

The Impact of Invasive Plants on Detrital Food Webs

Final report: 30 June 2006



Introduction

A system's dominant plant type often drives a number of its ecosystem and community properties; plants of disparate functional types produce habitats with differing physical structure and nutrient availability through both the living and dead plant tissue (litter) (Fig. 1).

Litter is often the principal contributor to detritus (any non-living organic matter) in terrestrial and aquatic systems, and therefore makes up the main component of energy recycled through the system. Over

90% of all terrestrial energy flows through the detrital system (Heal and MacLean 1975) and inclusion of detritus in food web theory alters conclusions about food web structure, stability and length (Moore et al. 1993). Food web models including detritus produce longer, more energetically feasible systems with faster return times (Moore et al. 2004). Yet detritus is generally ignored when asking fundamental questions about community organization (Moore et al. 2004).

Though ecosystem science has included detritus in many theories and models since the development of the discipline (Lindeman 1942), detritus and the organisms which use it as a direct food resource have been excluded from most of the main debates of community ecology. For example, decomposers were explicitly considered in the original "Green World Hypothesis" (Hairston et al. 1960), but left out of many future debates (Murdoch 1966, Oksanen et al. 1981). With continually more work integrating community and ecosystem ecology, there is increasing importance to understanding both the community and ecosystem impacts of plant detritus (Wardle et al. 2004) (Bardgett et al. 2005).

Plant invasions often change a system's dominant plant type, producing dramatic effects on a system's litter dynamics. Many studies have found *a posteriori* that invasive litter plays an important role in altering ecosystem dynamics (MacDougall and Turkington 2005) (Ogle et al. 2003) (Gruner 2004), but few studies have focused on community-level effects of invasive litter. Recent studies examining invasive versus native plant litter have found that invasives generally improve a system's litter quality (higher nitrogen and phosphorus concentrations and faster decay rates) which leads to increased rates of decomposition and nutrient cycling (Allison and Vitousek 2004).

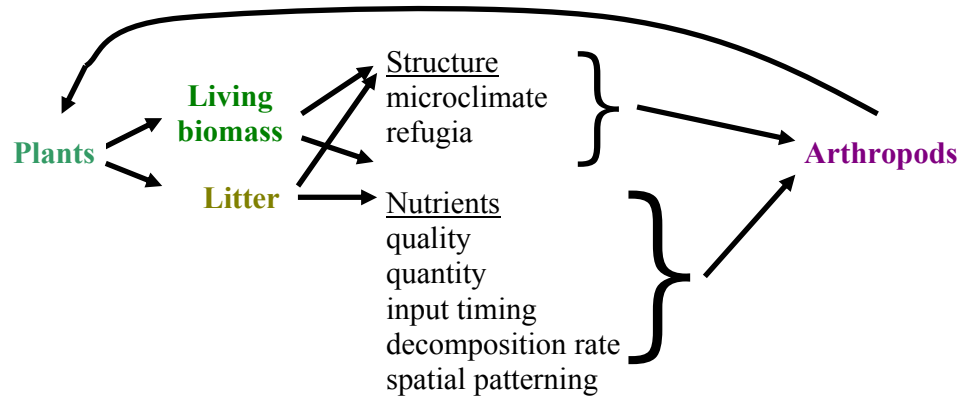


Figure 1: Plant composition can affect an ecosystem's arthropods through both its living and dead tissue leading to changes in the system's nutrients and structure.

Mediterranean annual grasses are widespread invasives (Gurevitch and Padilla 2004) that have been present in many of their non-native habitats for over a century and led to many shrubland to grassland conversions (Cione et al. 2002). In southern California they established in the threatened habitat of coastal sage scrub (henceforth CSS), a semi-arid deciduous shrub system, sometime before the last century and have expanded over the past 70 years (Minnich and Dezzani 1998).

Because the invasive grasses in CSS are of a different functional plant type than the native co-dominants, the system provides an excellent opportunity to examine the effects of extreme changes in detritus. The ontogenies of each litter-type are of distinct temporal scales: invasive grasses (primarily *Bromus* spp., *Vulpia* spp., *Avena* spp. and *Brachypodium* sp.) produce abundant litter that generally turns over in one year (Jackson et al. 1988), while the native co-dominant shrubs, (*Artemisia californica* and *Eriogonum fasciculatum*) produce leaf litter that turns over in 3-5 years (T. Zink, *pers. comm.*).

After several years of observational work, we were able to use CIPM Seed Money funding to begin experimental approaches to identify changes in soil communities and ecosystem properties due to changes in litter composition. Using the invasion of CSS for field studies, we are interested in how changes in a system's dominant functional plant type, especially related changes in system detritus, impact the soil community and associated ecosystem functioning. This work will serve as a major contribution to linking the role of detritus in both the brown and green webs. Additionally, this work will test restoration techniques for CSS by removing litter from areas with differing amounts of invasion.

Hypotheses & Predictions

Because grass litter has the ability to alter the physical structure, nutrient lability and availability of the habitat we hypothesized that CSS's shift from shrub to grass domination would produce changes in the soil food web. Specifically we predicted that detritivorous arthropods would respond negatively to increasing non-native grass litter (Belnap and Phillips 2001) due to reduced movement ability and because they would not consume non-native grass litter due to its novelty. This expected decrease in detritivorous mesofauna may then lead to a decrease in their major predators (certain Formicidae and Araneae).

In contrast, we expected the microbial community would show an overall positive response to increasing non-native grass litter, driven by bacteria. Empirical studies of *Bromus* have found increased amounts of active bacteria along with decreases in the richness and abundance of soil fungi and invertebrates (Belnap and Phillips 2001). In addition, fungi are generally able to decompose more recalcitrant litter than bacteria (Moore et al. 2004) (Wardle et al. 2004), thus a change from fungi-dominated to bacteria-dominated soil communities is expected.

The influx of abundant labile grass litter into a formerly shrub-dominated community may cause a number of ecosystem functioning changes. Increased surface and soil moisture from a layer of litter thatch may lead to faster litter decomposition and nutrient cycling rates in areas of high non-native grass litter. Consequently, it follows that there will be higher total soil carbon and soil nitrogen due to increased aboveground productivity. Productivity increases can lead to greater soil organic matter stabilization by

the microbial community (Kaye and Hart 1997) and possibly due to changes in nitrogen input timing which may allow greater stabilization by microbes (Eviner 2004). All predicted changes have feedbacks to arthropod communities (Klironomos and Kendrick 1995).

To study these changes we have used observational approaches for two years and began a litter removal/addition experiment in spring 2005. The experiment consists of litter removal, litter addition, and control treatments in areas with either naturally high or naturally low grass litter, as well as a removal control of litter from naturally high areas for a total of seven treatments (see below for more detail). This design will allow us to continue to monitor soil community, ecosystem, and shrub growth properties in areas of naturally high and

low non-native grass litter via the control plots. Additionally it will allow identification of effects of litter via the removal and addition treatments and will allow us to identify whether these effects differ based on the pre-experimental condition (naturally high or low grass litter).

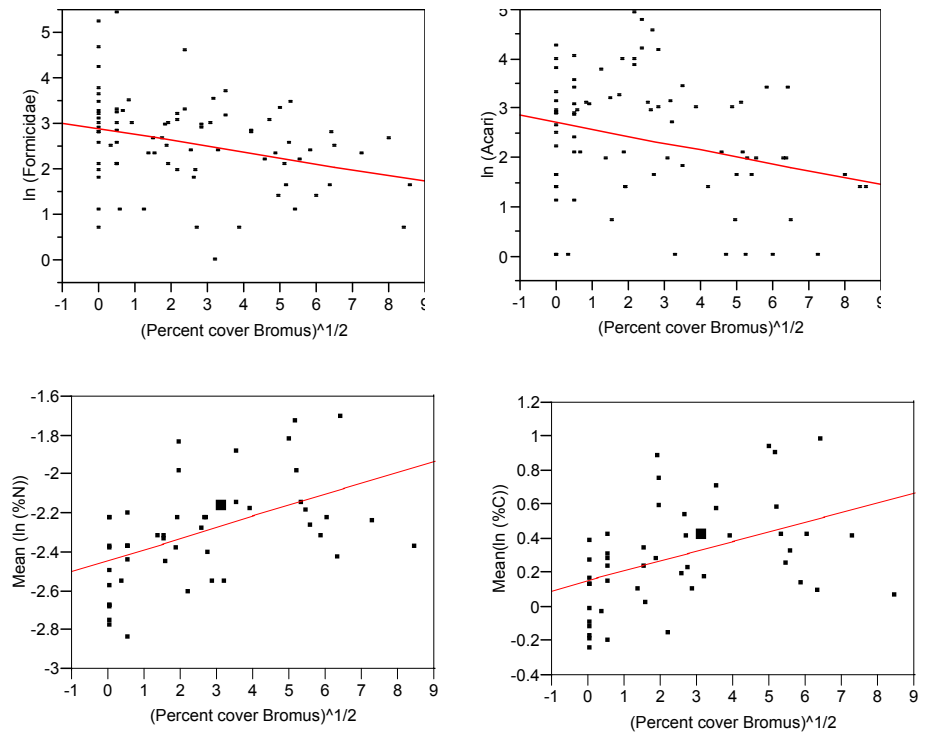


Figure 2: Relationships between *Bromus* and Acari and Formicidae and soil nitrogen and carbon: $\ln(\text{Formicidae}) = 2.9 - 0.13 \text{ Bromus}^{1/2}$ ($p < 0.005$); $\ln(\text{Acari}) = 2.7 - 0.14 \text{ Bromus}^{1/2}$ ($p < 0.05$); $\ln(\%N) = -2.44 + 0.06 \text{ Bromus}^{1/2}$ ($p < 0.001$); $\ln(\%C) = 0.15 + 0.06 \text{ Bromus}^{1/2}$ ($p < 0.001$).

Observational work

A pilot study conducted by the project group in spring 2004 in areas of naturally varying *Bromus* cover found that most ground-dwelling arthropod taxa decline with increasing *Bromus* while total soil carbon and nitrogen increased. We sampled arthropods with pitfalls installed under *Artemisia californica* and *Eriogonum fasciculatum* shrubs in areas of variable *Bromus* cover across three aspects (east/west, north, south); we took two soil cores from each plot for basic soil analysis. Neither shrub species nor aspect were significant predictors of arthropod abundance ($p > 0.1$). Acari and Formicidae, the two most abundant groups, showed similar decreases with increasing *Bromus* cover, while total soil nitrogen and carbon content showed increases, suggesting grass litter is being decomposed and incorporated into the soil (Fig. 2, previous page).

We conducted additional observational work in 2005 in areas of high and low non-native grass. We found a general decline in arthropod taxa (mites: $F_{1,54}=10.86$ $p<0.01$; collembola: $F_{1,54}=2.10$ $p=0.15$; a number of scavenger ant species, among them *Forelius mccooki*, *Pheidole vistana*, see Fig. 3; and larger spiders: $F_{1,54}=5.76$ $p<0.01$) and increase in soil moisture and organic matter (moisture: $F_{1,54}=13.65$ $p<0.001$; organic matter: $F_{1,54}=3.84$ $p=0.055$).

These results provide general support for the outlined hypotheses. As expected many detritivorous arthropods (mites, collembola, most ant species, >3 mm spiders) showed a decline in areas of higher grass. However, two proxies for microbial abundance, soil respiration ($F_{1,54}=1.12$ $p=0.29$) and microbial biomass ($F_{1,54}=0.69$ $p=0.41$) showed no relationship with grass, however, these values were taken near the end of the rainy season and changes may be more apparent during times of higher microbial activity such as in the early to mid-rainy season (December to March). Proposed future work includes soil sampling during the winter.

Experimental work

In May 2005 we began a litter addition and removal experiment which consists of three and four treatments across two different levels of naturally present non-native grass: areas with naturally low amounts of non-native grass litter (L), and areas with naturally high amounts of non-native grass litter (H). The four treatments are replicated eight times

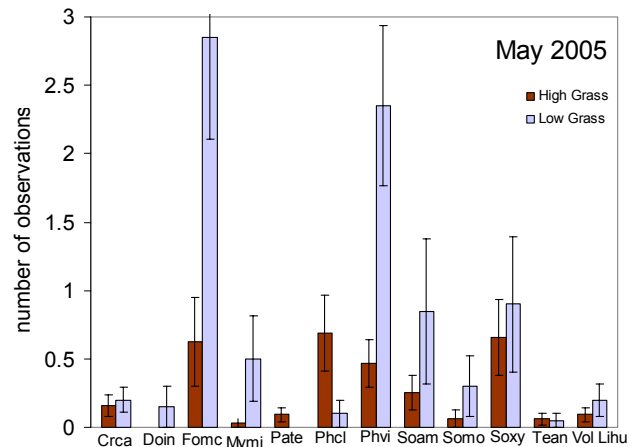


Figure 3: Ant species abundance in areas of high and low non-native grass. Codes are left to right: Crca: *Crematogaster californica*, Doin: *Dorymyrmex insanus*, Fomc: *Forelius mccooki*, Mymi: *Myrmecocystus mimicus*, Pate: *Paratrachina* c.f. *tericola*, Phcl: *Pheidole clementensis*, Phvi: *Pheidole vistana*, Soam: *Solenopsis amblychila*, Somo: *Solenopsis molesta*, Soxy: *Solenopsis xyloni*, Tean: *Temnothorax Andrei*, Vol Lihu: *Linepithema humile*.

for each factor and are: 1) C: control: no change; 2) R: Removal: litter removed by raking, shaken within plot to remove most arthropods and removed from plot; 3) RC: Removal control: litter removed by raking, shaken and returned to plot; 4) A: Addition: litter added (taken from removal plots and additional areas, air-dried and gently

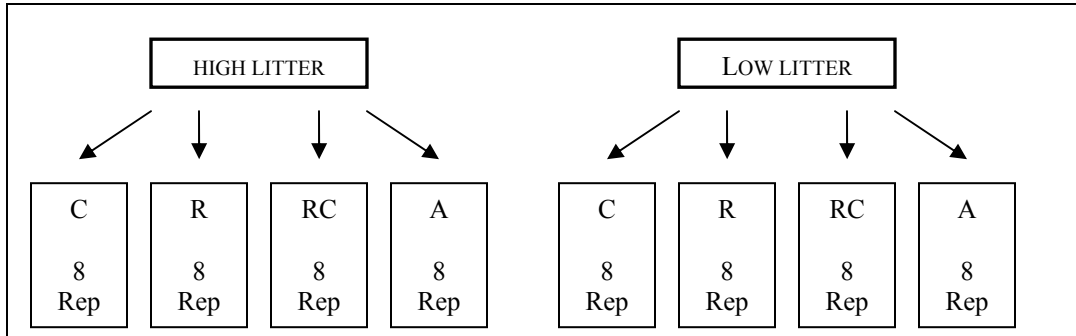


Figure 4: Design of addition/removal manipulation. See text immediately above for treatment codes.



Figure 5: Photos of manipulated plots, June 2006: Top: a control plot with naturally low grass litter (LC), Middle: a plot with naturally low litter to which litter was added in 2005 (LA) and in 2006 (bottom).

homogenized) to two times the amount of litter in plots with naturally high litter (Figs. 4-5). In total an estimated 60 kg of dry weight grass litter was moved in late May 2005 for the experiment and changes in community and ecosystem dynamics will be followed for a minimum of 36 months.

We gathered arthropod and soil samples from the manipulated plots in March through mid-June 2006. We expect to have the majority of these samples processed by the fall and present here only some of the data we will eventually have. Analyses on soil organic matter, moisture and microbial biomass carbon show trends towards some of the predicted results (Fig. 6).

Future work

We plan to continue monitoring the ecosystem and community effects of manipulation at a minimum until June 2007, with sampling in winter and spring 2007. Some research funding will be provided by an EPA Science to Achieve Results (STAR) Fellowship (to Wolkovich) and we are currently pursuing additional funding through California's

Exotic and Invasive Pests Research Program.

This proposal funded the first collaborative work between Bolger and Cottingham and, thus, some of the first combined ecosystem and community work on exotic annual Mediterranean grasses and in coastal sage scrub. Furthermore, the work was supported by a number of local scientists at both UC-San Diego and San Diego State University which we expect will lead to future partnerships. Dr. David Holway (UCSD) provides space for arthropod sorting and expertise in ant identification. Dr. David Lipson (SDSU) provides assistance for soil methods and sample storage.

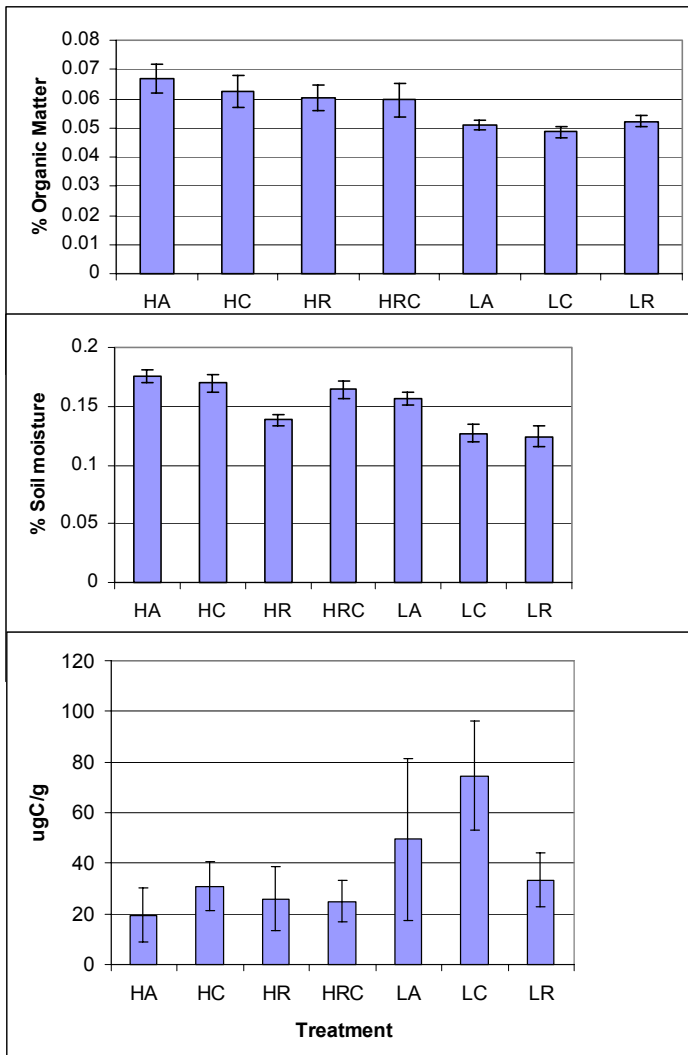


Figure 6: Results from manipulation: Soil organic matter (top) and moisture (middle) shows a trend towards increasing in plots with added litter, while soil microbial biomass carbon (bottom) is highest on naturally low grass litter unmanipulated plots. Bars are +/- 1 SE. See text for treatment codes.

Value of CIPM Seed Money Grant

The CIPM Seed Money grant provided start-up funding to begin what is now a multi-year grass litter manipulation. We would likely not have been able to conduct our 2005 observational work or complete the manipulation in June 2005 without this funding. Now that the experiment has begun we are collecting data on ecosystem and community changes and will continue to do so through June 2007 with other funding. We expect this will lead to several publications in peer-reviewed journals and will probably lead to follow-up studies.

The findings of this project are expected to be transferable to a number of other Californian areas and systems. The results should be widely applicable to other conserved areas of Diegan CSS, and generally applicable to areas of CSS throughout its range in California and Mexico. Additionally these grasses are considered invasive in desert and grassland regions of California

(Brooks 2003) (Seabloom et al. 2003b). In particular, invasion of grasses into CSS also provides an interesting mirror of shrub invasion into desert grasslands. Several studies

have found the invasion of shrubs into the southwestern US has led to changes comparable to those observed in CSS, which may allow generalizations of the consequences of changing a system's dominant plant functional type (Bestelmeyer 2005) (Nash et al. 2000). Results from this study will provide refuge and park managers with a more detailed understanding of how non-native grasses impact native shrubs, their soil communities and ecosystem properties and whether established plans for grass removal are beneficial. Conclusions will also inform future work aimed at elucidating how invasive litter alters soil food webs and will provide excellent insights and data for future studies.

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