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Facilitation of tiger moths by outbreaking tussock moths that share the same host plants

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Summary

1. Ecologists have argued about the commonness and strength of interspecific competition between insect herbivores, but facilitation between herbivores has received much less consideration. We previously found that when two species of folivorous caterpillars co-occurred on a shared host plant, feeding by early season tiger moth caterpillars reduced the growth and reproduction of later season tussock caterpillars. However, densities of tussock caterpillars in summer were positively correlated with densities of tiger moth caterpillars the following spring.

2. In this study, we experimentally manipulated numbers of feeding tussock caterpillars and found that they facilitated tiger moth caterpillars.

3. The depth of the litter layer beneath host lupine bushes was positively correlated with the number of tussock caterpillars feeding on each bush. Experimental additions of litter beneath lupine canopies during summer resulted in increased numbers of tiger moth caterpillars in the following spring, indicating a causal role of litter. Litter potentially provides food, habitat and protection from desiccation and predation. We failed to find evidence that tussock caterpillars facilitated tiger moth caterpillars by mechanisms independent of litter.

4. Our study demonstrates that facilitation may operate between insect herbivores, across life-stages through indirect interactions that are non-trophic. Facilitation operated by a novel mechanism, the accumulation of litter which was a by-product of feeding by one species was valuable to a second species. Facilitation persisted in time and space far beyond the creation of litter by tussock caterpillars which should be considered important ecosystem engineers from the point of view of tiger moths. Facilitations that involve habitat modification may generally connect species that do not interact directly or trophically, and have not previously been considered to affect one another.

Key-words: caterpillar, competition, ecosystem engineer, food web, herbivore, interactions, litter

Introduction

Almost every plant is fed upon by several herbivore species, although these herbivores may be separated in space (which plant tissues they exploit) and in time (when they are active). Traditionally, interactions between different herbivore species were assumed to be relatively weak and unimportant (Hairston, Smith & Slobodkin 1960; Lawton & Strong 1981) and to involve mainly interference or exploitative competition. More recently, researchers have come to appreciate that indirect interactions between herbivores are common and important (Karban 1986; Kaplan & Denno 2007; Ohgushi 2008). In particular, herbivores frequently alter their shared host plant (Karban & Baldwin 1997), their shared natural enemies (Holt & Lawton 1994), or their shared physical habitat (Jones, Lawton & Shachak 1994, 1997). Such alterations can have profound indirect effects on co-occurring herbivore species. When the interacting species do not overlap in time and space, it becomes important to explicitly include their indirect effects as these significant elements may be easily overlooked (Hastings *et al.* 2007; Ohgushi 2008).

Coincidental with this appreciation of indirect interactions, there has also been a slower realization that many interactions among species involve facilitation (Bertness & Callaway 1994; Bruno, Stachowicz & Bertness 2003; Crain & Bertness 2006; Ohgushi 2008). Some of the under-representation of positive interactions in the literature stems from a difficulty in elucidating the responsible mechanisms. For example, there have been many reported cases of 'induced susceptibility,' in which prior feeding by one herbivore

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*Correspondence author. E-mail: rkarban@ucdavis.edu appears to make the host plant more suitable to a second herbivore (Karban & Baldwin 1997:116–119). However, this common empirical finding has not been incorporated into ecological theory because we have not understood the mechanisms involved. For example, early work by Williams & Myers (1984) showing that trees attacked by tent caterpillars subsequently supported larger populations of fall webworm caterpillars was interpreted as 'contradicting' reports of induced resistance, but not as demonstrating a different and important phenomenon of facilitation because mechanisms responsible were unknown.

Positive interactions have been hypothesized to be most important in environments with high levels of abiotic stress or high consumer pressure (Bertness & Callaway 1994; Bruno, Stachowicz & Bertness 2003; Crain & Bertness 2006). Under these conditions, facilitation allows species to thrive where conditions would otherwise be inhospitable. When abiotic stress is great, positive interactions help to ameliorate these conditions, as exemplified by 'nurse plants' that provide shade and moisture (e.g., Callaway 1992) or 'foundation species' that provide habitat for other species (e.g., Dayton 1971; Irving & Bertness 2009). Under conditions where herbivore pressure is high, positive interactions allow palatable species to escape by making them less detectable or less vulnerable to herbivores (e.g., Barbosa *et al.* 2009). When species affect each other indirectly by modifying their shared physical environments we refer to these species as 'ecosystem engineers' (Jones, Lawton & Shachak 1994, 1997). Interactions involving ecosystem engineering often persist over time and extend over large spatial scales (Hastings *et al.* 2007; Ohgushi 2008).

This study examines the relationship between two externally feeding macro-lepidoptera that share *Lupinus arboreus* as a primary host plant. Early experiments with these two caterpillars examined whether feeding by each of the species affected the other. Tussock moth caterpillars grew less quickly, attained smaller female pupal weights, and produced fewer eggs when fed on leafy branches that had previously hosted tiger moth caterpillars (Harrison & Karban 1986). In a later common garden study, *L. arboreus* plants that had supported higher numbers of tussock caterpillars during the summer of 1997 also supported higher numbers of tiger moth caterpillars during the spring of 1998, the opposite of *a priori* predictions based on an expectation of induced resistance (Karban & Kittelson 1999). In this common-garden study, we did not experimentally manipulate the levels of tussock caterpillars which prevented us from distinguishing effects that were caused by tussock caterpillars from other differences among bushes that both caterpillar species may have responded to in a correlated manner.

In the present study, we sought to evaluate the effects of tussock caterpillars active during summer on abundances of tiger moth caterpillars active from summer through the following spring, as well as the causes for those effects. We experimentally removed or added tussock caterpillars to lupine bushes at 12 sites during the summer, and monitored the number of tiger moth caterpillars that were present on those bushes during the following spring. As tussock moth caterpillars had positive effects on tiger moth caterpillars we sought to determine the ecological mechanisms responsible. Differences in the abundance of tiger moth caterpillars could have been caused by indirect effects mediated by shared predators or by changes in the quality and quantity of lupine litter, the habitat of early instar tiger moth caterpillars. We evaluated these two possibilities by assaying survival of tiger moth caterpillars exposed to predation and by measuring litter depth at bushes that had received varying levels of tussock caterpillars. Finally, we conducted an experiment in which we added or removed litter from beneath the canopies of lupine bushes to examine if this habitat characteristic affected numbers of tiger moth caterpillars.

Materials and methods

STUDY SYSTEM

Western tussock moths (*Orgyia vetusta* Boisduval, Lymantriidae) occur in localized outbreaks that exceed 100 caterpillars per bush, and outbreaks may persist for at least a decade at sites along the coast of California (Harrison 1997). During non-outbreak years, this species becomes rare and densities fall below detectable levels. Western tussock moths generally have a single generation per year and caterpillars may defoliate lupine bushes during the summer. Bushes that were attacked and even defoliated by tussock moth caterpillars often recovered and produced full complements of leaves, flowers and seeds in the following growing season (Harrison & Maron 1995). At the study site, tussock moths overwinter as eggs, and caterpillars feed most actively during summer on *L. arboreus* and to a lesser extent on *L. chamissonis* (Harrison & Maron 1995; Harrison 1997).

The ranchman's tiger moth (*Platyprepia virginalis* Boisduval, Arctiidae) is also found in association with *Lupinus arboreus* and to a lesser extent with other host species (Karban *et al.* 2010). Although its populations vary widely among years (by almost three orders of magnitude), this species never reaches the outbreak densities of the tussock moth and does not defoliate lupine bushes (Karban & de Valpine 2010). Mating occurs in the late spring and early instar caterpillars pass the summer and autumn feeding in lupine litter. Later instar caterpillars feed on leaves of lupine and other host species during winter and spring before pupating in late spring (Karban *et al.* 2010). Like the tussock moth, the ranchman's tiger moth is univoltine although most feeding occurs in spring. Both caterpillar species are attacked by parasitoids, primarily tachinids, although there is no overlap in the parasitoid species that attack the two moth species (Brodmann, Wilcox & Harrison 1997; Karban & English-Loeb 1999). Ants, particularly *Formica lasioides*, are important predators of caterpillars of both species, particularly small caterpillars (Harrison & Wilcox 1995 and R. Karban, personal observation). *F. lasiodes* have been found to become satiated at sites of high densities of tussock caterpillars which may allow individuals of both caterpillar species to escape predation during tussock outbreaks (Harrison & Wilcox 1995).

Lupinus arboreus is the most common shrub throughout the reserve, although its densities fluctuate over time (Barbour *et al.* 1973; Strong *et al.* 1995). Bushes are roughly 1 m tall with a radius of 1–2 m and they occur in both wet and dry habitats. Litter accumulates during summer, reaching depths > 15 cm thick in summer, but it decays during winter months. The litter layer is underlain by organic material or mineral soil, depending upon microsite.

EFFECTS OF THE NUMBER OF TUSSOCK CATERPILLARS ON TIGER MOTH CATERPILLARS

We added or removed tussock caterpillars from lupine bushes (*L. arboreus*) and recorded the number of tiger moth caterpillars on these bushes the following spring, once they became conspicuous. These experiments were conducted at 12 sites in largely grassland and dune habitats at the Bodega Marine Reserve, CA (sites are described in Appendix A; one site was excluded from this experiment because an insufficient number of *L. arboreus* bushes were present). We selected 15 healthy bushes separated by at least 5 m at each site and randomly assigned five bushes to each of three treatments consisting of tussock caterpillar addition, tussock caterpillar removal and unmanipulated controls. The three treatments were unbiased with respect to initial litter depth on 14 August (ANOVA $F_{2,161} = 0{\cdot}37$, $P = 0{\cdot}69$). We removed all visible tussock caterpillars from removal bushes on 15 August, 23 August, 26 August and 7 September 2009 and added them to the caterpillar addition bushes. We transferred a mean of 19·2 (± 3·2 SE) tussock caterpillars per bush. We recorded the number of tiger moth caterpillars on these same bushes on 27 February 2010, by which time they had become large enough to be conspicuous. We had observed that the ground beneath the canopy of bushes that were defoliated by tussock moths accumulated a thick layer of shed leaves, partly consumed leaf fragments and frass in late summer. This is the time when early instar tiger moth caterpillars are living hidden in the litter. We measured the thickness of the litter layer beneath each bush on 23 August 2009, 1 week after applying the tussock caterpillar treatments.

As appropriate for count data with frequent zero values (e.g., Crawley 2007), we analysed the number of tiger moth caterpillars observed on each bush using General Linear Models (GLM's) with a Poisson distribution of sampling error and a natural logarithmic link function performed. The analysis was performed in R version 2·13·1 (R Development Core Team 2011) with site as a random factor, tussock caterpillar treatment (removal, addition, control) as a fixed factor and litter depth as a covariate. We used model selection based on Akaike's Information Criterion (AIC), where models were preferred if AIC values were lower and the change in AIC (ΔAIC) was $< 2{\cdot}0$. As the model with the lowest AIC value and the next best model differed by $\Delta\text{AIC} < 2{\cdot}0$, out of parsimony we selected the model with the fewest parameters as our preferred model (e.g., Crawley 2007). We considered all possible models up to the three way interaction of site*tussock treatment*litter depth interaction. The tussock caterpillar addition treatment was more effective at increasing the number of tussock caterpillars than the removal treatment was at producing bushes that were completely free of tussock caterpillars. Addition treatments had approximately 50% more tussock caterpillars than controls, but removals were not noticeably different than controls (personal observation).

One possible mechanism that could affect numbers of tiger moth caterpillars associated with tussock treatments is predation by ants, particularly *F. lasioides*, a common ant at our study site (Harrison & Wilcox 1995). We have found that most caterpillars are removed by ants within the first 72 h that they are experimentally placed at sites with ants (personal observation). We tested whether ant access reduced caterpillar survival. We placed one-second-instar tiger moth caterpillar in a plastic deli container (11 cm diameter, 540 ml; Solo Cup Co., Highland Park, IL, USA) beneath the canopy of each of the 15 bushes at each of the 11 sites and recorded the fates of the caterpillars over a 72 h period during August 2010. Deli containers were modified to contain fiberglass window screen (mesh opening 1·1 mm) on the bottom to allow contact with the soil and to allow workers of *F. lasioides* and other ants to enter and leave at will. Lids on the containers prevented the caterpillars from leaving and several flowering stems of lupine were placed in each container to provide food for the caterpillars. We compared survival of tiger moth caterpillars beneath bushes which had had tussocks added, removed, or unmanipulated controls using a G-test of association (Sokal & Rohlf 1969).

EFFECTS OF TUSSOCK MOTH CATERPILLARS ON LITTER DEPTH AND QUALITY

We hypothesized that prior feeding by tussock moths increased litter depth and altered litter composition beneath lupine canopies. We selected lupine bushes and measured the number of tussock caterpillars on each bush, the depth of the litter beneath that bush and the ratio of carbon to nitrogen in the litter for use in correlational tests. Three bushes were haphazardly selected at each of the 12 sites (Appendix A) that had not been used in the tussock manipulation experiment and an additional 12 bushes were selected from one of the sites ('Artemisia'). We estimated the mean number of tussock caterpillars feeding on each selected bush during weekly visual censuses in August, 2008, when they were most abundant. We measured the depth of litter beneath each bush on 13 August by placing a ruler through the litter until it hit the mineral soil. This is the time when early instar tiger moth caterpillars are living in the litter. We obtained an estimate of litter quality by examining the concentrations of C and N in litter samples collected at this time from 24 bushes (one bush from each of the 12 sites plus the additional 12 bushes from the 'Artemisia' site). Litter samples were dried in an oven, ground, and analysed for total carbon and nitrogen at the UC Davis Analytical Lab (http://anlab.ucdavis.edu). We hypothesized that feeding by tussock caterpillars increased litter depth and affected litter quality. We analysed the relationship between the number of tussock caterpillars on each bush and the litter beneath it using linear regression with the number of tussock moths on each bush as a predictor and litter depth and C to N ratio as responses variables in two analyses.

EFFECTS OF LITTER DEPTH ON TIGER MOTH CATERPILLARS

We hypothesized that the positive effect of tussock caterpillar feeding on tiger moth caterpillars was mediated by an increase in litter depth; we tested this hypothesis by experimentally manipulating the litter beneath bushes during the summer of 2010, and observing the number of tiger moth caterpillars on those bushes the following March. We selected 90 *L. arboreus* bushes east of the 'housing' at the reserve (38·319°N, 123·058°W) and randomly assigned them to one of the three treatments: litter addition, litter removal, or an unmanipulated control. We selected this site for this experiment because it consistently supported high densities of tiger moth caterpillars making it more likely that we would have a sufficiently large number of caterpillars to measure a result. We collected the existing litter and aboveground vegetation (all forb and grass species in the understory) from beneath those bushes assigned to the litter removal treatment on 5 July, before *P. virginalis* oviposition occurred for the season. It was difficult to separate the litter from living forbs and grasses. As such, our litter addition and removal treatments included lupine litter as well as other plant material in small amounts. This litter was added beneath the canopies of those bushes assigned to the litter addition treatment at approximately the same time that litter was naturally accumulating beneath bushes hosting tussock moth caterpillars. It also coincides with the time when tiger moth caterpillars reside in the litter. We measured the depth of litter on 16 August to assess the success of our treatments. We visually assayed the number of tiger moth caterpillars on each bush on 17 March 2011 and analysed the effects of our litter manipulation treatments using a simple single factor GLM with Poisson errors and a natural log link function conducted in R.

Results

EFFECTS OF THE NUMBER OF TUSSOCK CATERPILLARS ON TIGER MOTH CATERPILLARS

The preferred General Linear Model showed that lupine bushes to which we added tussock caterpillars had, on average, approximately 90% more tiger moth caterpillars that survived the following spring as unmanipulated bushes or those from which we removed tussock caterpillars (Fig. 1, Table 1b, $z = 2{\cdot}69$, 1 d.f., $P = 0{\cdot}007$). The preferred model included site, tussock moth addition/removal treatment as factors and litter depth as a covariate. We conducted censuses of tiger moth caterpillars in February, when they became more conspicuous, although the effect could have occurred any time between August and the following February. In fact, most mortality occurs during the summer when tiger moth caterpillars are early instars in the litter.

Recalling that earlier investigations indicated an absence of induced effects through plants (Karban & Kittelson 1999), this effect (Fig. 1) could potentially have been caused by differences in litter depth or quality associated with tussock caterpillar feeding. Litter depth, measured 1 week after the first manipulation (addition/removal) of tussock caterpillars, had a statistically significant and substantial effect on tiger moth caterpillar numbers (z-values in Table 1b, Fig. 1). However, removing site from the preferred model produced a large change in AIC, indicating a strong effect of site on tiger moth caterpillar numbers (Table 1a; in addition, based on z-values in Table 1b four sites differed from site 1 in tiger moth caterpillar numbers at $P < 0{\cdot}05$). Alternatively, the effect we observed (Fig. 1) could have been caused by differences in predation rates experienced by early instar tiger moth caterpillars beneath bushes with different densities of tussock caterpillars. However, we found no differences in rates of survival of tiger moth caterpillars associated with the three tussock caterpillar treatments during a 72-h assay conducted during summer (Table 2; $G = 0{\cdot}20$, d.f. = 2, $P = 0{\cdot}90$). Nonetheless, 18·4% of tiger moth caterpillars were consumed in 72 h, showing that predation rates on exposed caterpillars can be substantial.

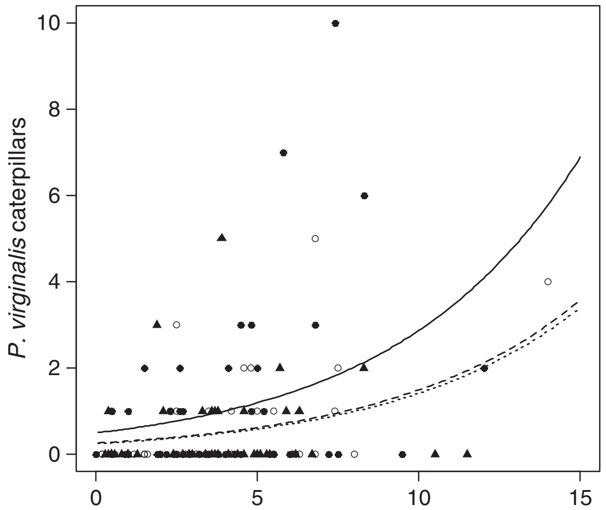

Fig. 1. The number of *Platyprepia virginalis* (tiger moth) caterpillars on bushes with tussock caterpillars added (solid circles and solid line), removed (solid triangles and dashed line), or unmanipulated controls (unfilled circles and dotted line). The dotted and dashed lines overlap. Curves are exponential curves because they are back-converted from ln(number of tiger moth caterpillar) that are used in Poisson models. Mean numbers (± 1 SE) of tiger moth caterpillars on bushes with tussock caterpillars added was 0·93 ± 0·26, on control bushes was 0·49 ± 0·15 and on bushes with tussock caterpillars removed was 0·49 ± 0·14.

EFFECTS OF TUSSOCK MOTH CATERPILLARS ON LITTER DEPTH AND QUALITY

Bushes with more tussock caterpillars naturally occurring had deeper litter than those with fewer caterpillars (Fig. 2, $R^2 = 0{\cdot}49$, d.f. = 47, $P = 0{\cdot}001$). This litter contained frass from the tussock caterpillars, partially consumed leaf fragments and damaged leaves that had been abscised. There was no detectable relationship between the number of tussock caterpillars feeding on a bush and the C to N ratio of the litter beneath that bush (data not shown, $R^2 = 0{\cdot}07$, d.f. = 23, $P = 0{\cdot}20$) although we had a smaller sample size and less power to detect this effect.

EFFECTS OF LITTER DEPTH ON TIGER MOTH CATERPILLARS

Our litter manipulations created bushes with the desired differences in litter depths: by 16 August, 6 weeks following the manipulations, mean litter depths were 0·82 ± 0·23 (SE) cm for removal, 2·51 ± 0·39 cm for control and 2·83 ± 0·52 cm for addition treatments, and these were statistically distinguishable ($F_{2,86} = 14{\cdot}4$, $P = 0{\cdot}001$). Most of the change in litter depth came from the litter removal treatment. The litter manipulations affected the number of tiger moth caterpillars found on bushes of the three treatments in the following spring (Fig. 3, $\chi^2 = 22{\cdot}5$, $P < 0{\cdot}001$). Comparisons of tiger moth caterpillar numbers for litter treatments indicated that the differences were primarily between the litter addition treatment and other two treatments, which were similar to one another (comparison of GLM parameter estimates using z-tests: $z = 3{\cdot}7$, $P < 0{\cdot}001$ for addition vs. control, $z = 4{\cdot}1$ $P < 0{\cdot}001$ for addition vs. removal, $z = 0{\cdot}6$ $P = 0{\cdot}5$ for control vs. removal). Number of tiger moth caterpillars in the litter-addition treatment was 86% greater than controls.

Table 1. Effects of experimental manipulation of tussock caterpillars on number of *Platyprepia virginalis* caterpillars from general linear models with Poisson errors and a log link function

(A) Model fit comparisons

Model	Model terms	Residual d.f.	AIC	Δ AIC
1. Full model	S + L + T + S*L + S*T + L*T + S*L*T	94	323·6	45·5
2. Full model – S*L*T	S + L + T + S*L + S*T + L*T	114	294·1	16
3. Model 2 – S*L	S + L + T + S*T + L*T	124	288·3	10·2
4. Model 3 – S*T	S + L + T + L*T	144	278·1	0
5. Model 4 – L*T	S + L + T	146	279·2	1·1
6. Model 5– L	S + T	147	300·6	22·5
7. Model 5 – T	S + L	148	287·6	9·5
8. Model 5 – S	L + T	156	371·62	93·52

(B) Parameter estimates for model 5

	Estimate	SE	*z*-value	*P*
Intercept (Site 1, Tussock addition)	−0·701	0·374	−1·87	0·06
ΔSite 2	−1·85	1·06	−1·75	0·08
ΔSite3	−17·8	1367	−0·01	0·99
ΔSite 4	0·43	0·42	1·04	0·30
ΔSite 5	−1·63	0·78	−2·09	0·04
ΔSite 6	0·67	0·43	1·54	0·12
ΔSite 7	−2·25	1·05	−2·13	0·03
ΔSite 8	−17·3	1452	−0·01	0·99
ΔSite 9	−2·23	1·05	−2·11	0·04
ΔSite 10	1·16	0·38	3·06	0·002
ΔSite 12	0·03	0·44	0·06	0·95
Tussock removal	−0·66	0·24	−2·69	0·007
Tussock control	−0·71	0·25	−2·86	0·004
Litter (slope)	0·175	0·036	4·82	< 0·001

In A models with the lowest AIC value are preferred and those with ΔAIC < 2 are considered to be equivalent in fit and simpler models of equivalent fit are preferred. ΔAIC is expressed relative to the model with the lowest AIC value. S, Site; L, Leaf litter; T, tussock moth caterpillar treatment; and d.f., degrees of freedom. B presents the parameter values for the preferred model (Model 5 in A). Values expressed with a delta value are differences in intercepts of Ln(tiger moth caterpillars) from site 1 tussock addition treatment.

Table 2. Fates of second instar tiger moth caterpillars over 72 h beneath bushes with tussock caterpillars added, removed or unmanipulated controls

Treatments	Survived	Died	Total	% survived
+ tussocks	44	11	55	80
Control	45	9	54	83
– tussocks	44	10	54	81

Discussion

We initially expected these two herbivore species to compete either directly for food or habitat or indirectly by changing the quality of their *L. arboreus* hosts or through a shared predator. This expectation was fulfilled in part as bushes that supported tiger moth caterpillars were diminished as hosts for tussock caterpillars that feed later in the season (Harrison & Karban 1986). These negative effects were substantial and resulted in reductions in larval growth rates of 10–27%, reductions in female pupal weights of 25% and reductions in egg production of 48%. However, bushes that had supported tussock caterpillars hosted greater, not reduced, numbers of tiger moth caterpillars, suggesting a positive interaction rather than competition (Karban & Kittelson 1999). Our present results corroborated this pattern as bushes to which we added tussock caterpillars had an average of approximately 90% more tiger moth caterpillars than control bushes

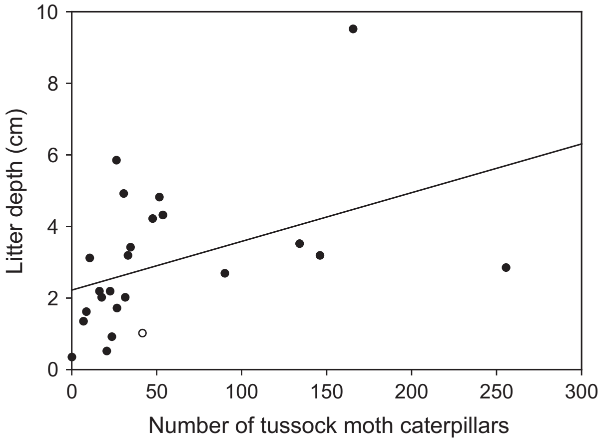

Fig. 2. The depth of litter beneath 48 bushes as a function of the number of tussock caterpillars feeding on those bushes. The line shows the least squares regression.

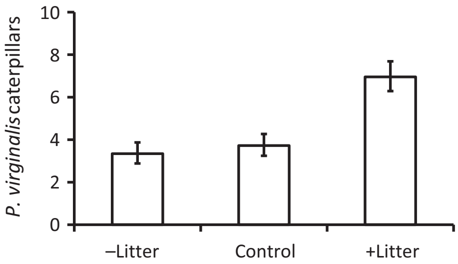

Fig. 3. The number of *Platyprepia virginalis* (tiger moth) caterpillars (mean ± 1 SE) on bushes beneath which litter had been added (+), removed (−), or unmanipulated controls. Error bars are asymmetric because values were back-converted from ln-values.

or those from which we removed tussock caterpillars (Fig. 1). The experimental manipulation confirmed that tussock caterpillars caused the increase in tiger moth caterpillar numbers. The interaction between these two species was highly asymmetric; tiger moth caterpillars reduced the success of tussock caterpillars whereas tussock caterpillars increased the numbers of tiger moth caterpillars. In this case, the positive effect size of facilitation was greater than the negative effect size, although the two are not necessarily directly comparable.

Tussock caterpillars acted as ecosystem engineers, converting lupine leaves into litter. Tussock caterpillars caused an increase in the litter depth beneath bushes (Fig. 2) and adding litter increased numbers of tiger moth caterpillars (Fig. 3). It is not clear why a small increase in litter depth achieved by our litter addition treatment translated into a large increase in tiger moth caterpillar numbers. Litter serves as a food source for early instar tiger moth caterpillars and provides habitat that may protect them from natural enemies, desiccation and other dangers. These services are difficult to isolate and evaluate independently. We doubt that tiger moth caterpillars ever experience absolute food shortages as they never defoliate lupine bushes and there always is live lupine foliage available to them (RK personal observation). In optimal, wet, habitat there was no detectable relationship between lupine cover and abundance of tiger moth caterpillars although in suboptimal, upland habitat the correlation between lupine cover and caterpillar numbers was strong (unpublished data). This pattern fits with recent generalizations that ecosystem engineers and facilitation may both have stronger effects in suboptimal environments and are less likely to be important where conditions are otherwise more favourable (Bruno, Stachowicz & Bertness 2003; Crain & Bertness 2006).

Our results consistently indicate that litter is important for early instar tiger moth caterpillars, but do not indicate the precise mechanisms involved. In addition to food, litter may also provide a complex habitat that makes it harder for predators, such as ants, to find or handle young caterpillars (Freitas & Oliveira 1992). Young tiger moth caterpillars were also more vulnerable to entomopathogenic nematodes when there was no litter and spent most of their time above the soil surface and away from nematodes when this was possible (Karban *et al.* 2011). At the study site, outbreaks of tussock caterpillars had no measurable effects on numbers of foraging ants, but the percentage of tussock caterpillars attacked by ants was reduced in areas with outbreak densities of tussock caterpillars (Harrison & Wilcox 1995). We have observed ant predation of early instar tiger moth caterpillars and hypothesized that a similar benefit may accrue to them in the litter beneath bushes supporting outbreaks of tussock caterpillars. If this mechanism was operating, we expected that rates of mortality of early instar tiger moth caterpillars would be reduced beneath bushes with added tussock caterpillars, although our data failed to meet this expectation (Table 2). One possible explanation for these negative results is that our experiments in deli-containers may not have allowed caterpillars to hide in the leaf litter. We failed to find evidence that predation on caterpillars by invertebrate or vertebrate predators, other than ants, was important (unpublished data).

Litter may provide other benefits important to young caterpillars. *P. virginalis* has a large range throughout western North America, although most of the locations where it is found are at higher elevations with cooler temperature regimes than the study site, as well as close proximity to water (Opler *et al.* 2011). Caterpillars in lab colonies do poorly on warm days, but survive in a refrigerator (personal observation). Thick litter may allow caterpillars to find microhabitats that are cooler and moister than litter-free conditions.

By indirectly causing a thick accumulation of litter under bushes that they defoliated (Figure 2), tussock caterpillars facilitate tiger moth caterpillars (Fig. 3). This unexpected result adds to a growing list of examples of facilitation among species that live with stressful abiotic conditions and the threat of predation (see Introduction). Most of the published examples of facilitation involve plants and marine invertebrates, although numerous examples of positive interactions between herbivores have been reported (Karban & Baldwin 1997; Denno & Kaplan 2007; Ohgushi 2007). These literatures dealing with facilitation and with interactions between herbivores have historically been poorly integrated, and (as our study reveals) the mechanisms behind such positive effects merit more attention.

Facilitation of one herbivore by the actions of another has been reported to occur by one of several mechanisms: feeding by one herbivore (i) improves the apparency or nutritional quality of a shared host plant, (ii) causes the shared host plant to regrow highly suitable tissues, or (iii) involves the construction of structures that provide habitat, food, or enemy-free space for other species (Marquis & Lill 2007; Ohgushi 2007). The mechanism described here involves a waste product or induced plant response to feeding by tussock caterpillars in the lupine canopy that provides food, habitat and probably improved microclimate and enemy-free space in a different microhabitat, the litter layer, for tiger moth caterpillars. There are several other examples of above-ground feeding by herbivores that change the quality of litter inputs below-ground, although these emphasize decomposition and mineralization processes in the soil and do not link herbivory in the canopy to feeding on living or decaying leaves at the soil surface (Bardgett, Wardle & Yeates 1998). At this time, it is unclear whether facilitations of the sort described here will prove to be common as ecologists have only recently begun to examine interactions between above-ground herbivores and those that reside or feed on or in the soil (Bardgett, Wardle & Yeates 1998; Bardgett & Wardle 2003; van der Putten *et al*. 2009; van Dam & Heil 2011). Regardless of the mechanisms involved, it is clear that this facilitation involves 'ecosystem engineering' of the physical environment rather than the trophic interactions that ecologists have examined in the past. Although we do not know the precise mechanisms of facilitation, in this example it probably involves differences in mortality rather than movement as early instar tiger moth caterpillars seldom move between bushes (unpublished data). This facilitation occurs between two herbivores that are separated in both time and space. Separation may by common for interactions involving induced plant responses to herbivory (Karban & Baldwin 1997) or ecosystem engineering (Hastings *et al*. 2007). The consequences of negative interactions between organisms that are separated in time and space can have important theoretical and management implications (Ratikainen *et al*. 2008) and further consideration of consequences for positive interactions is merited as well. We agree with Ohgushi (2008) that a broader consideration of interaction webs, rather than trophic food webs, will enable our field to progress most rapidly.

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Appendix A

Location and description of study sites.

Site Name	Latitude – 38°N	Longitude – 123°W	Habitat
S curve	0·3137	0·0618	Grassland
NE of curve	0·3145	0·0616	*Juncus*
Lower draw	0·3143	0·0666	Grassland
Across from lab	0·3183	0·0698	wet grassland
Top of the hill	0·3185	0·0693	Dune
Hemlock	0·3191	0·0710	wet grassland
Artemisia	0·3217	0·0749	Grassland
N dune	0·3215	0·0724	Dune
Top of Mussel Pt.	0·3221	0·0766	Grassland
Dorm marsh	0·3194	0·0572	*Juncus* near marsh
Rabbit valley[a]	0·3207	0·0593	Dune
Edge of marsh	0·3201	0·0567	Grassland near marsh

[a] Not included in experiment manipulating tussock caterpillars.