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ORIGINAL PAPER

Litter legacy increases the competitive advantage of invasive *Phragmites australis* in New England wetlands

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Abstract Exotic plant invaders that form monocultures and exclude native plants are often the most detrimental to native diversity and the hardest to eradicate. To generate a monoculture, the invader must garner more resources than resident natives and, once established, persist despite high densities of conspecific neighbors. Coincident with expansion and long-term persistence, successful invaders typically accumulate senesced material, but the role of this litter in mediating the invader's ability to establish and maintain monospecific dominance has rarely been investigated. We used stands of the common reed, *Phragmites australis*, a prolific wetland invader in North America, to explore the impact of litter on interspecific competition with the native rush, *Juncus gerardii,* and intraspecific competition among live shoots. In 10 × 10 m areas positioned on *Phragmites* expansion fronts, we removed litter to isolate its effect from live *Phragmites* on light availability, aboveground biomass and community composition. Compared to adjacent, unmanipulated fronts, light availability nearly tripled and *Juncus* biomass increased >170% in litter removal areas after 4 months. Although the positive response of *Juncus* and native forbs was most pronounced on the leading edge of *Phragmites* stands, litter removal triggered a 271% increase in native plant biomass even in the interior of stands where *Phragmites'* live stem density was highest. Litter treatment did not significantly affect *Phragmites* biomass, but more, shorter stems emerged in litter removals revealing *Phragmites* modifies stem phenotype in response to local litter and light conditions. These results suggest that litter plays a central role in *Phragmites'* invasion process, from initial establishment to subsequent monospecific dominance. Thus, prescribed litter removal may be an effective strategy to enhance coexistence of native plant populations in wetlands where eradication of invasive monocultures is not an ecologically or economically feasible option.

Keywords Competition · Intraspecific interactions · Invasive species · *Juncus gerardii* · Monoculture · Tidal marsh · Wetland management

Introduction

Due to the global impacts of exotic plant invasions, understanding the mechanisms that mediate the invasion process, from dispersal to establishment and subsequent proliferation, has become a central goal in

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ecology (Seabloom et al. 2003; Levine et al. 2003 and 2006; MacDougall et al. 2009). As a process, a species' invasion into a novel ecosystem takes place over multiple growth and dispersal cycles with its success in one cycle or year often affecting its success in the next (Levine et al. 2003). These inter-annual effects, such as plant-soil feedbacks or density-dependent growth, may be positive or negative in nature and drive patterns in the distribution and abundance of the invader and resident natives over time (Levine et al. 2006; Farrer et al. 2010). For invasive plants that form expansive monocultures, like cheatgrass (*Bromus tectorum*) in the dry plains of the western US, it seems implicit that an invader's growth in one year generates positive feedbacks that locally enhance its success in the next year (Evans et al. 2001; Healy and Zedler 2010). Litter, which can accumulate over successive growth cycles in the monoculture matrix, often alters the availability of nutrients, light or water (De Jong and Klinkhamer 1985; Evans et al. 2001; Windham and Ehrenfeld 2003; Minchinton et al. 2006; Farrer and Goldberg 2009) and may be a primary mechanism underlying these positive feedbacks and competitive dominance of some species. Despite a breadth of studies on litter impacts on resource availability, nutrient cycling and community structure (Tilman and Wedin 1991; Maron and Jefferies 2001; Marushia and Holt 2008; Farrer and Goldberg 2009), less is known about its role in the development, expansion and maintenance of plant monocultures (but see Evans et al. 2001). Here we investigate the degree to which litter enhances or inhibits dominance of the Eurasian common reed, *Phragmites australis*, a perennial C_3 grass whose monospecific stands are displacing wetland plant communities throughout the central and eastern US (Chambers et al. 1999; Saltonstall 2002), and use this mechanistic insight to detail management strategies for ecosystems invaded by monoculture-forming exotics that are devastating to native plant diversity and challenging to remove (Healy and Zedler 2010).

In wetlands throughout North America, highly productive grasses are becoming increasingly dominant at the expense of native plant assemblages (Farnsworth and Meyerson 2003; Zedler and Kercher 2004). Research has linked these compositional shifts with species introductions and widespread eutrophication of wetlands (Chambers et al. 1999; Bertness et al. 2002; Silliman and Bertness 2004; Zedler and Kercher 2004; Quinn et al. 2007), which has shifted resource limitation from nutrients to light, thereby altering competitive hierarchies in favor of tall plants that are dominant light competitors (Bertness et al. 2002). In particular, nutrient enrichment has been shown to fuel the spread of reed canary grass, *Phalaris arundinacea* (Maurer and Zedler 2002), cattail hybrid, *Typha* × *glauca* (Woo and Zedler 2002; Zedler and Kercher 2004), giant reed, *Arundo donax* (Quinn et al. 2007) and common reed, *Phragmites australis* (Bertness et al. 2002; Minchinton and Bertness 2003; Silliman and Bertness 2004). All of these species expand vegetatively to form extensive monospecific stands and produce tough, lignified stems that decay slowly and accumulate in thickets within the monoculture matrix (Windham and Ehrenfeld 2003; Farnsworth and Meyerson 2003; Farrer and Goldberg 2009). As a legacy of prior growth, litter is often dense in older, interior regions and more sparsely distributed across the leading edge of these expanding monocultures.

Since litter is a common characteristic of these prolific invaders, recent studies have begun to investigate its influence on community structure and resource availability in invaded wetlands. Minchinton et al. (2006) for instance, found that *Phragmites'* litter engineers the environment to exclude native forbs in the early stages of their life history, primarily by shading and obstructing seed delivery and germination. As a result, forbs that are common in high marsh meadows tend to be extremely rare within *Phragmites'* monocultures where few seeds get dispersed and even fewer seedlings emerge through the litter mat (Minchinton et al. 2006). In other studies, the invasion of monocultures that change the quantity and quality of litter have been shown to both increase and decrease soil N availability and N-mineralization rates (Evans et al. 2001; Windham and Ehrenfeld 2003; Farrer and Goldberg 2009), redox potential and water availability (Windham and Lathrop 1999), which have cascading effects on community composition and the productivity of invasive and native plants (e.g., Windham 2000). The role of litter in mediating the invasion of *Phragmites* into dense turfs of native rushes and grasses, the historically dominant space holders in wetlands that spread largely through vegetative growth and harbor forbs and sedges, has yet to be investigated however. In New England marshes, senesced *Phragmites* stems that break and fall to the ground (wrack litter, hereafter wrack) often get lodged within the stand matrix and form persistent mats at the interface of *Phragmites* stands and resident turfs (Minchinton 2002). Since *Phragmites* has thick, pointed tillers capable of penetrating the wrack, we suspect that litter disproportionately smothers native plants at this interface and, thus, plays a key role in driving the expansion of *Phragmites* and corresponding retreat of native turfs.

Additionally, litter can initiate environmental feedbacks that influence the growth of the invader itself (i.e., intraspecific effects). In Great Lakes coastal marshes, for instance, litter generated by cattail hybrid has been shown to increase soil NH_4^+ availability and N mineralization rates within stands compared to the adjacent open marsh, which may explain the taller stem heights and more vigorous growth of cattail transplants grown within a natural litter matrix than transplants grown with its litter removed (Farrer and Goldberg 2009). Aboveground, litter also provides structural support to live stems and may mediate their height and density within a monoculture. The standing dead shoots of *Phragmites*, *Typha, Arundo* and *Phalaris* stands create a tall (1–3 m), rigid framework that buffers wind stress and enhances crowding of interstitial live stems (Fig. 1a, b), which has been shown in other species to induce taller, thinner stem morphologies relative to plants grown in low densities or isolation (Ellison 1987; Holbrook and Putz 1989; Harley and Bertness 1996). Consequently, as stands age and standing dead shoot densities increase, positive soil and structural feedbacks between litter and live stems may give rise to taller stems of invaders like *Phalaris, Typha, Arundo* and *Phragmites* and reinforce their ability to shade out shorter native plants.

Accumulated litter may have negative intraspecific effects on invading monocultures as well. In a study of perennial grassland productivity dynamics, Tilman and Wedin (1991) found that time-delayed inhibitory effects of litter drove chaotic biomass oscillations over time. Grass grown in moderate and high nutrient treatments produced significantly more biomass over the first two growing seasons compared to grass grown in low nutrient treatments, but accumulated litter in fertilized plots stifled tiller emergence and drove a collapse in live biomass in the third year (Tilman and Wedin 1991). Since nutrient enrichment is commonly associated with the success of invasive grasses, like *Phalaris, Typha* and *Phragmites,* and litter production is notoriously high for each of these species (Farnsworth and Meyerson 2003; Zedler and Kercher 2004; Silliman and Bertness 2004), we might expect similar inhibitory effects of litter to drive a reduction in their productivity and slow their expansion over time. At the very least, the slowly decomposing litter of these invaders may immobilize significant pools of nitrogen (Windham and Ehrenfeld 2003) and interfere with the growth of interstitial live stems by blocking tiller emergence and depleting the availability of light and space (Minchinton 2002). As far as we are aware, these litter-mediated intraspecific interactions have not been investigated for invasive wetland grasses. Understanding the nature of these intraspecific interactions between litter and live growth, specifically whether soil and structural feedbacks are positive or negative, will provide useful insight into mechanisms that sustain high productivity

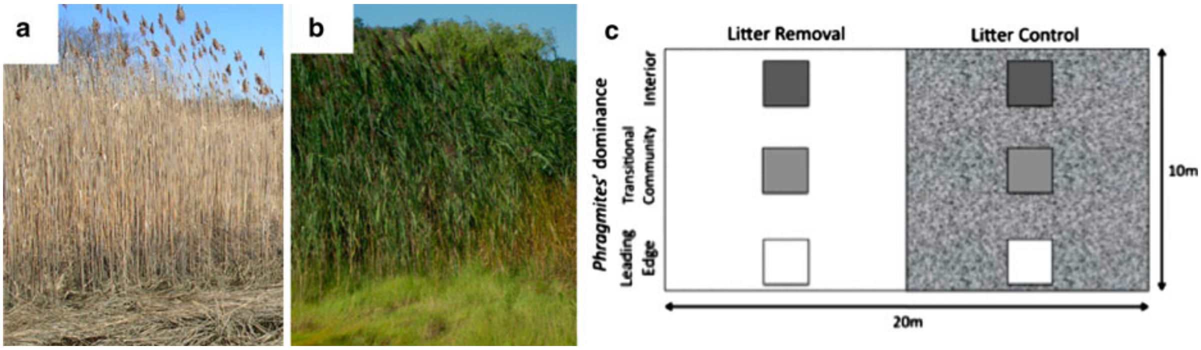

Fig. 1 Expanding monoculture of *Phragmites* at Palmer River Marsh, Rehoboth, MA in March 2008 (**a**), and in August 2008 (**b**), and our experimental design (**c**). This image shows an example of one complete block

of common, invasive monocultures, like *Phalaris, Typha, Arundo* and *Phragmites,* and inform predictions about their long-term persistence.

Furthermore, although the effects of litter on resource availability and competitive interactions have been previously explored, the majority of studies have either assessed litter impacts on relatively small scales ($<6\ \mathrm{m}^2$, Tilman and Wedin 1991; Minchinton et al. 2006; Farrer and Goldberg 2009) or simply compared invaded and non-invaded habitats (Windham and Ehrenfeld 2003). As a result, these approaches have been unable to evaluate the degree to which litter accumulation influences the invasion process of monocultures (but see Windham and Lathrop 1999; MacDougall and Turkington 2005). More specifically, our understanding of litter's contribution to the initial exclusion of resident natives (monoculture formation) or its effect on conspecific growth (long-term persistence) remains tenuous. In this study, we conducted a removal experiment to examine the effect of litter on community composition, primary productivity and light availability across 10 × 10 m areas spanning the sparsely-colonized edge to heavily-colonized interior of *Phragmites'* monocultures. By quantifying the response of both the native plant assemblage and live *Phragmites* stems to litter removal across this gradient, we identify the inter- and intraspecific feedbacks that arise as litter accumulates over successive growth cycles. We then use this mechanistic insight to explore management strategies for ecosystems heavily impacted by monoculture-forming species, like *Phragmites, Typha, Phalaris* and *Arundo,* that aim to disrupt positive feedbacks between litter and invading stands and promote the recovery and coexistence of native with invasive plants.

Materials and methods

Study site

Field studies were performed at the Adolf Rotundo Wildlife Sanctuary (41°46′36.85″N, 71°17′2.24″W) on the Palmer River in Rehoboth, Massachusetts, USA. The upland border of this tidal oligohaline (salinity 0–12 ppt) marsh is heavily colonized by monospecific stands of *Phragmites*, which currently cover ~30% of the total marsh area (see Minchinton and Bertness 2003 for full site description). The species composition of the remaining marsh is similar to other marshes in the northeastern United States with the black rush, *Juncus gerardii*, forming expansive, contiguous turfs throughout the high marsh. Less abundant forbs and sedges, including *Solidago sempervirensis*, *Atriplex patula* var. *hastata*, *Potentilla ansersina*, *Pluchea purpurascens* and grasses, *Agrostis stolonifera*, *Triglocin maritimum*, and *Distichlis spicata* (L.) Greene, are scattered throughout the marsh matrix.

Litter removal experiment

To test the relative importance of litter in driving and maintaining monospecific dominance as it accumulates from young, expanding edges to the older, interior of invading stands, we manipulated the presence of litter in *Phragmites*' stands abutting *Juncus* turfs at the Palmer River study site. In March 2008, prior to the emergence of new growth, we flagged 6- 10 × 20 m blocks along *Phragmites*/*Juncus* borders positioned >25 m from marsh creeks to minimize differences in inundation, split each block in half (2 adjacent 10-m^2 areas) and arbitrarily assigned either a litter removal or control treatment to each half (Fig. 1c). Within each litter treatment block, we marked 1-m^2 plots at three stand positions: the leading edge (4–10 dead shoots/m^2), transitional community (20–30 dead shoots/m^2) and interior (70–100 dead shoots/m^2). We positioned plots in the middle of litter treatment areas to minimize edge effects and, in litter removals only, cleared all the dead shoots at the marsh surface using a brush trimmer and extracted residual wrack from the entire block. Every 3 weeks for the duration to the experiment, we cleared loose *Phragmites'* wrack deposited by tides from litter removal areas. In control treatment areas, we did not manipulate ambient litter levels which where similar across our 6 blocks, but fitted a bungee cord 20 cm over the substrate and positioned 2 wooden stakes on each side of each plot to maintain the initial wrack cover. Bungee cords and stakes were needed to prevent significant changes in wrack cover over the duration of the experiment because wrack can be mobile, particularly along the leading edge of stands.

On a cloudless day in mid-July, we quantified light concentration as an integrated score of readings collected over 90 s with a Quantum light meter

(Spectrum Technologies, Plainfield, IL) in the open marsh to assess full sunlight concentrations (10–90 s light readings). We then collected 1–90 s reading at 5, 40 and 150 cm above the marsh surface in each experimental plot. These levels correspond to the mean height of new emerging growth, the *Juncus* canopy and *Phragmites* leaves. Light measurements were transformed to % full sunlight values (in plot concentration/mean full sunlight concentration %) to provide a relative measure of light available to *Phragmites* and native plants across our experimental treatments. To quantify the composition of the community, we removed any residual wrack and scored percent cover of bare space, *Phragmites*, *Juncus*, *Distichlis* and subordinate species (plants that accounted for <5% cover across all quadrats) using a 0.5-m^2 string grid evenly divided into 100 cells. Coverage was calculated by counting the number of cells occupied by each species (Crain et al. 2004). At the conclusion of the experiment in late August, we harvested aboveground biomass of all plants from 0.40-m^2 sampling quadrats positioned haphazardly in each plot. After sorting samples by species, we counted the total number of live *Phragmites* stems and then measured the height of 8 randomly chosen *Phragmites* stems per plot. Biomass samples of each species in each plot were oven-dried for 72 h at 60°C and weighed.

Statistical analysis

Given that many forbs and sedges were present in only a few plots, we could not assess the individual species' trends across experimental treatments. In an earlier study conducted in this marsh, two forb species responded similarly to litter removal within and outside *Phragmites* monocultures, suggesting that the mechanism underlying the distribution of rare annuals is not species-specific in this invaded landscape (Minchinton et al. 2006). Consequently, we pooled the percent cover and biomass data of all subordinate species together and treated this component of the community as a single response variable in our statistical analysis. Percent cover data were arcsine square-root transformed and biomass data were $\log_{10}(1 + x)$ transformed to meet the assumptions of normality for parametric statistics. Given our modified randomized complete block design, we assigned block and litter treatment nested within block (i.e., identifying each half of the block as a separate treatment unit) as random effects to account for the spatial structure of our experiment, and assigned litter treatment and stand position as fixed effects (see Fig. 1c for reference). We then used a standard method of moments ANOVA to evaluate the effect size and statistical significance of variation in light, community composition and aboveground biomass as a function of litter treatment, stand position, and their interaction (Quinn and Keogh 2002). All data were analyzed using JMP statistical software (SAS Institute 2001).

Results

Litter removal experiment

The removal of litter increased light penetration to the understory and initiated conspicuous changes in the composition of the plant community and growth of *Phragmites* stems after 4 months. At the marsh surface (5 cm) and *Juncus*-canopy (40 cm), we detected an interactive effect of litter treatment and stand position on light (litter × stand position, $F_{2,\ 20} \geq 3.79$, $P \leq 0.0401$), such that plots positioned along the leading edge and interior experienced larger increases in light availability with litter removal relative to those positioned in the transitional community (Fig. 2). The effect of litter removal was dampened in the transitional community for two reasons; relative to the leading edge, less light filtered through the full canopy formed by live *Phragmites* stems in the transitional community so overall increases in light with litter removal were less pronounced, and less wrack and dead shoots were extracted from transitional areas than from the heavily-littered interior, leading to differences in the magnitude of litter removal effects on light in these positions. Across all stand positions, light concentrations increased from 1.9 to 10.2% and 20.2 to 54.8% of full sunlight with litter removal at the marsh surface and *Juncus* canopy, respectively, compared to unmanipulated control stands. In addition, as live *Phragmites* stem density increased in transition and interior positions, light concentrations decreased by an order of magnitude at 40 and 5 cm relative to concentrations recorded along the leading edge (Fig. 2 a, b). At the *Phragmites'* canopy (150 cm), light levels also decreased from the leading edge to the stand

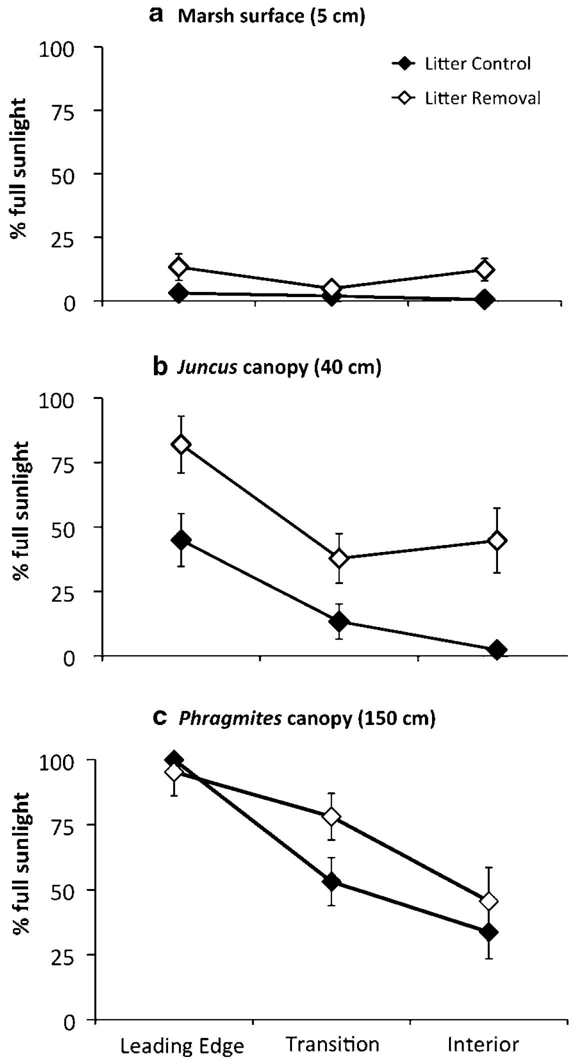

Fig. 2 Effect of litter and stand position on the concentration of light reaching the marsh surface, *Juncus* canopy and *Phragmites* canopy measured on a cloudless day in July. Light concentrations are represented relative to full sunlight concentrations taken in the open marsh. Data are shown as mean ± standard error for 6 replicate treatments

interior, from ~1,300 to 500 mol m^{-2} s^{-1} (stand position, $F_{2,\ 20} = 11.57$, $P = 0.0005$), but litter removal had a negligible effect on light levels at this height (litter, $F_{1,\ 5} = 2.69$, $P = 0.1622$, Fig. 2c).

The removal of litter also triggered changes in the coverage of bare space and composition of the plant community across *Phragmites* invasion fronts (Fig. 3). In unmanipulated plots, litter maintained significant swaths of bare space at the leading edge (72 ± 5% cover, mean ± standard error), transitional community (39 ± 6%) and stand interior (23 ± 10%). In litter removals, however, *Juncus* and subordinate species aggressively revegetated this bare space. The recovery of the native assemblage was greatest along the leading edge and transitional communities where these plants reduced bare space to <10% cover (litter × stand position, $F_{2,\ 20} = 26.18$, $P < 0.0001$, Fig. 3d–f). The positive response of *Juncus* and subordinate species to litter removal was manifested in both percent cover (litter, $F_{1,\ 5} \geq 9.88$, $P \leq 0.0256$) and biomass measures (litter, $F_{2,\ 20} \geq 6.74$, $P \leq 0.0485$, Fig. 3). Although the response of native plants to litter removal was most pronounced on the leading edge of stands (Fig. 3), even in the stand interior *Juncus* cover and biomass recovered to 23.7% and 14.3 g m^{-2}.

In contrast to the positive aboveground biomass response of *Juncus* and subordinate species to litter removal, *Distichlis* did not respond measurably to litter treatments (percent cover and biomass, $P \geq 0.1355$). *Distichlis* was regularly observed within small, exposed pockets under wrack mats (CH, *personal observation*) and thus persisted as a marginal space holder regardless of litter presence or removal in the leading edge and transition region of stands. In the stand interior, however, *Distichlis* cover and biomass fell to 0 regardless of litter treatment (Fig. 3).

As native plant coverage diminished from the leading edge to interior regions, *Phragmites* percent cover and biomass increased steadily (Fig. 4). With increasing dominance, live *Phragmites* stems grew taller and denser than those on the sparsely colonized leading edge (Table 1). Although aboveground biomass was not strongly influenced by litter, more, shorter live stems emerged in litter removals than in control stands. In the interior positions where we cleared the most standing dead shoots per plot from litter removals (~85 dead shoots removed on average), the mean stem height decreased from 165 to 130 cm, a difference that was not statistically significant but visible in the field, and live stem densities doubled, from 27.5 ± 3.2 in natural control stands to 57.3 ± 6.8 stems/m^2 with litter removal (Fig. 4, Table 1). Also, at leading edge of stands where standing dead shoots are sparse, the effect of litter removal was dampened and *Phragmites* stems were generally shorter and live stem densities lower.

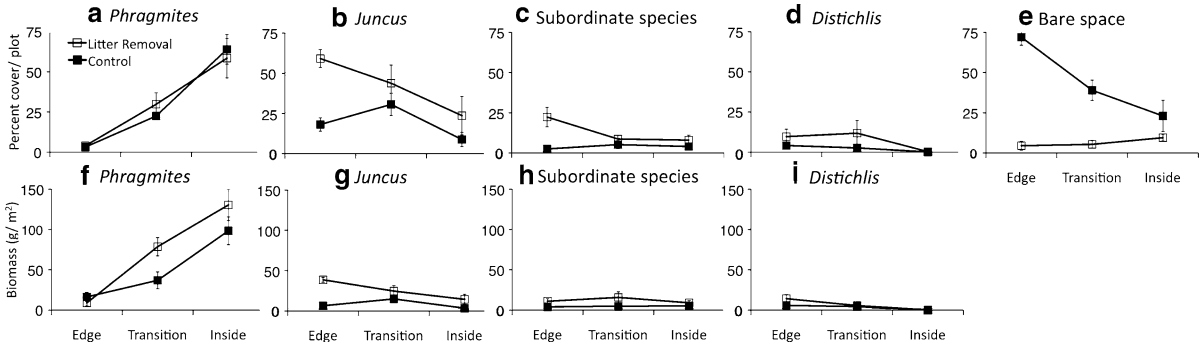

Fig. 3 Effect of litter on the percent cover (**a**–**e**) and aboveground biomass (**f**–**i**) of marsh plants at three levels of *Phragmites*' dominance. Data are shown as mean ± standard error for 6 replicate treatments

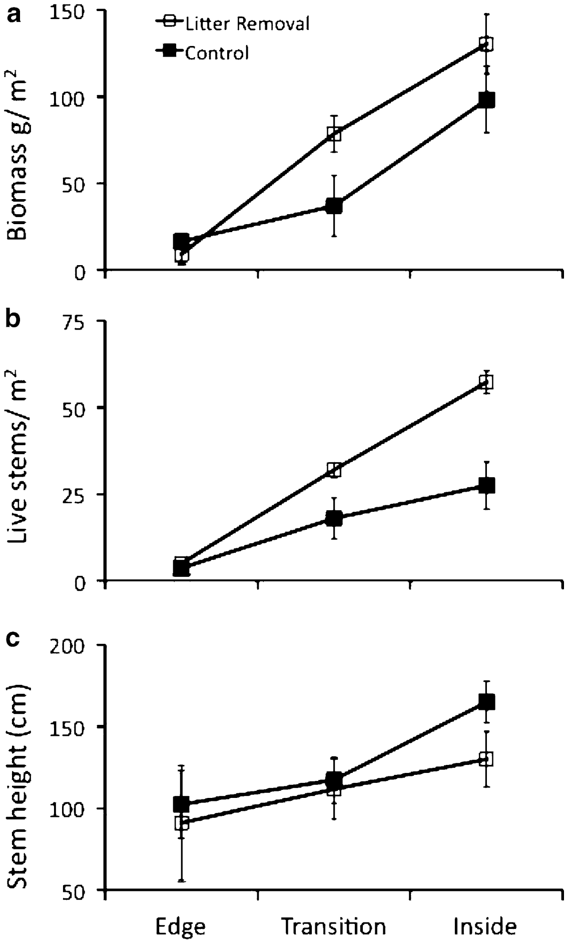

Fig. 4 Effect of stand position and litter treatment on the aboveground biomass (**a**), live stem density (**b**) and stem height (**c**) of *Phragmites*. Data are shown as means ± standard error

Discussion

Our results reveal that litter plays a central role in the transformation of wetland plant communities to monospecific stands of invasive grasses. By persisting in wrack mats that inhibit the emergence of native plants and in matrices of standing dead shoots that shade the understory and support the vertical growth conspecific stems, litter generates positive feedbacks that allow *Phragmites* to monopolize light and maintain high growth rates and production. Consequently, removing litter to counteract these positive feedbacks and reducing nutrient run-off from anthropogenic sources to reduce litter production could prove an effective management approach to maintaining plant diversity and ecosystem function in wetlands where monocultures of invasives are too robust to eradicate.

Litter interference, light, and loss of native plants

These data provide considerable evidence that litter mediates community composition and productivity along invasion fronts, based on the significant increase in native species' percent cover and biomass following litter removal. This increase, or recovery of native vegetation, was most evident along the leading edge of monocultures where, despite low densities of live *Phragmites* stems, wrack mats can maintain large swaths of bare space. Even in the transitional community and interior stand positions, however, native plants rapidly revegetated approximately 50

Table 1 Summary of results from standard method of moments ANOVA for *Phragmites* aboveground biomass, live stem density and live stem height response to experimental treatments. Random effects are not shown

	Aboveground biomass		Live stems/m^2		Stem height (cm)	
Effect	*F*	*P*	*F*	*P*	*F*	*P*
Stand position ($df = 2, 20$)	32.65	<0.0001	90.94	<0.0001	8.86	0.0019
Litter ($df = 1, 5$)	0.54	0.4946	9.24	0.0288	1.23	0.3167
Position × litter ($df = 2, 20$)	2.16	0.1411	0.6119	0.5522	0.86	0.4393

and 30% of ground cover exposed by litter removal, emerging conspicuously in the broad interstitial space between live *Phragmites'* stems left bare. Both the dominant turf, *Juncus*, and the subordinate forbs, sedges and grasses responded to litter removal across all three stand positions indicating that dispersal was not detectably limiting for particular species or functional groups within the scale of our study. We suspect that this vigorous response may be partially a result of our experiment being located on the boundaries of *Phragmites* stands where seeds and rhizomes of native plants remained viable beneath the wrack mat. If litter were removed from expansive, well-established *Phragmites* monocultures at a larger scale, the emergent, native community would likely reflect species-specific differences in dispersal, since few plants would germinate locally from the seed bank or sprout from live rhizomes (see Minchinton et al. 2006 for further discussion). Specifically, species that produce wind- or tide-dispersed seeds able to infiltrate the *Phragmites* stand would be more likely to recolonize interior regions than native turf grasses or rushes that spread primarily via vegetative growth. Regardless of scale, native forbs, sedges and grasses appear able to coexist as a mixed community with *Phragmites* if the thick layer of litter is reduced.

The species-diverse and rapid recovery of the native plant assemblage in litter removals also suggests that light is the key limiting resource mediating plant growth, a finding consistent with other productive, grass-dominated ecosystems (see MacDougall and Turkington 2005 for review). Although soil properties and edaphic factors, such as salinity, soil moisture, redox potential, and water level are known to differ in *Phragmites*-dominated areas compared to un-invaded habitats (Windham and Lathrop 1999; Windham 2000), we found no evidence that these variables or other allelopathic effects inhibit the growth of natives as twelve different species emerged within the monoculture matrix over the course of our experiment. In fact, *Solidago sempervirens* and *Atriplex patula* var. *hastata*, common halophytic forbs in New England marshes, were shown to grow better in soil extracted from *Phragmites* stands than soil from *Juncus* turfs in an earlier study, which further supports the idea that soil or edaphic conditions are not the principle driver of native plant loss observed in *Phragmites* monocultures (Minchinton et al. 2006). Given that belowground conditions are not excluding natives and that native species emerged only when litter was removed, we can infer that changes in aboveground conditions (i.e., light) are primarily responsible for mediating community composition. By filtering light to the *Juncus* canopy as standing dead shoots and essentially eliminating light reaching the marsh surface as wrack, litter significantly enhances *Phragmites* ability to intercept and monopolize light. In invader-dominated grasslands and savannahs, mowing experiments have reported similar impacts of litter on light resources and community structure with the removal of the aboveground biomass of dominant invaders prompting the recovery of native vegetation (Maron and Jefferies 2001; MacDougall and Turkington 2005; Coleman and Levine 2007). The widespread success of invasive species that monopolize light via litter accumulation indicate that it is an effective strategy to become established and persist in novel environments and is likely the key mechanism underpinning the proliferation of productive plant invaders in eutrophic habitats where belowground competition for nutrients is relaxed and competition for light is intensified (Bertness et al. 2002; Silliman and Bertness 2004).

In addition, our data also support the prediction that litter initiates positive, intraspecific feedbacks that enhance and sustain the productivity of the monoculture over time. By congregating in wrack mats that get lodged against the leading edge of invading stands, litter smothers underlying vegetation to create large patches of bare space along the interface of invading stands and *Juncus* turfs. Although we observed small patches of *Juncus* and *Distichlis* opportunistically poking through breaks in the wrack and thriving in mixed assemblages with *Phragmites* where the wrack was absent, these historically dominant clonal species were largely displaced even in the recently invaded, sparsely colonized areas of the marsh. Over successive years, *Phragmites* infiltrates in this bare space using its thick rhizomes to forage through the substrate and dense, pointed tillers to pierce through the wrack. Since our experiment was only conducted over a single growing season, we were not able to detect whether the presence of wrack influences the rate or directionality of stand expansion. Results from Minchinton and Bertness (2003), however, showed that clearing matrix vegetation along *Phragmites'* borders increases the density, height and biomass of *Phragmites* stems relative to control borders where the matrix vegetation was left intact. Consequently, wrack may play a key role in both ensuring the success of *Phragmites'* invasion and accelerating the rate of its expansion across marsh landscapes (Minchinton 2002).

The morphological response of live *Phragmites* to litter removal provides additional insight to long-term persistence of this invader. In interior regions of monocultures, live stems typically grow extremely tall (>3 m) but are relatively sparse with individual live stems often spaced at distances >10 cm. *Phragmites* sustains high levels of productivity with this 'few, but tall stems' morphology because the rigid framework of standing dead shoots provides structural support to emerging stems, enabling them to reach full sunlight and maintain high rates of photosynthesis (Farrer and Goldberg 2009; Mozdzer and Zieman 2010). When we removed litter, rhizomes produced twice as many shorter stems than in the adjacent control stands, demonstrating that *Phragmites* stem traits are not fixed, but plastic, and acutely responsive to light and crowding conditions (Minchinton and Bertness 2003). This litter (light)-associated variation in stem traits was also apparent on the leading edge of stands where ample light reaches the understory and, consequently, *Phragmites* stems typically do not grow taller than 1 m. Thus, stands adjust the density and height of live stems to access adequate light as the rhizomes develop and litter load thickens, resulting in positive feedbacks between litter and live neighboring stems that enhance the height and thickness of the canopy over time (Farrer and Goldberg 2009).

Coincident with changes in stem height and density, aboveground biomass increased in transitional areas and the stand interior with litter removal but this response was not significant over the time span of our experiment. This suggests that litter accumulation may moderately stifle growth but does not elicit strong inhibitory effects as described in Tilman and Wedin's study of oscillatory productivity dynamics in grasses (Tilman and Wedin 1991). We suspect that *Phragmites* and other wetland invaders are less vulnerable to litter-mediated inhibition because of a number of hallmark characteristics; their sharply pointed tillers, tall, lignified stems and fast growth rates. These traits enable these species to persist within the litter matrix, even in eutrophic environments where litter production is high. Thus, rather than driving a collapse in the productivity, litter appears to secure the dominance, productivity and persistence of these invaders over time.

Management recommendations and the future of North American wetlands

Attempts to eradicate invasive species are often futile due to the tremendous human effort and financial resources these conservation efforts require (see Levine et al. 2003). A more practical option, therefore, may entail changing the goals of invasive species management from species removal to impact mitigation. Specifically, implementing strategies that aim to counteract the effects that invaders have on the environment (i.e., plant-soil feedbacks) or facilitate the recovery of resident natives will likely prove a more economically feasible and sustainable approach (Maron and Jefferies 2001). In our study, simply removing litter from *Phragmites* stands with a brush trimmer prompted the vigorous revegetation of native plants, a response consistent with mowing studies performed in a number of other heavily invaded grassland ecosystems (Maron and Jefferies 2001; MacDougall and Turkington 2005). In shifting the community composition from a monoculture to a mixed plant community, we suspect that litter removal also enhanced the quality of this wetland habitat for higher trophic level species, including birds, invertebrates and mammals whose foraging may be altered by the thick litter matrix (Benoit and Askins 1999; Warren et al. 2001) and insects that preferentially utilize forbs and sedges for food and habitat (Tewksbury et al. 2002). Generally, our findings suggest that efforts focused on disrupting positive feedbacks between litter and live growth within monoculture-forming invasives can be quite effective in maintaining viable native plant populations and restoring community structure. Further studies that investigate the effects of timing (spring versus summer or fall trimming), target (live stems only, litter or both) and replication (one or multiple trimmings) of aboveground biomass removal, as well as research that quantifies ecosystem services in control versus litter-removed stands, would provide additional valuable information about the efficacy of different litter removal methods in restoring ecosystems.

In addition to managing established populations of invasive species within a given wetland, identifying the landscape-level factors associated with their establishment and proliferation is also crucial to our ability to develop long-term, sustainable strategies to minimize their impacts (Zedler and Kercher 2004). Throughout North America, the eutrophication of wetlands stimulated by increased use of fertilizers and the removal of woody, buffer zones that filter nutrient run-off has been causally linked with the success of the most detrimental invasive plants, *Phalaris, Arundo, Typha* and *Phragmites* (Maurer and Zedler 2003; Silliman and Bertness 2004; Quinn et al. 2007; Farrer and Goldberg 2009). High nutrient inputs fuel the spread of these species that tower over native plants and stimulate the production of thick mats of their litter. Consequently, active restoration of the woody buffer zone surrounding wetlands and policies to reduce fertilizer run-off, strategies to shift resource limitation from light back to nutrients, are necessary to mediate the competitive advantage and slow further expansion of these robust invaders.

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