidae (Insecta), Gammaridae and Oniscidae (Crustacea), *Polydora nuchalis* (Polychaeta), Enchytraeidae (Oligochaeta), *Assiminea californica* and *Melampus olivaceus* (Gastropoda) had ^{15}N values that indicated that between 5 and 20% of their N was derived from labeled tamarisk detritus. Coleoptera larvae, Chironomidae larvae, Cincindelidae adults, Dolichopodidae larvae sp. 1, *Ephydra* sp. 1, and *Hydrophyillid* sp. 1 (all Insecta) derived <5% of their N from labeled tamarisk detritus. Finally, *Cerithidea californica* (Gastropoda), Hydrophillidae sp. 1 (Insecta), *Transorchestia traskiana* (Crustacea) exhibited minor uptake of ^{15}N-label (0.1–1%) (Table 1).

Uptake in surface versus subsurface animals

Surface utilization of tamarisk-derived N was greater than sub-surface utilization by microalgal feeders in both TAM and SP habitats at day 14 (microalgal grazers $F_{1,10} = 12.485$, $P = 0.005$; mixed diet feeders $F_{1,6} = 0.22$, $P = 0.654$).

Taxonomic comparisons

A comparison of the tamarisk utilization (change in $\delta^{15}N$ signatures from background signatures) revealed taxon differences at the surface only after 270 days. After 270 days in the surface treatment, mites had higher uptake than crustaceans, insects, and gastropods, and insects and crustaceans had higher uptake than gastropods (Appendix 2 of Electronic supplementary material). Unlike surface treatments, after 14 days all taxonomic groups in the subsurface treatment differed in tamarisk utilization with ^{15}N uptake by insects being substantially greater than that of oligochaetes and gastropods, which utilized more tamarisk-derived N than crustaceans (Appendix 2 of Electronic supplementary material). Use patterns were similar at 90 days in the subsurface treatment (oligochaetes and insects showed more utilization than crustaceans) (Appendix 2 of Electronic supplementary material).

Table 1 Percent of N in invertebrate diets that was derived from δ^{15}N labeled-tamarisk detritus at 1, 4, 14, 90 and 270 days after deployment of surface-deployed labeled material

Species	T1	T4	T14	T90	T270
Tamarisk-absent (SP) marsh					
Gastropoda					
Assiminea californica	2.66	0.81	13.69	0.73	1.18
Cerithidea californica	0.53	0			
Melampus olivaceus	0.87	0.45	19.21		0.63
Insecta					
Ceratapogonidae larvae			2.19	6.46	1.17
Coleoptera larvae		2.66	0	2.81	
Chironomidae larvae					1.84
Cincindelidae adult					1.54
Dolicopodidae larvae		1.72		4.05	
Ephydra sp. 1					0.92
Hydrophilid sp. 1				0.21	
Psychodidae			62.45	0.27	
Staphylinidae adult				7.22	
Staphylinidae larvae		16.6			
Crustacea					
Gammaridae			16.56		
Littorophiloscia richardsonae		3.52		3.03	2.04
Polychaeta					
Polydora nuchalis		1.62	4.88		
Oligochaeta					
Tubificoides browniae				0.69	
Enchytraeidae		5.77	13.45		
Other					
Acaria sp. 1				0.93	3.29
Tamarisk-present TAM) marsh					
Gastropoda					
Assiminea californica		1.1	21.52	1.81	0.76
Cerithidea californica		0.37			
Melampus olivaceus	0.22	0.32	19.33		0
Insecta					
Ceratapogonidae larvae		0		0.54	1.51
Coleoptera adult		0.85			
Coleoptera larvae		0.41	0.12	2.2	
Dolicopodidae larvae				0.61	
Ephydra sp. 1					0.96
Poduridae				12.33	
Staphylinidae adult		2.35	4.26	1.6	
Staphylinidae larvae				18.34	1.33
Stratiomyidae		7.78	2.9	1.78	1.15
Tapinoma sessile		0.11			
Unk fly adult #1					3.89
Unk. larvae #1		0.08			
Crustacea					
Gammaridae		9.98	0		3.07
Grandidierella japonica				49.89	
Littorophiloscia richardsonae	2.71	4.63	2.16		1.36
Transorchestia traskiana				0	0.09
Other					
Turbellarian sp 1			0		
Acaria sp. 2		1.72		1.61	6.28

Missing values indicate that that species was not collected at that time point. Percentages are calculated from a single isotope, two-source mixing model for δ^{15}N in which labeled tamarisk detritus was treated as one food source and unlabeled (background) native food sources (i.e. microalgae, POM and SOM) were treated as a second food source

Feeding groups

Uptake of tamarisk-derived ^{15}N differed by food preference type, with greater uptake in detritivores than in microalgal and mixed-diet feeders after 4 days and greater uptake by mixed-diet feeders than detritivores and microalgal feeders after 270 days (Fig. 4). Species-level comparisons at each time period indicated several species exhibited increased N uptake relative to the rest of the species. The greatest tamarisk-derived ingestion, as indicated by elevation of δ^{15}N signatures above background ($\Delta\delta^{15}$N) at 14 days (surface and subsurface) and 90 days (surface only) was by species normally considered to be mixed-diet feeders (Psychodidae sp. 1) or detritivores (*Grandidierella japonica*) (Figs. 5, 6). ^{15}N-labeled tamarisk contributed greater than 50% of the N in these animals at different time points (Table 1). Lesser uptake of ^{15}N label was observed in many other taxa, including microalgal consumers (Figs. 5, 6, Table 1).

Discussion

The spread of tamarisk through the southwestern United States has substantially altered freshwater ecosystems, causing significant changes in flooding and erosion patterns, fire frequency, and both plant and animal diversity (Di Tomaso 1998). The effects of tamarisk as a detrital food source in these systems have recently been shown to be significant, and a factor to be considered in recovery post-eradication (Kennedy et al. 2005). Results of this study indicate that the consequences of tamarisk invasion in the salt marsh system could mimic the dramatic, ecosystem-altering impacts of tamarisk in freshwater environments, by affecting the entire food web from the bottom up.

Is tamarisk available as a food source? Vertically falling tamarisk detritus reaches the sediment surface of the

Table 2 Feeding behavior designations for the macroinvertebrates found in isotope samples

Species	Taxonomic grouping	Feeding behavior
Mite sp. 1	Acaria	Mixed diet[a]
Mite sp. 2	Acaria	Mixed diet[a]
Mite sp. 3	Acaria	Mixed diet[a]
Gammaridae	Crustacea	Detritivore[b]
Grandidierella japonica	Crustacea	Detritivore[b]
Littorophiloscia richardsonae	Crustacea	Mixed diet[c]
Transorchestia traskiana	Crustacea	Detritivore[b]
Assiminea californica	Gastropoda	Microalgal grazer[b]
Cerithidea californica	Gastropoda	Microalgal grazer[b]
Melampus olivaceus	Gastropoda	Microalgal grazer[b]
Ceratapogonidae larvae	Insecta	Mixed diet[d]
Chironomidae larvae	Insecta	Microalgal grazer[d]
Cincindelidae adult sp. 1	Insecta	Detritivore[d]
Coleoptera larvae	Insecta	Detritivore[d]
Coleoptera sp. 1	Insecta	Detritivore[d]
Dolicopodidae larvae	Insecta	Mixed diet[e]
Ephydra sp. 1 pupae	Insecta	Mixed diet
Hydrophilidae sp. 1	Insecta	Microalgal grazer[d]
Muscidae larvae	Insecta	Mixed diet[d]
Poduridae sp. 1	Insecta	Mixed diet[d]
Psychodidae larvae	Insecta	Mixed diet[f]
Staphylinidae adult	Insecta	Mixed diet[g]
Staphylinidae larvae	Insecta	Microalgal grazer[d]
Stratiomyidae larvae	Insecta	Detritivore[d]
Tapinoma sessile	Insecta	Mixed diet[h]
Unk. larvae #1	Insecta	Microalgal grazer[d]
Unknown adult fly	Insecta	Mixed diet[d]
Enchytraeidae	Oligochaeta	Detritivore[i]
Tubificoides browniae	Oligochaeta	Detritivore[j]
Polydora nuchalis	Polychaeta	Detritivore[b]
Turbellarian	Turbellaria	Mixed diet

These designations are based on natural abundance signatures and/or published literature

[a] Di Sabatino et al. (2000), [b]Levin and Currin (2005), [c]Carefoot (1973), [d]Moseman et al. (2004), [e]Bickel and Dyte (1989), [f]Schlein and Muller (1995), [g]D. Holway (personal communication), [h]S. Menke (personal communication), [i]Dash and Cragg (1972), [j]Wavre and Brinkhurst (1971)

marsh in the summer. The observed "very low" standing stocks (below 50 g/m^2 as defined by Olson 1963) indicate that tamarisk is being consumed by detritivores, decomposed, and/or carried out of the system. Leaf degradation rates (K_t) are influenced by temperature, humidity, soil pH, and aeration, in addition to consumption (Moore et al. 2004). The observed difference between leaf residence times based on Kd (29 days) and Kt (0.7 days) is most likely due to factors not considered in this study, such as tidal export. In addition, this was a short-term study that does not consider temporal fluctuations in standing stock or leaf litter production. Although there was a temporal gap between macroinvertebrate sampling in 2004 and litter sampling in 2005 and 2006, the data demonstrate a pattern of tamarisk availability over several years. The observations of a short residence time for tamarisk combined with relatively low C:N values and rapid uptake by infauna support our hypotheses that tamarisk is an available and labile food source comparable to many dominant native plants in the salt marsh, and thus its addition to the environment as detritus has the potential to alter the food web and influence consumers.

Which species derive nitrogen from ^{15}N-labeled tamarisk? Does utilization vary with depth or habitat? Because there were no significant differences in change in δ^{15}N among species when offered different ^{15}N-enriched tamarisk parts, data from root, stem and leaf litter bags were analyzed together. We hypothesized that labeled ^{15}N from tamarisk could end up in consumer tissue through (1) direct detritus consumption, (2) leaching of N and uptake by algae, (3) remineralization by bacteria and subsequent ingestion by bacterivores or grazers, or (4) consumption of animals that had obtained ^{15}N by 1–3. Leaching treatments collected at 90 days after experiment initiation suggest that the leaching and remineralization utilization pathways are minor compared to direct detritus consumption, except at

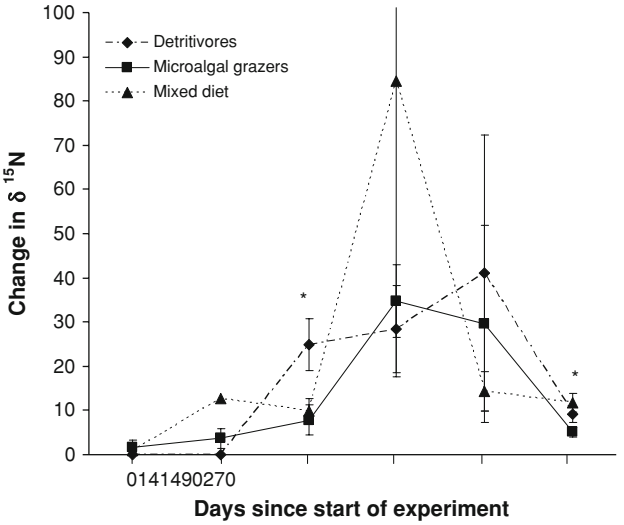

Fig. 4 Mean (±SE) change in δ^{15}N signatures (δ^{15}N experiment − δ^{15}N background) of three infaunal invertebrate feeding groups, detritivores (*line with diamond*), microalgal feeders (*square*), and mixed diet feeders (*dotted line with triangle*), following periods of exposure to ^{15}N-labeled tamarisk detritus at the sediment surface. The scale of *y* axis eliminates the full range of the error bars (up to 160) for day 14, mixed diet feeders. The absence of *error bars* indicates very small error terms or $n = 1$. *Asterisks* indicate a posteriori differences among treatments (ANOVA, T4: $F_{2,20} = 4.85$, $P = 0.019$; T270: $F_{2,16} = 3.09$, $P = 0.053$)

270-day time points. The isotope enrichment data reflect consumption of tamarisk-derived N by species from many taxa and feeding groups, equally in both TAM and SP habitats (Table 1).

Although most species were able to derive N from tamarisk detritus (Fig. 6), Psychodidae and *Grandidierella japonica* incorporated significantly more than did other species. *Grandidierella japonica* is an exotic corophiid amphipod first reported in the United States in San Francisco Bay, CA, in 1966 (Chapman and Dorman 1975) and was first identified in the Tijuana Estuary in 1994 although it may have been present prior to this date (Williams et al. 2001). Rapidly reproducing, opportunistic species, like Psychodidae and *G. japonica*, are capable of taking advantage of expanded resources, such as an input of tamarisk detritus (Zajac and Whitlatch 1982; Greenstein and Tiefenthaler 1997; West et al. 2003).

Detritivore species had the greatest tamarisk-derived N signals, while microalgal feeders (primarily insects) had significantly lower amounts of tamarisk-derived N (Fig; 5). In some cases, mixed diet feeders, such as Acarina and Pscychodidae, also exhibited high levels of tamarisk-derived ^{15}N uptake, suggesting a possible shift from consumption of native plant and sediment organic matter to tamarisk use in higher trophic levels (Fig; 6). Some tamarisk N uptake in microalgal feeders, such as insect larvae and gastropods, may have been due to increased microalgal colonization on the surface of tamarisk detritus and subsequent grazing.

What are the overall food web effects? At the species level, there was coherence between ability to derive nitrogen from tamarisk detritus and the macrofaunal abundance patterns in TAM and adjacent SP marsh. The most abundant or second-most abundant species in the TAM blocks (the oniscid isopod, *Littorophiloscia richardsonae*) and several species whose abundance did not change (Staphylinidae adults) were major consumers (detritivores and mixed-diet feeders), able to incorporate tamarisk-derived nitrogen (Fig; 6). In contrast, the species that were less abundant in the TAM blocks (*A. californica*, enchytraeid oligochaetes, coleoptera larvae) were minimal or intermediate consumers of ^{15}N-labeled tamarisk detritus (Fig; 6). These observations support the hypothesis that macrofaunal composition differences between tamarisk and non-tamarisk areas were influenced by the increase in available detritus. These results mirror trophic patterns and consumption of the invasive *Spartina* hybrid in San Francisco Bay (Levin et al. 2006).

Our results indicate that the macroinvertebrate community and trophic structure are significantly different between our TAM and SP habitats. The causes underlying these site differences are unknown; it is possible that the observed effects are due to historical differences between the habitats that predated the tamarisk invasion. However, close proximity and similar climate and soil characteristics do not explain the significant differences between habitats. First, observed changes in macroinvertebrate community composition could be due to pre-existing differences in plant community composition or amount of shading (Whitcraft and Levin 2007). In addition, the observed isotopic differences in SOM and microalgae, common to both TAM and SP habitats (lighter δ^{13}C and heavier δ^{15}N in natural habitats), imply differences in several factors between these habitats (Fig; 3). The algal and SOM signatures could reflect the signatures of organic matter exuded by vascular plants, *S. pacifica*, more dominant in the blocks where tamarisk was absent, has lighter δ^{13}C than tamarisk, the more dominant plant in tamarisk environment. In addition, the isotopic value differences could be due to C-limitation and fractionation associated with increased shading in natural areas (Whitcraft 2007), or to greater contribution of cyanobacteria in natural areas. Because cyanobacteria tend to be more dominant in shady, wetter environments, this could be an example of how structural alterations can change the growth of a food source (Whitcraft and Levin 2007). Different bacterial or fungal communities could contribute to the patterns found. Finally, although our results suggest that some changes in TAM habitats are bottom-up processes, other factors, including top-down control, grazer access to food sources,

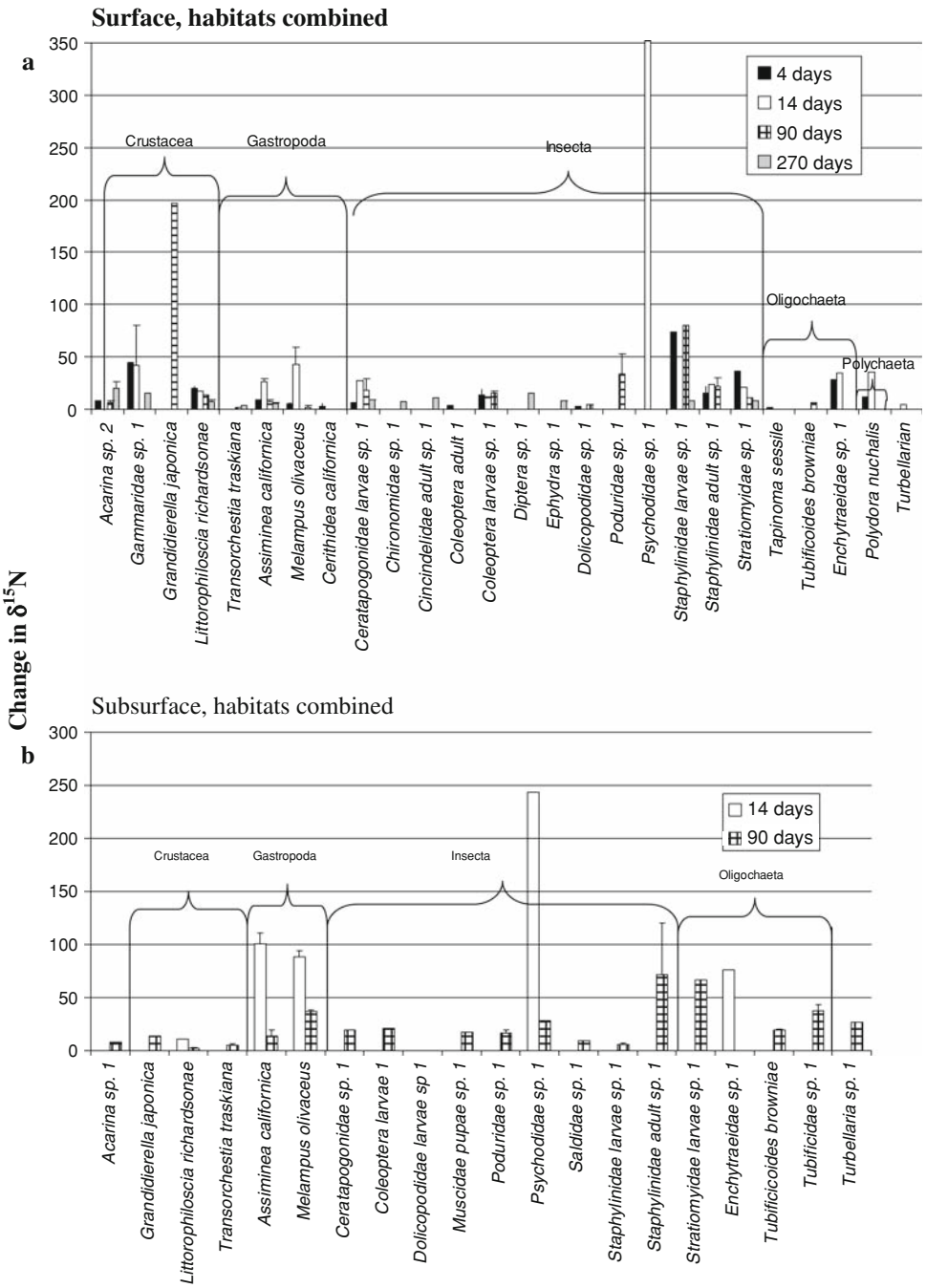

Fig. 5 Mean (±1 SE) change in δ^{15}N signatures from background δ^{15}N signatures of infaunal invertebrate species and families following periods of exposure to ^{15}N-labeled tamarisk detritus at the sediment surface and at subsurface depth of 1 cm in litterbags. The legend numerals refer to sampling days after experiment initiation

flow regime modifications, and indirect changes in food supply, may also structure this benthic ecosystem and differ between TAM and SP habitats as demonstrated for *Spartina* (cordgrass) invasions (Neira et al. 2006).

The study of invasive species is a challenging field because documenting differences between invaded and uninvaded areas brings into question inherent differences about the historical susceptibility of the areas to invasion. Paired block designs that take advantage of a natural arrangement of plants, such as this study, have limitations that complicate identification of underlying mechanisms, but remain an effective method for evaluating invader impacts and critical for identifying patterns (Ashton et al. 2005). Using this type of experimental design, we demonstrate the incorporation of tamarisk into the food web through input of labile detritus. These findings have major implications for understanding how trophic shifts can occur, for appreciating crucial functional differences among invaders, and for increasing our knowledge of how best to manage invasions. The demonstrated food web effects of tamarisk raise interesting parallels with other invasive plant species and may guide understanding of why

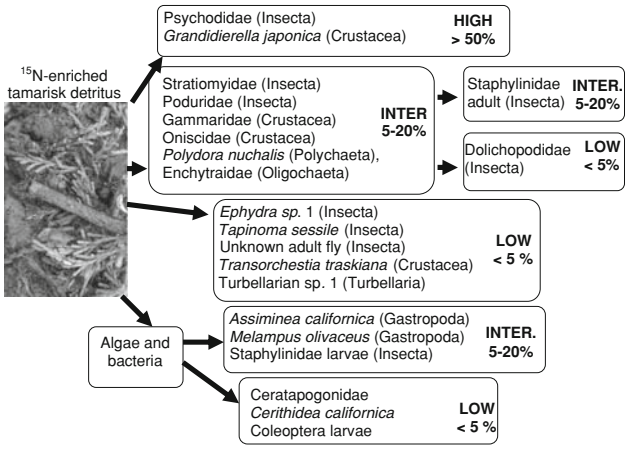

Fig. 6 Hypothesized model based on ^{15}N tamarisk detritus utilization (maximum percent of tamarisk derived-^{15}N that occurred in an individual species is listed). *Inter* Intermediate ^{15}N tamarisk detritus utilization

some wetland plants are more successful or invasive than others. *Phragmites australis* (reed canary grass) in the northeast United States, perhaps the best-studied invader in North American coastal wetland habitats, has multiple effects on higher trophic-levels (Able et al. 2003; Osgood et al. 2003). A second example, a hybrid of *Spartina alterniflora* × *foliosa* (cordgrass) in San Francisco Bay, shifts the dominant primary producers from algae to taller, dense stands of cordgrass (Neira et al. 2007) and shifts the invertebrate community from mainly algal grazers to detritivores (Levin et al. 2006).

Our research also demonstrates that isotopic enrichment of wetland plants is a powerful method to track the fate of introduced plants within food webs and, thus, to potentially assess the impacts of an invader or the recovery of a system. Natural abundance stable isotope methods have proved valuable for tracking food sources into consumers provided that the organic matter sources have distinct signatures (Fry and Sherr 1984; Petersen et al. 1985; Currin et al. 1995; Kwak and Zedler 1997; Levin et al. 2006). However, in situations where important food source signatures overlap, as occurs in the TR NERR mid-marsh, isotopic enrichment experiments allow researchers to identify key consumers of the enriched species, and to identify trophic succession (directional change in abundances of feeding groups) as a possible cause of potential community changes (Levin et al. 2006, this study). Understanding of trophic succession can also be used to evaluate trophic recovery following management action.

Although our study was conducted in a small section (approximately 100 m^2) of low marsh habitat within TR NERR, the area is representative of a significant amount of habitat within TR NERR (20%) as well as an important habitat regionally in southern California. TR NERR shares important features with numerous regional estuaries (seasonal flooding, disturbance from surrounding land use, dominance by wetland habitat, sedimentation) indicating that additional estuaries in southern California are susceptible to invasion by tamarisk. Our results demonstrate that tamarisk has the potential to alter the habitat and detrital cycling of the low intertidal habitats within these marshes. Thus, vigilant monitoring for incipient invasions and rapid, coordinated responses in southern California marshes will be essential to effective management.

Genera such as tamarisk (*Tamarix*), reed canary grass (*Phragmites*), and cordgrass (*Spartina*) act as ecosystem engineers (Bruno and Bertness 2001; Crooks 2002), greatly altering the structure of an invaded site and potentially shifting hydrological conditions and animal communities. Integrating detrital pathways into the study of these and other plant invasions has proved to be crucial in understanding, predicting and mitigating the effects of wetland plant invaders both in the salt marsh and other invaded ecosystems. In the case of tamarisk, enrichment experiments demonstrate that several native consumers can modify their diets to include N derived from invasive tamarisk and that input of tamarisk detritus serves as one mechanism of overall macrofauna community change.

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