

Holcus lanatus invasion slows decomposition through its interaction with a macroinvertebrate detritivore, *Porcellio scaber*

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Abstract Detritus based food webs may mediate the impacts of invasive species on ecosystem processes. *Holcus lanatus* (L.) is an invasive perennial grass that is rapidly spreading in the coastal prairie of California. We used litterbags to determine if *H. lanatus* altered the rate of litter decomposition through its interaction with the dominant macroinvertebrate detritivore at our study site, the isopod *Porcellio scaber* (Latreille). Over the course of a year, *H. lanatus* litter loss was 15% less than annual grasses, a difference that was directly attributable to *P. scaber*. Although there was no effect of isopods on litter loss during the winter, when most decomposition occurred, isopods had substantial effects on litter loss of annual grasses during the summer. *P. scaber* had no effect on litter loss of *H. lanatus* litter. Our findings suggest that *H. lanatus* invasion slows decomposition in the coastal prairie because it is unusually refractory to an important detritivore. The decreased decomposition of *H. lanatus* litter, along with increased production during the growing season,

lead to a doubling of the end-of-season litter biomass where *H. lanatus* had invaded.

Keywords California grasslands · Decomposition · Detritus based food web · *Holcus lanatus* · Introduced species · Litterbags · Litter dynamics · *Porcellio scaber* · Seasonality

Abbreviations

BMR Bodega Marine Reserve

Introduction

Invasive species can impact resident species, the diversity of invaded communities, as well as ecosystem processes. Although conservation concerns primarily focus on their direct impacts on native species and communities, the influence of invasive species can also be indirect, mediated through changes to ecosystem processes (Vitousek et al. 1987; Vitousek 1990). Decomposition is one of the fundamental ecosystem processes and is responsible for the recycling of nutrients in dead biomass (Swift et al. 1979). Invasive plants have had a wide variety of impacts on decomposition and nutrient cycling in terrestrial systems (Ehrenfeld 2003).

Although invasive terrestrial plants are known to impact both decomposition (Ehrenfeld 2003) and detritus based food webs (Lindsay and French 2006;

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Standish 2004; Kourtev et al. 1999; Kourtev et al. 2002), there have been few experimental studies of the role of detritus based food webs in mediating the impacts of invasive species. The interactions between invasive plants and the detrital food webs of invaded communities are likely to be important in understanding the impacts of invasive species on decomposition and nutrient cycling. For example, different plant species typically harbor distinct soil microbial assemblages (Bardgett et al. 1999; Grayston et al. 1998; Bardgett and Walker 2004), and macroinvertebrate detritivores exhibit preferences among litter types (Nicolai 1988; Hendriksen 1990; Tian et al. 1993). Cameron and Spencer (1989), for example, have suggested that the terrestrial isopod *Armadillidium vulgare* may play a role in the increased nutrient turnover following Chinese tallow (*Sapium sebiferum*) invasion in a coastal prairie in Texas.

California grasslands are among the most heavily invaded ecosystems in the world. Prior to European colonization, California grasslands are believed to have been dominated by perennial grasses (Heady 1988). European annual grasses were introduced with the earliest European settlements (Hendry 1931), and have long since dominated inland California grasslands (Heady 1988). Native perennial grasses have remained more abundant in coastal prairie (Stromberg et al. 2001), where they are competitively superior to many introduced annual grasses (Corbin and D'Antonio 2004). However, *Holcus lanatus* (velvet grass or Yorkshire fog), an invasive perennial grass native to Europe, appears to be competitively superior to resident species in the coastal prairie, where it is considered a conservation threat (Anderson et al. 1999). *H. lanatus* forms dense monocultures (Peart 1989) that spread extensively during the latter 20th century and now threaten native plant species that have been able to coexist with introduced annuals (Kotanen 2004). The spread of *H. lanatus* is therefore considered a threat to native plant species even when it is a secondary invader of heavily invaded grasslands.

We examined the effects of *H. lanatus* invasion on litter decomposition in an annual-dominated coastal prairie, and the extent to which an abundant detritivore, the sowbug *Porcellio scaber*, mediates these effects. Native perennial grasses were not used in this study because they now account for only a small fraction of the litter produced in our study site (Maron and Jeffries 2001). Because both

H. lanatus and the annual grasses used in this experiment are introduced to California, this experiment does not test for a difference between native and exotic species; instead, our results document the ecosystem consequences of a secondary invasion and test a possible mechanism for these ecosystem changes.

Methods

This experiment was carried out at the Bodega Marine Reserve (BMR). BMR is a 146 ha reserve located in Sonoma Co., California USA (38° 19' N, 123° 4' W). The reserve receives an average of 86 cm of rain a year (SD 35 cm, Bodega Ocean Observing Node 2006), the majority of which (>80%) falls between November and March. Frequent fogs moderate the summer drought and serve to extend the growing season. This experiment was conducted during a year with average rainfall (83 cm). The western portion of BMR has sandy loam soils and supports coastal prairie vegetation, including a mix of annual and perennial grasses and forbs. Although native perennial grasses are abundant at some locations within the coastal prairie, we conducted this study at the border between a *H. lanatus* monoculture and an annual-dominated grassland comprised primarily of exotic grasses. BMR is naturally treeless and contains only three species of shrubs.

The dominant macroinvertebrate detritivore at BMR is the terrestrial isopod *P. scaber*, which reaches densities of 350/m² (Bastow unpublished data). Although native to Western Europe, *P. scaber* is now found throughout the world (Harding and Sutton 1985) and has been present in California for over a century (Richardson 1905). It is unclear if terrestrial isopods occurred in California grasslands prior to European contact; all terrestrial isopod species reportedly found in California grasslands at present are introduced from Europe, as are most terrestrial isopod species found throughout North American grasslands (Jass and Klausmeier 2000). Terrestrial isopods are generalist scavengers that feed primarily on dead plant matter (Sutton 1972), although they also consume seedlings (Paris and Sikora 1965), insect eggs (Ehler 2002), feces (Hassall and Rushton 1982; Zimmer and Topp 2002) and dead arthropods. *P. scaber* is active at BMR from spring until early fall (Bastow unpublished data). Other

macrodetritivores found on the reserve include a second species of terrestrial isopod, *Armadillidium vulgare* (Latreille), as well as millipedes, earthworms and termites. Neither *A. vulgare* nor termites are found at the particular sites used in this study. Millipedes and earthworms are present, albeit at lower abundance than *P. scaber*, and are active during the wet Mediterranean winter (Bastow unpublished data).

Experimental design

We used litterbags to measure litter mass loss in an annual grassland site and a *H. lanatus* monoculture (Falconer et al. 1933). *H. lanatus* forms a single large monoculture at BMR, along with scattered individual bunches. Because we were interested in decomposition in the *H. lanatus* monoculture, we were unable to replicate habitat patches. In order to separate the effects of litter and site, we performed a full reciprocal transplant, in which we transplanted both *H. lanatus* and annual grass litter into both the *H. lanatus* monoculture and the adjacent annual grassland site. In order to estimate the contribution of *P. scaber* to litter loss, we used both isopod exclusion litterbags and isopod access litterbags (Crossley and Hoglund 1962). We thus had three factors (litter type, site and isopod access) and a total of eight treatment combinations. We constructed 12 litterbag replicates of each treatment combination (96 litterbags total), half of which we collected after each of two sampling periods (6 and 12 months).

Litterbags

We constructed litterbags out of fiberglass window screen (1.5 mm mesh). Litterbags were 10 cm by 10 cm in area and litterbags in the isopod-access treatment were each perforated with ten holes (6 mm diameter). It is possible that intact litterbags excluded other detritivores in addition to *P. scaber*, although *P. scaber* accounts for the majority of macroinvertebrate detritivores at our site. We used the presence or absence of other invertebrates in collected litterbags, along with differences in the seasonal phenology of macroinvertebrate detritivores, to make inferences about the relative contributions of *P. scaber* and other invertebrates to observed treatment effects.

We collected litter from the annual grassland site and the *H. lanatus* monoculture in August of 2002.

Litter was air-dried in the lab for 5 days prior to assembling the litterbags. To measure the initial moisture content of our litter and estimate initial dry weights of litter, we oven-dried six samples of each litter type at 50°C to constant mass. We placed 3.00 g (± 0.10 g) of air-dried litter into each litterbag. Litter used in the litterbags was not oven-dried, because of the possibility that oven-drying may alter the chemical composition of the litter (Harmon et al. 1999). Litter from the *H. lanatus* monoculture and the annual grassland were predominately (>95% by mass) *H. lanatus* and annual grass litter, respectively. The most abundant annual grasses at this site were *Bromus diandrus*, *Lolium multiflorum*, and *Vulpia bromoides*. We placed the litterbags in the field in September 2002. In order to measure over-winter litter mass loss, we collected half of the litterbags in March 2003 (after 6 months). The remaining litterbags were collected in September 2003, to measure litter mass loss after a full year. We were unable to locate one of the litterbags from the 6-month set and four of the litterbags from the 12-month set. Arthropods were then removed from the litterbags, identified and counted. Litter was rinsed to remove sediment, and oven dried at 50°C to constant mass.

Data analysis

In order to evaluate the effectiveness of the isopod access manipulation in this experiment, we analyzed the effect of punching holes in the litterbags on the number of isopods found inside the litterbag. Because the number of isopods was not normally distributed among litterbags, we used the Median test (Steel et al. 1997). We analyzed the proportion of litter lost with factorial ANOVAs on arcsine square root transformed data. Litterbags collected in March and September were analyzed in separate ANOVAs. Litter type, isopod access and site were included as factors, along with all of their two-way and three-way interactions. We performed pair wise treatment comparisons of interactions with Tukey tests. We performed all analyses using JMP IN 4.0.3 (SAS Institute).

Estimating litter accumulation

In order to estimate how differences in decomposition affect litter accumulation in *H. lanatus* invaded and annual grasslands, we used Olson's equation for litter

accumulation in a system with discrete annual litter fall (Olson 1963). Olson's equation, $T = L/k'$, relates the annual peak litter biomass (i.e., litter biomass immediately after litter fall), T , to the biomass of annual litter fall, L , and the annual decomposition rate, k' . This relationship assumes that both production and decomposition are roughly constant from year to year (i.e., a constant fraction of litter decomposes each year, as in exponential decay models of decomposition (Swift et al. 1979)). We also assumed that both sites are annual systems, meaning that aboveground vegetation dies at the end of the growing season. Aboveground biomass at the end of the growing season could then be used as an estimate of annual litter fall, L . Although we did not measure aboveground biomass at the end of the 2002–2003 growing season, when we measured decomposition, we did measure aboveground biomass in both the *H. lanatus* invaded site and the adjacent annual grassland at the end of the 2001–2002 and 2004–2005 growing seasons as part of ongoing surveys. We measured aboveground biomass by clipping all standing plant biomass within eight 0.25 m² quadrats in the *H. lanatus* invaded and the adjacent annual grassland of two (in 2002) or three (in 2005) sites along the margin of the *H. lanatus* monoculture. The *H. lanatus* invaded areas used for biomass surveys were mowed during the summer of 2004 by BMR's reserve steward as a control effort. This did not affect our litterbag experiment (which took place before the mowing) and by the time of our 2005 biomass survey the area had had a full year to produce new growth.

Results

Isopod exclusion

Our manipulation of isopod access was effective. The number of *P. scaber* in hole-punched litterbags collected in March, after 6-months, 3.71 ± 1.25 isopods/litterbag, or 371 ± 125 isopods/m², was within the range of field densities observed at BMR, and was an order of magnitude greater than the number found in intact (unpunched) litterbags, 0.17 ± 0.12 isopods/litterbag (mean \pm SE). The hole-punched litterbags collected in September, after 12-months, had fewer isopods, 0.75 ± 0.30 isopods/litterbag, and we found no isopods in the intact litterbags collected in September. In both cases the hole-punched litterbags

had many more isopods than intact litterbags (March: $\chi^2 = 9.38$, $P = 0.0022$; September: $\chi^2 = 8.15$, $P = 0.0043$). *P. scaber* was the only macroinvertebrate detritivore we found in the litterbags, although small numbers of spiders were also observed.

Litter mass loss

Isopods increased litter mass loss of annual grass litter over the full year, but had no effect on over-winter decomposition (Tables 1, 2, Fig. 1). Litterbags collected after a full year that excluded isopods showed a reduction in decomposition from $59.7 \pm 2.7\%$ litter mass loss to $49.8 \pm 1.1\%$ (averaging over both litter types and sites). There was an interaction between isopod access and litter type in the full year litter mass loss analysis (Litter type X Isopod access). Neither the interaction between isopod access and site (Isopod access X Site) nor the three-way interaction (Litter type X Isopod access X Site) were significant over either sampling period (See Appendix A for a full ANOVA tables).

Litter type had the clearest and most consistent effect on litter mass loss across both sampling periods (Table 1). Annual grass litter lost more mass ($45.6 \pm 2.1\%$ over-winter, $58.8 \pm 2.3\%$ over the full year, averaging over sites and isopod access) than *H. lanatus* litter ($37.5 \pm 2.0\%$ over-winter, $49.7 \pm 1.6\%$ over the full year) in both sampling periods. Although isopods did not affect litter mass loss over-winter (when isopods are relatively inactive), they increased annual grass litter loss over the full year (by 17.6%). Isopods did not increase litter loss of *H. lanatus* litter.

Site of litter decomposition affected over-winter litter mass loss, but this effect was not significant for the full year (Table 2). Over-winter litter mass loss was 8.1% greater in the *H. lanatus* monoculture than in the annual grassland site. Because of the lack of site replication, it is not possible to attribute this difference to either habitat effects of *H. lanatus* or characteristics of sites more readily invaded by *H. lanatus*. In any case, decomposition did not differ between sites by the end of the summer. Isopods increased full year litter mass loss in both the annual grassland and *H. lanatus* invaded sites (11.8% in the annual grassland, 8.1% in the *H. lanatus* invaded, averaging over litter types).

In order to combine the effects of site and litter type into an estimate of the decomposition rates that

Table 1 The effect of litter type and isopod access on litter mass loss over the first 6 months and the full year, averaging over both sites. Different letters indicate significant differences

within the same time period (ANOVA, with Tukey Test on the litter X isopod interaction term)

Litter	% Litter loss over winter without isopods	% Litter loss over winter with isopods	Difference attributable to isopods	% Litter loss full year without isopods	% Litter loss full year with isopods	Difference attributable to isopods
<i>H. lanatus</i>	39.1 ± 1.9	36.0 ± 3.4	-3.1 ± 5.3	48.7 ± 1.8 ^a	51.0 ± 2.9 ^a	2.3 ± 4.7
Annual grasses	45.3 ± 1.4	45.8 ± 4.0	0.5 ± 5.4	50.8 ± 1.3 ^a	68.4 ± 2.5 ^b	17.6 ± 3.8 [†]

† indicates litter types where isopods significantly increased litter mass loss

Table 2 The effect of site and isopod access on litter mass loss over the first 6 months and the full year, averaging over both litter types. Different letters indicate significant differences

within the same time period (ANOVA with Tukey Test on the site X isopod interaction term)

Site	% Litter loss over winter without isopods	% Litter loss over winter with isopods	Difference attributable to isopods	% Litter loss full year without isopods	% Litter loss full year with isopods	Difference attributable to isopods
<i>H. lanatus</i> invaded	45.6 ± 1.3	45.5 ± 2.1	-0.1 ± 3.3	51.6 ± 1.7 ^{ac}	59.7 ± 2.7 ^b	8.1 ± 4.4 [†]
Annual grassland	38.8 ± 1.9	36.3 ± 4.9	-2.5 ± 6.8	47.9 ± 1.3 ^a	59.7 ± 4.6 ^{bc}	11.8 ± 5.9 [†]

† indicates sites where isopods significantly increased litter mass loss

naturally occur in these habitats, we considered the mass loss of each litter type in its site of origin. We compared the decomposition of annual grass litter in the annual grassland and *H. lanatus* litter in the *H. lanatus* monoculture (“within-site decomposition”, Fig. 1). There were no differences in over-winter within-site decomposition. By the end of the full year, however, the annual grassland had greater litter mass loss than the *H. lanatus* site in the isopod access treatment, but there was no difference in the isopod exclusion treatment.

Estimates of litter accumulation

The end of season aboveground biomass for the *H. lanatus* invaded grassland was $797 \pm 264 \text{ g/m}^2$ (mean ± SD) in 2002 and $874 \pm 210 \text{ g/m}^2$ in 2005. Aboveground biomass in the annual grassland was lower in both years: $534 \pm 179 \text{ g/m}^2$ in 2002 and $534 \pm 134 \text{ g/m}^2$ in 2005. Although there is considerable variation in aboveground productivity within years, the difference between *H. lanatus* invaded and annual grasslands was large and of similar magnitude in both years. We used the means of these 2 years of data, 836 g/m^2 for the *H. lanatus* invaded grassland and 534 g/m^2 annual grassland, as values for annual litter input (L) in our estimates of litter accumulation.

Annual grass litter in the annual grassland lost 69.7% of its mass when isopods were present, so that $k' = 0.697$ and $T = L / k' = 766 \text{ g/m}^2$. Excluding isopods decreased litter loss for the full year to 49.9% for the annual grass litter in the annual grassland site, so the estimated equilibrium litter biomass in the absence of isopods would be $1,070 \text{ g/m}^2$.

H. lanatus litter in the *H. lanatus* invaded site lost 54.4% of its mass during the year, which translates into an estimated equilibrium litter biomass of $1,537 \text{ g/m}^2$. The mean litter mass loss when isopods were excluded from *H. lanatus* litter in the *H. lanatus* invaded site was 51.5%, which would increase standing litter biomass to $1,623 \text{ g/m}^2$.

Discussion

H. lanatus appears to be competitively superior to annual grasses in the coastal prairie of BMR, and is rapidly displacing them. While the abundant *P. scaber* contributes greatly to the decomposition of annual grasses, *H. lanatus* is refractory to its influence. *H. lanatus* invasion thus slows decomposition in the coastal prairie, primarily through its interaction with *P. scaber*. *H. lanatus* decomposes more slowly and is more productive than the annual grasses it displaces,

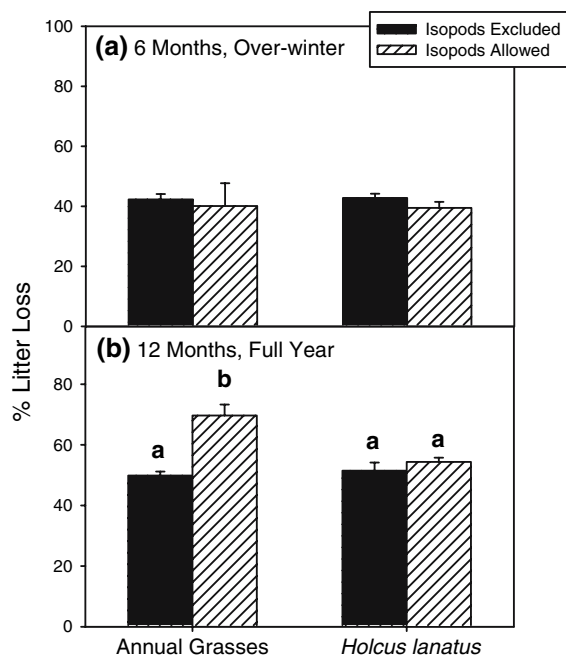


Fig. 1 The within-site decomposition rates for annual grasses and *Holcus lanatus*. We looked at the decomposition rates of litter in its site of origin in order to incorporate site and litter effects into an estimate of naturally occurring decomposition rates. Excluding isopods had no effect on decomposition during the first six months (a), but decreased decomposition of annual grasses over the entire year (b) (Different letters indicate significant differences as determined by mean separation of the three way interaction term in the ANOVA, $P < 0.05$)

causing a dramatic increase in the aboveground standing litter in invaded portions of the coastal prairie (from 766 g/m^2 in the annual grassland to $1,537 \text{ g/m}^2$ in the *H. lanatus* monoculture). Although *P. scaber* had a strong effect on within-site litter decomposition of annual grasses, increasing annual litter loss from 49.9% ($\pm 1.3\%$, SE) to 69.7% ($\pm 3.6\%$), *P. scaber* did not contribute to within-site decomposition of *H. lanatus* (Fig. 1). This was an effect of litter type: *P. scaber* increased decomposition of litter transplanted into the *H. lanatus* invaded grassland (Table 2), but did not affect the decomposition of *H. lanatus* litter (Table 1). While within-site litter mass loss in the isopod access treatment was significantly less for *H. lanatus* litter than annual grass litter ($54.4 \pm 1.4\%$ and $69.7 \pm 3.6\%$, respectively), litter mass loss in the isopod exclusion treatment did not differ. This suggests that *H. lanatus* invasion slows decomposition in the coastal prairie because it is refractory to the dominant macrodetritivore, *P. scaber*.

Our surveys of aboveground biomass show that *H. lanatus* invasion increases production by 57% (from 534 g/m^2 in the annual grassland to 836 g/m^2 in the *H. lanatus* monoculture). Additionally, decreased litter loss rates of *H. lanatus* in the invaded prairie lead to a 29% increase in litter accumulation (from 1.43 L in annual grassland to 1.84 L in the *H. lanatus* monoculture, where L = annual litterfall). The increase in *H. lanatus* production and decrease in decomposition together contribute to a 101% increase in end of growing season aboveground biomass (from 766 g/m^2 to $1,537 \text{ g/m}^2$). Ehrenfeld (2003) found that invasive plants in terrestrial ecosystems typically grow faster than the vegetation they displace, but also typically have higher decomposition rates, so that litter accumulation is relatively unchanged. *H. lanatus* is therefore unusual, although by no means unique, among invasive species in its impact on decomposition. Litter accumulation has been shown to suppress seedling germination (Foster and Gross 1998; Reynolds et al. 2001) and reduce native forb cover and species richness in California grasslands (Coleman and Levine 2007). The slow decomposition of *H. lanatus* litter may therefore contribute, along with its high aboveground productivity, to its negative impact on resident plant species.

The use of litterbags to measure *P. scaber*'s role in decomposition

Selective exclusion of macroinvertebrate detritivores in litterbag studies has long been used to estimate their contribution to decomposition (Crossley and Hoglund 1962). Although this manipulation could have affected other macroinvertebrate detritivores, we believe that *P. scaber* accounts for most or all of the observed effect. *P. scaber* accounts for most of the macroinvertebrate detritivores caught in pitfall traps at BMR and is active during the spring and summer (Bastow unpublished data), when we observed significant differences in litter mass loss between intact and hole-punched litterbags. Millipedes and earthworms are active during the winter at BMR, when there was no significant difference between the two litterbag treatments. *P. scaber* is the only macroinvertebrate detritivore we found inside litterbags, and was significantly more abundant in hole-punched litterbags than intact litterbags. The contribution of macroinvertebrate detritivores to decomposition may be over-estimated in

litterbag studies, because litter can fall out of the larger mesh sizes at a larger size. Most of the litter mass loss in our study occurred during the winter, but we observed no effect of isopod access on litter mass loss during this period. Therefore, we believe that this potential artifact had a negligible contribution to the differences we observed.

The seasonality of decomposition in the coastal prairie

Cold and dry conditions potentially limit decomposition by limiting the activity of the detritus based food web (Swift et al. 1979). Most of the litter mass loss in this study occurred during the cool, wet winter months (September through March). There was no difference between the isopod access and isopod exclusion treatments during the winter months, indicating that decomposition during this period was carried out by leaching, microbes (bacteria and fungi) and microfauna (collembolans, mites and nematodes). Overall, there was little decomposition during the summer months in the isopod exclusion treatment (from $42.3 \pm 1.3\%$ in March to $49.8 \pm 1.1\%$ in September, averaging over both litter types and sites), indicating that microbes and microfauna are relatively inactive during the summer period. However, in the isopod access treatment, litter mass loss increased from $40.9 \pm 2.8\%$ in March to $59.7 \pm 2.7\%$ in September. Summer litter mass loss in the isopod access treatment, along with pitfall trapping from this site (Bastow unpublished data), indicates that *P. scaber* is active throughout the summer months. This suggests that the activity of *P. scaber* is primarily limited by low winter temperatures at BMR, while the activity of microbes and microfauna are primarily limited by low summer moisture. Interestingly, this seasonal pattern is opposite that observed for *P. scaber* in more inland California grasslands, where *P. scaber* is most active and abundant in the winter months, and becomes restricted to moist spots during the summer drought (Paris 1963; Grosholz 1993). This difference is most likely attributable to the frequent summer fogs at BMR, which may alleviate desiccation during the summer. It is likely that summer fogs therefore regulate the importance of *P. scaber* in the detritus based food web, although comparable litterbag

studies on the role of terrestrial isopods have not been published from inland California grasslands.

Macroinvertebrate detritivores such as *P. scaber* are believed to contribute to decomposition primarily by reducing the particle size of the litter and thus increasing its surface area, an effect termed comminution (Swift et al. 1979). Macroinvertebrate detritivores stimulate microbial activity by increasing the exposed surface area of litter (Ponge 1991; Kautz and Topp 2000), while microbial conditioning of litter makes the litter more appealing for macrodetritivores (Stöckli 1990; Daniel et al. 1997). It remains to be seen whether such facilitative interactions still occur when microbial conditioning and litter comminution are seasonally separated, as they appear to be at BMR.

H. lanatus invasion and the population biology of *P. scaber*

The fact that isopods had no effect on litter loss of *H. lanatus* suggests that *P. scaber* does not consume this invasive grass. Although resident consumers often ignore invasive species because they have not evolved the means to consume the invasive species, or simply do not recognize them as food, this is unlikely to be the reason *P. scaber* did not consume *H. lanatus* litter in this experiment. *P. scaber* is believed to be native to Western Europe (Sutton 1972), where *H. lanatus* is also native. *H. lanatus* litter has long been noted to be poor forage that is generally ignored by livestock (Beal 1887; Davies 1960), perhaps because it has a high C/N ratio (Bastow unpublished data) or because it is mildly cyanogenic (Muenscher 1951; Fuller and McClintock 1986). It is possible that these characteristics make *H. lanatus* litter a poor quality resource for *P. scaber* as well.

We have shown that *H. lanatus* slows decomposition in the coastal prairie of northern California through its interaction with the macroinvertebrate detritivore *P. scaber*. Although the increased production and litter accumulation that result from *H. lanatus* invasion are readily apparent, the role that the reduced decomposition plays in the increased litter accumulation could only be detected in an experiment incorporating macrodetritivores. Although litterbags are among the most frequently used tools for understanding detrital dynamics, such studies frequently exclude macroinvertebrate

detritivores from all litterbags, which would have precluded observing a difference between *H. lanatus* and annual grasses in this system. The value of incorporating specific members of the detritus based food web into studies of invasive plants is likely to increase as ecologists' understanding of the interactions between detrital and biotic foodwebs improves.

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Appendix A

Results from ANOVAs on arcsine square root transformed percent litter mass loss

Over-winter (6 months)				
Source	df	MS	F	P
Litter type	1	0.0831	7.54	0.009 [†]
Isopod access	1	0.00329	0.30	0.59
Site	1	0.0927	8.41	0.006 [†]
Litter type X Isopod access	1	0.00318	0.29	0.59
Litter type X Site	1	0.000207	0.019	0.89
Isopod access X Site	1	0.00304	0.28	0.60
Litter type X Isopod access X Site	1	0.00308	0.28	0.60
Error	39	0.0110		
Full year (12 months)				
Source	df	MS	F	P
Litter type	1	0.106	20.93	0.0001 [†]
Isopod access	1	0.110	21.69	0.0001 [†]
Site	1	0.00737	1.45	0.24
Litter type X Isopod access	1	0.0646	12.74	0.001 [†]
Litter type X Site	1	0.0143	2.82	0.10
Isopod access X Site	1	0.00148	0.29	0.59
Litter type X Isopod access X Site	1	0.00295	0.58	0.45
Error	36	0.00507		

[†] P < 0.05

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