Nonnative grass litter enhances grazing arthropod assemblages by increasing native shrub growth

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Abstract. Recent theory and research have highlighted how the brown (detritus-based) world may control the trophic structure of the green (grazing) world. Detritus can alter bottom-up control of green webs by affecting autotroph biomass and quality through its ability to alter ecosystem properties, including soil moisture and nutrient cycling. Additionally, the role of detritus as the food resource base of brown webs may subsidize omnivorous predators that can provide top-down control of green webs. Brown–green connections may be especially important following plant invasions, which often lead to increased detritus and altered food webs. I combine field experiments, observational data, and path analysis to understand how nonnative grasses impact native arthropod communities in a semiarid shrub system. Theory and correlative evidence predict that decreased shrub growth and nutritional quality, and increased feeding of detrital predators on the grazing web, would decrease the abundance of shrub arthropods. In contrast, I found nonnative litter increased shrub growth via increased soil moisture and produced a strong bottom-up increase of the grazing arthropod web; effects of detrital predators and plant quality were comparatively unimportant. I link these findings to the apparent lack of overlapping predators between the brown and green webs, and to the important abiotic role of litter in this xeric system, which increased native plants and the abundance and richness of arthropods on them.

Key words: Artemisia californica (California sagebrush); bottom-up control; coastal sage scrub, southern California, USA; detritus; exotic and alien species; harvestmen (Opiliones); leafhoppers (Auchenorrhyncha: Cicadellidae); Mediterranean climate cf. xeric systems; PERMANOVA; plant quality; resource-shunt hypothesis; spiders (Araneae).

INTRODUCTION

For decades ecological theory of how basal resources (bottom-up) and consumers (top-down) influence trophic structure and dynamics has focused on the "green" world—living autotrophs and the grazing webs they support (Hairston et al. 1960, Oksanen et al. 1981). However, recent theory (Rooney et al. 2006), and research in both aquatic (Vander Zanden and Vadeboncoeur 2002) and terrestrial ecosystems (Wise et al. 1999, Pringle and Fox-Dobbs 2008) have demonstrated that detritus and its associated "brown" webs can be critical to the relative magnitude of top-down or bottom-up control of green webs. At the same time research has highlighted the role of detritus as an important modulator of ecosystem properties (Moore et al. 2004), often altering the quantity and quality of autotrophs (Cebrian and Lartigue 2004, Nowlin et al. 2008), and thus possibly consumers as well (Ritchie 2000).

Top-down effects of brown webs on green webs can occur through a "resource shunt" (Oksanen 1997), where brown and green webs are connected by omnivorous predators. According to the resource-shunt hypothesis, bottom-up increases in the detrital food web lead to increased abundance of predators that then feed additionally on the green web and depress green-web consumers. Theory predicts resource shunts should be ubiquitous (Rooney et al. 2006) and they have been documented in both aquatic and terrestrial systems (Wise et al. 1999, Vander Zanden and Vadeboncoeur 2002). In lakes, predatory fish exert strong top-down control on pelagic grazing webs, but only because they are heavily subsidized by feeding on benthic, often detrital-based webs (Schaus and Vanni 2000, Vander Zanden and Vadeboncoeur 2002). Similarly, in several forest and crop systems increased plant litter enhances spider populations that then depress arthropod herbivores (Settle et al. 1996, Wise et al. 1999, Miyashita and Takada 2007).

Detritus and its associated brown web may also produce bottom-up control by altering key ecosystem properties related to autotroph quantity and quality, especially in terrestrial systems. Plant quantity (biomass), and plant quality, often assessed as the percentage of nitrogen (N) or C:N in leaf tissue, are strongly controlled by a system's nutrient cycling that itself is linked to detritus (Moore et al. 2004). Detritus can alter

nutrient cycling through its quality and its control over microclimate (Facelli and Pickett 1991); such changes in temperature and soil moisture may favor establishment and growth of certain plants (Facelli 1994). By altering the type, quantity, and quality of plants detritus may then influence the abundance and diversity of herbivores, and of their green-web predators. In systems with especially low-quality terrestrial plant materials, plant litter may limit herbivores and slow nutrient cycling, producing bottom-up control (Borer et al. 2005).

The effect of the brown world on green webs may be especially important to arthropod food webs in systems undergoing plant invasions. Plant invasions generally increase plant litter (Liao et al. 2008) and produce associated bottom-up increases of detrital arthropod abundance (Gratton and Denno 2005, Topp et al. 2008). Concurrently arthropod grazing webs often show declines in the overall abundance and diversity of arthropods following invasion. Thus, invaded landscapes shift to having most arthropod abundance occurring in the brown, rather than the green, web, and a concomitant reduction in richness of the green web only (Gratton and Denno 2005, Topp et al. 2008).

The three mechanisms outlined above—resource shunt, plant quantity, and plant quality—may explain the observed declines in grazing-web arthropods following invasion. The resource-shunt hypothesis predicts declines in herbivores and also in specialist grazing-web predators, which may decrease due to competition for herbivore prey with ground predators, or through intraguild predation (Wise 1993). Declines in native plants due to invasion (Levine et al. 2003) could result in decreased quantity of native-plant biomass to support grazing webs. Finally, because the most common hypothesis for decline of terrestrial native plants is competition between native and nonnative plants for soil nitrogen (Levine et al. 2003), reduced available soil nitrogen following invasion may reduce leaf nitrogen in native plants. This reduction in native-plant quality could then limit herbivores and their grazing-web arthropod predators. Understanding which of these three mechanisms controls how nonnative plant litter alters grazing webs has important applications to both basic and invasion biology. For basic ecology the study of nonnative litter's impacts on grazing webs provides a novel opportunity to examine how detritus affects the trophic structure of terrestrial systems. For invasion biology, understanding mechanisms controlling the impacts of invasive plants is often key to predicting which nonnative plants may become invasive species detrimental to native species (Levine et al. 2003).

I examined the impacts of invasive plants and their litter on grazing webs in coastal sage scrub. Coastal sage scrub is a shrub-dominated semiarid habitat of southern California (USA) (Westman 1981) that has recently seen large increases in the cover of nonnative annual grasses (Minnich 2008). These grasses produce abundant litter that transforms the habitat, converting most interstitial spaces between shrubs from a crust/bare ground mosaic to areas covered by nonnative grass and its litter (Wolkovich et al. 2009b). Invasion has also been associated with declines of the dominant shrub, *Artemisia californica*, hypothesized to be due to competition for soil nitrogen (Eliason and Allen 1997).

Integrating expectations of decreased native-plant quantity and native-plant quality, due to competition with nonnative grass, and increased abundance of omnivorous predators due to the resource shunt, predicts declines in the abundance of arthropods in the grazing webs of *A. californica* shrubs in areas of increased nonnative grass and its litter. I combined an observational study with a two-year experiment and path analysis to identify the most likely mechanisms controlling impacts of nonnative litter on *A. californica* shrub grazing webs. I measured shrub growth (quantity), shrub leaf nitrogen (quality), and the ground arthropod predators (resource shunt) as well as shrub arthropod herbivores and predators. Contrary to predictions I found increased abundance of both arthropod herbivores and predators on shrubs with increased grass and its litter, and no evidence of effects of plant quality or ground arthropod predators on the shrub arthropod web. I link these findings to the abiotic role of litter and the separation of arthropod predators between detrital and grazing webs.

MATERIALS AND METHODS

Study site

I conducted all studies in 50 ha of coastal sage scrub (hereafter CSS) habitat of the San Diego National Wildlife Refuge's Sweetwater Unit (California, USA). I selected areas >0.5 km from any urban edge to avoid confounding effects of the nonnative Argentine ant (*Linepithema humile*), an invasive species abundant at habitat edges (Holway 1999). I studied effects on *Artemisia californica,* a drought-deciduous shrub, codominant and type-specific in CSS (Westman 1981). Dominant nonnative grasses at the study site were *Brachypodium distachyon*, *Bromus madritensis* ssp. *rubens*, and *Avena barbata*.

Shrub sampling

I estimated aboveground shrub biomass and leaf nitrogen from shrub clippings in May of 2004, 2006, and 2007. I clipped a small section of each shrub and visually estimated the number of similarly sized clippings present on the shrub. For each clipping I separated, dried, and weighed current (foliage and non-lignified stem, hereafter referred to as "shrub growth") and previous (woody) growth in the laboratory. Foliage samples from 2007 were analyzed for carbon and nitrogen content (Carlo Erba NA 1500 series 2 [CE Elantech, Lakewood, New Jersey, USA]). I used leaf tissue percentage nitrogen as my plant-quality metric because trends in the C:N ratio were driven almost entirely by variation in nitrogen.

Shrub arthropod sampling

I used a modified leaf-blower (Stewart and Wright 1995) to vacuum-sample (for 60 s) *A. californica* shrubs. Vacuum-sampling provides a reliable estimate of arthropod grazing communities and is comparable to more intensive and destructive methods (Brook et al. 2008). Additionally, pilot work in March–May 2004 showed that: (1) vacuum-sampling captured a greater abundance and diversity of arthropods than beating or fogging and (2) earlier-season sampling captured an extremely high proportion of immature arthropods with a similar representation of families as late-season sampling, suggesting synchronous phenology of arthropods. Thus I sampled only once later in the growing season (9–10 May 2004, 30 May 2006, and 20 May 2007). I placed all vacuum samples on ice immediately in the field and kept them frozen until sorting.

I sorted shrub arthropods under a dissecting microscope. Most taxa were sorted to morphospecies (Oliver and Beattie 1996), including all non-Sternorrhyncha Hemiptera, Araneae, Coleoptera, Formicidae, and Psocoptera. I identified the most common Auchenorrhyncha (herbivore) and Araneae (predator) morphospecies to species (listed in Appendix C). Voucher specimens are retained by E. Wolkovich.

Observation

To characterize natural variation in the study system, I selected 21 *A. californica* shrubs of typical size (0.3–1.4 m^2) along a natural gradient of high to low nonnative grass cover. In May of 2004, I measured percent grass cover visually within a 4-m^2 area centered around each shrub and quantified shrub growth and the shruboreal arthropod community (arthropods adapted for living in and moving about shrubs) as described above.

Experiment

Design.—To test whether variation of arthropod communities of *A. californica* shrubs was influenced by nonnative grass litter, I manipulated invasive grass litter. I first selected 56 *A. californica* shrubs of roughly the same size (1 m^3), in high- and low-grass areas, and centered 3 × 3 m plots around them. The experiment consisted of two factors: the pre-manipulation invasive grass cover (Factor 1, *Invasion level*), categorized as high or low, and whether I added, removed or left unchanged (control) invasive grass litter (Factor 2, *Litter*), for a total of six treatments (*Invasion level × Litter*). I performed the initial manipulation at the end of the growing season in June 2005 when all grass had senesced and dried. For additions I brought all plots (high and low *Invasion level*) up to two times the abundance of grass litter in highly invaded areas (271 g/m^2). In removal plots I cut all litter at the ground level, shook it to remove unattached seeds and arthropods, and removed it from the area. A removal control treatment tested for artifacts of the removal process (see Appendix

A). Each treatment was replicated eight times. I repeated the manipulation in 2006; precipitation, and therefore productivity, was much lower than in 2005 (74% of the 50-year mean vs. 190% in 2005) so I added or removed less litter (67 g/m^2, the natural abundance of litter in highly invaded areas in 2006). Measurements included numerous response variables, including growth of nonnative grass (Wolkovich et al. 2009a). I sampled shrub growth and shrub arthropods as described earlier.

Vegetation sampling.—I assessed the percentage of ground cover that was nonnative litter by the point-intercept method (Heady et al. 1959, Barbour et al. 1999), recording cover at 18 points in each plot as either nonnative grass litter or other cover. Points were separated every 0.5 m along two diagonal transects stretched across each plot. I divided total litter hits by 18 to obtain percent ground cover out of 100%.

Ground arthropod sampling.—I sampled the ground Araneae and Opiliones (spiders and harvestmen, respectively) by pitfall trapping in 2007. Pitfall-trap captures represent an integrated measure of abundance and activity, which makes absolute numerical comparisons difficult, especially among taxa. However, pitfall traps allow comparison of the effects of grass litter cover within taxa because they are repeatable throughout a season, sample across several days and nights, and provide an effective way to sample ground arthropod communities across a gradient of vegetation structure (Curtis 1980, Perner and Schueler 2004). Pilot sampling determined the timing and duration of pitfalls. Pitfalls were open for two 8-d periods during the growing season (10–18 March and 21–29 May 2007). I sorted pitfall contents, recording all Opiliones and Araneae, and further sorting all mature Araneae to family.

Statistical analyses

Because changes to arthropod grazing webs may involve abundance and/or species composition, I used both multivariate and univariate statistics to assess arthropod and plant responses to nonnative grass and its litter. I used Pearson correlation to analyze relationships among nonnative grass, shrub growth, and shrub arthropods in the observational study. I used permutational (PER)MANOVA to assess responses by multiple taxa to the experiment. PERMANOVA (formerly called "nonparametric MANOVA") is similar to traditional parametric multivariate analysis of variance (MANOVA) in simultaneously testing multiple response variables to factors, but relaxes the assumption of a multivariate normal distribution, which is rarely met with taxa count data (see Appendix B). It achieves this by converting data to dissimilarity or distance measures, then obtaining a distance-based pseudo-F statistic by expectations of mean squares, similar to a traditional MANOVA, and a P value based on permutations of the data (Anderson 2001, Anderson et al. 2008). Here I used a two-way PERMANOVA based on my experimental design, using Bray-Curtis

TABLE 1. Comparisons of six a priori path models that contrasted links between nonnative grass litter, shrub growth, plant quality (shrub leaf tissue %N) and detrital web predators to shrub arthropods.

Model	Description of model	χ^2	df	P	ΔAIC
A	full model: detrital food-web predators and plant quality linked to grazing food web	7.24	6	0.30	12.77
B	Model A without plant quality linked to shrub arthropods	7.48	7	0.38	12.53
C	Model A without detrital web predators linked to shrub arthropods	8.62	8	0.38	11.39
D	Model A without plant quality	4.46	4	0.35	5.55
E	Model A without detrital web predators	4.42	4	0.35	5.59
F	simple bottom-up model, no plant quality or detrital web predators	2.01	3	0.57	0

Notes: Model A is the most complex, while Model F is the simplest. A *P* value of >0.05 indicates that the model fits the data, while the AIC compares model fit, where the lowest AIC (and ΔAIC = 0) is the best-fitting model. See also Fig. 4.

similarity on square-root-transformed data with 9999 permutations.

Because PERMANOVA uses dissimilarity measures, it can detect differences in treatment groups due to differences in community composition, community sizes, the multivariate dispersion (similar to variance in multivariate space), or any combination of these (Anderson et al. 2008). Thus I examined PERMANOVA results with a suite of additional tests. I assessed community differences by nonmetric multidimensional scaling (NMDS), univariate analyses, and PERMDISP. PERMDISP provides a method to test for homogeneity of multivariate dispersion for any given grouping factor and obtains permutation-based *P* values (Anderson et al. 2008). Because PERMDISP makes comparisons to a factor's group centroid, analyses of two-way designs must be considered by analyzing single factors (Anderson et al. 2008). I used PERMDISP for the experiment by combining *Invasion level* and *Litter* into a single factor with six levels, and used the same transformed data as for PERMANOVA (with 9999 permutations). For univariate analyses of shrub arthropods (total leafhoppers, spiders, richness) in the experiment I used two-way repeated-measures (RM-)ANOVA based on the experimental design (Invasion level × Litter). I analyzed the responses of *A. californica* growth to the manipulation with the same two-way RM-ANOVA model, but with an additional covariate for previous growth (see *Shrub sampling*, above). For all RM-ANOVAs I used a variance–covariance matrix with unstructured variance because it was an equally good (leafhoppers) or better (spiders, richness, shrub growth) fit than a matrix with compound symmetry, as assessed with Akaike's information criterion (AIC). Tests included all possible interactions between Invasion level, Litter, and Year. For brevity however, I do not report interactions where $P > 0.2$. I square-root-transformed all 2006 and 2007 arthropod and shrub growth data to reduce heteroscedasticity. Also, the degrees of freedom for some similar models vary slightly due to loss of samples in transport. I estimated the morphospecies richness of leafhoppers and spiders as the number of morphospecies per shrub (Colwell and Coddington 1994).

To contrast the three possible pathways of litter's effects on the grazing web—resource shunt, plant quantity, and plant quality—I used path analysis, a subset of structural equation modeling that allows the comparison of competing causal models that involve direct and indirect effects (Shipley 2002). I developed six a priori models based on the three possible pathways by which litter may affect the grazing web. All models included a bottom-up effect via plant growth, but varied connections of litter to the grazing web through the detrital predators (resource shunt) and through plant quality (Table 1). The most complex model (A) included all such links, while the most basic model (F) included only a simple bottom-up direct effect through shrub growth to shrub arthropods. I used AIC to compare model fits, where models with the lowest AIC best fit the data. I used 2007 data for the path analysis because 2007 was the predetermined end date of the experiment and therefore also the year when I measured a complete set of all response and predictor variables.

I conducted analyses in JMP 5.0 (SAS Institute 2005), PERMANOVA+ PRIMER 6 (PRIMER-E 2008), and R 2.7.1 (R Development Core Team 2007) including the packages car, nlme, MASS, sem, and vegan.

RESULTS

Arthropod species and species pools

I collected a total of 5117 arthropods by vacuum-sampling (334 in 2004, 2230 in 2006, 2553 in 2007) belonging to 71 morphospecies (Appendix C). The Cicadellidae (leafhoppers, within Auchenorrhyncha) was the most abundant group numerically (51% in 2004, 63% in 2006 and 59% in 2007). Spiders (Araneae) were the next most abundant group (19%, 11%, and 12% in each year, respectively). Within each of these groups, one morphospecies dominated: the leafhopper *Empoasca alboneura* Gillette (Typhlocybinae) (of total cicadellids: 30% in 2005, 35% in 2006, and 44% in 2007), and the spider *Ceraticelus* sp. 1 (Linyphiidae) (Prentice et al. 1998) (of total spiders: 65% in 2004, 35% in 2006, and 56% in 2007). All leafhoppers and spiders identified to genus or species were native (Prentice et al. 1998; R. Gill, *personal communication*). All other groups (Acarina, Coleoptera, Diptera, Formicidae, other Hemiptera, non-Formicidae Hymenoptera, Lepidoptera, Orthoptera, Psocoptera, Thysanoptera) represented 6% or less of arthropods. Thus I focused analyses on leafhoppers and spiders, which were the dominant herbi-
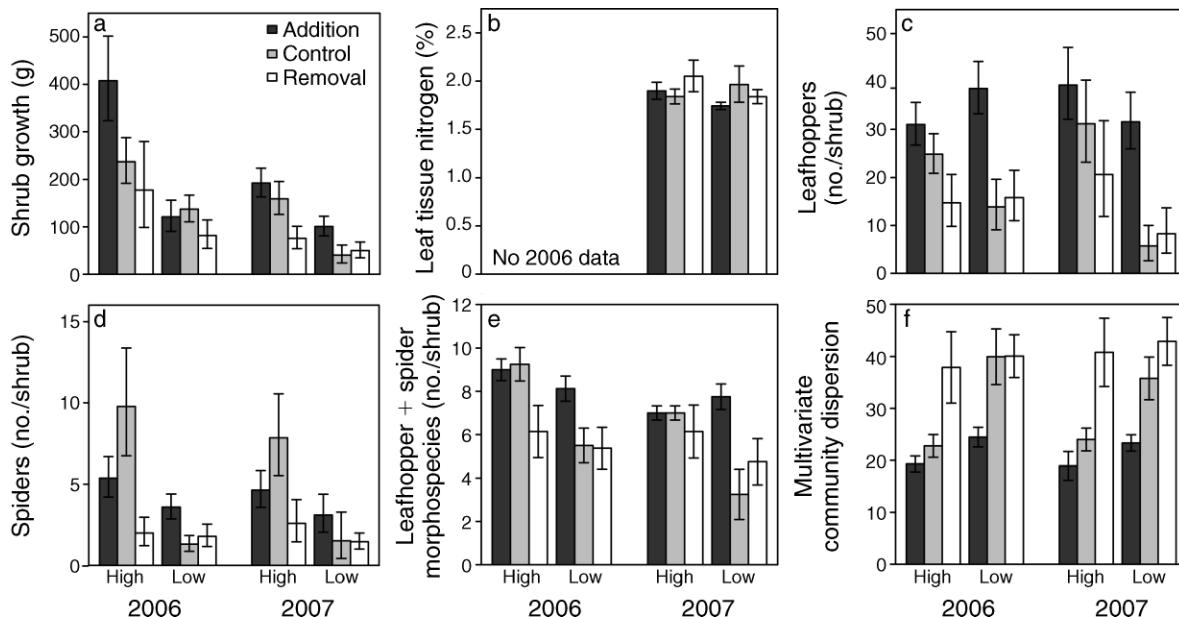
FIG. 1. (a) Native-shrub growth, (c) total leafhoppers and (d) total spiders on native shrubs, and (e) the morphospecies richness of the two groups combined showed similar positive responses to nonnative litter across years. (b) Native-shrub leaf tissue nitrogen percentage was not affected by litter. "High" and "Low" refer to the premanipulation invasion level, while "Addition," "Control," and "Removal" refer to the nonnative litter treatment. (f) Dispersion of the community of all leafhoppers and spider morphospecies was lowest in plots with greater nonnative litter cover (PERMDISP: $F_{5,41} = 5.74$, $P = 0.005$ in 2006; $F_{5,38} = 7.16$, $P < 0.002$ in 2007). "Dispersion" represents spread of leafhopper and spider community data in multivariate space; see *Materials and methods: Statistical analyses* for additional details. Data are shown as means ± SE and are back-transformed where appropriate.

vores and predators on *Artemisia californica* (see Plate 1).

I collected a total of 188 spiders (Araneae) and harvestmen (Opiliones) in 2007 from pitfall traps. The community was composed mainly of the spider families Lycosidae, Salticidae, Scytodidae, and Thomisidae, with Scytodidae (26% of community, all *Scytodes* sp. 1; Prentice et al. 1998) and Salticidae (21%) most common.

Observation

Contrary to the hypothesis that native shrub growth declines with grass invasion, shrub growth was positively correlated to nonnative grass cover ($r = 0.50$, $t_{18} = 2.46$, $P = 0.02$). The abundances of leafhoppers and spiders on the shrubs were also positively correlated with nonnative grass cover (leafhoppers, $r = 0.51$, $t_{19} = 2.57$, $P = 0.02$; spiders, $r = 0.63$, $t_{19} = 3.53$, $P = 0.002$), with shrub growth ($r = 0.37$, $t_{18} = 1.69$, $P = 0.11$; $r = 0.54$, $t_{18} = 2.75$, $P = 0.03$) and with each other ($r = 0.64$, $t_{19} = 3.63$, $P = 0.002$).

Experiment

The experiment confirmed the observational results, supporting the hypothesis that nonnative grass enhances shrub arthropod communities, and further indicated that beneficial effects were due to nonnative litter. The leafhopper and spider communities varied with premanipulation invasion level (Fig. 1c, d, pseudo-$F_{1,41} = 2.36$, $P = 0.04$ in 2006; pseudo-$F_{1,41} = 4.16$, $P = 0.0003$ in

2007) and in response to litter treatments (Fig. 1c, d, pseudo-$F_{2,41} = 1.91$, $P = 0.04$ in 2006; pseudo-$F_{2,41} = 1.98$, $P = 0.02$ in 2007, Invasion level × Litter, pseudo-$F_{2,41} < 1.0$, $P > 0.4$ both years). These results were consistent across various combinations of taxa considered (e.g., all taxa, various subsets of leafhoppers, and spiders). Morphospecies composition did not vary due to the manipulation, as shown by high overlap of all treatments in NMDS plots (Fig. 2). Results of NMDS with various other taxa combinations were similar.

Community changes detected by PERMANOVA were due to altered abundances of leafhoppers and spiders by litter ($F_{2,41} = 7.22$, $P = 0.002$ for leafhoppers; $F_{2,41} = 3.32$, $P = 0.05$ for spiders). Leafhoppers were more abundant in litter-addition plots, and less abundant in removal plots (Fig. 1c). Spiders exhibited similar trends to leafhoppers generally, but were less abundant in high invasion addition plots (Fig. 1d). Spiders additionally responded to invasion level ($F_{1,41} = 12.08$, $P = 0.001$) and its interaction with litter ($F_{2,41} = 4.67$, $P = 0.02$). This interaction occurred because treatments that reinforced the premanipulation state—additions of grass litter to areas already highly invaded, and minor removals of litter from areas with little grass invasion—showed reduced effects compared to other treatments (Fig. 1d). Leafhoppers showed the only variation among years: they were greater in high invasion areas in 2007 but not 2006 (Invasion level × Year, $F_{1,41} = 10.97$, $P = 0.002$; Fig. 1c). Increases in the overall abundance of

leafhoppers and spiders per shrub were not due to increased arthropod density: individuals/g leaf tissue of leafhoppers and spiders did not respond to the manipulation (two-way ANOVA results: all $F_{1-2,39} <$ 1.3, all $P > 0.25$ in 2006; all $F_{1-2,41} < 1.3$, all $P > 0.3$ in 2007). Thus, the increase in arthropod abundance per shrub was apparently due to increases in shrub size, not an increased density of arthropods on shrubs.

Matching the trends in abundance, richness of the leafhopper and spider community (Fig. 1e) was also greater in high invasion areas ($F_{1,41} = 4.27$, $P = 0.05$) and varied by litter treatment (Fig. 1e; $F_{2,41} = 6.81$, $P = 0.003$). Treatments that resulted in low litter cover (High invasion × Removal, Low invasion × Control, and Low invasion × Removal) showed much greater community dispersion than those with high litter cover (Fig. 1f).

Shrub growth did not show the predicted declines with increasing nonnative grass litter. Shrub growth was actually greater in high-invasion areas ($F_{1,41} = 4.61$, $P = 0.04$; Fig. 1a), growing more than twice as much in high-invasion areas (182 ± 1 g) as shrubs in low-invasion areas (70.5 ± 0.5 g) (mean $\pm$ SE; combined 2006–2007 data). Shrub growth also responded to litter ($F_{2,41} = 7.81$, $P = 0.001$; Fig. 1a), with shrubs in addition plots growing nearly three times as much as those in removal plots (190 ± 1 g vs. 65 ± 1 g, respectively). There was a modest interaction between invasion level and litter ($F_{2,41} = 3.84$, $P = 0.03$) due to treatments that reinforced the premanipulation state showing reduced effects. Experimental effects did not vary by year (all $F < 2.8$, all $P > 0.08$), but shrub growth itself varied by year ($F_{1,38} = 35.26$, $P < 0.0001$), and was positively related to previous growth ($F_{1,38} = 53.48$, $P < 0.0001$).

Plant quality and ground predators (spiders and harvestmen) were not affected by experimental treatments. Plant leaf nitrogen ranged nearly two-fold across shrubs, but did not vary due to the experimental manipulations (Invasion level, $F_{1,39} = 0.53$, $P = 0.47$; Litter, $F_{2,39} = 0.58$, $P = 0.56$; Invasion level × Litter, $F_{2,39} = 1.4$, $P = 0.27$; Fig. 1b). Ground arthropods also showed no effect of the experimental manipulations (Invasion level, $F_{1,42} = 0.02$, $P = 0.90$; Litter, $F_{2,42} = 1.7$, $P = 0.19$; Invasion level × Litter, $F_{2,42} = 0.44$, $P = 0.65$).

Path analysis

Path analysis supported a strong, but simple, positive bottom-up effect of litter on shrub leafhoppers and spiders via shrub growth (Figs. 3a–c, 4a). All six a priori models fit the data (Table 1, all $P > 0.05$), but the models that lacked plant quality (model D), ground predators (model E), or both (model F) had greatly improved fit (see ΔAIC, Table 1). Though ground predators did not show responses to the treatments, they were enhanced by litter (Fig. 4a). However, path analysis did not support any effect of this increase on shrub leafhoppers or spiders (Figs. 3d, e, 4a). Additionally, path analysis did not support any effect of plant quality on shrub leafhoppers (Fig. 4a), nor of nonnative
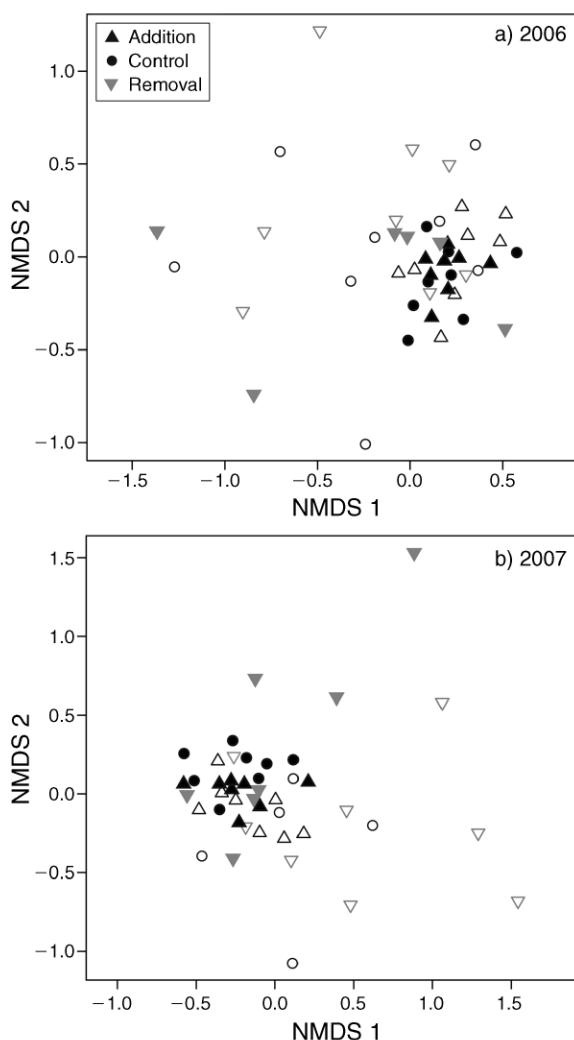

FIG. 2. Nonmetric multidimensional scaling (NMDS) plot of grazing-web community (a) in 2006 and (b) in 2007. Solid and open symbols represent areas of high and low grass invasion, respectively.

litter on plant quality (Fig. 4a). Instead, the best-fitting path model showed a simple bottom-up effect (Fig. 4b): nonnative litter increased native shrub growth, which increased the shrub herbivores (leafhoppers), which then increased the shrub predators (spiders). Models considering the role of the shrub growth (and thus potential habitat for spiders) in affecting shrub spiders did not alter these conclusions (Appendix D).

DISCUSSION

As hypothesized, native plant quantity strongly affected shrub arthropod communities, but its relationship with nonnative litter was directly opposite a priori predictions. Both observational and experimental results indicated that nonnative grass litter produced strong positive bottom-up control on native shrub herbivores (leafhoppers) and predators (spiders). Results did not
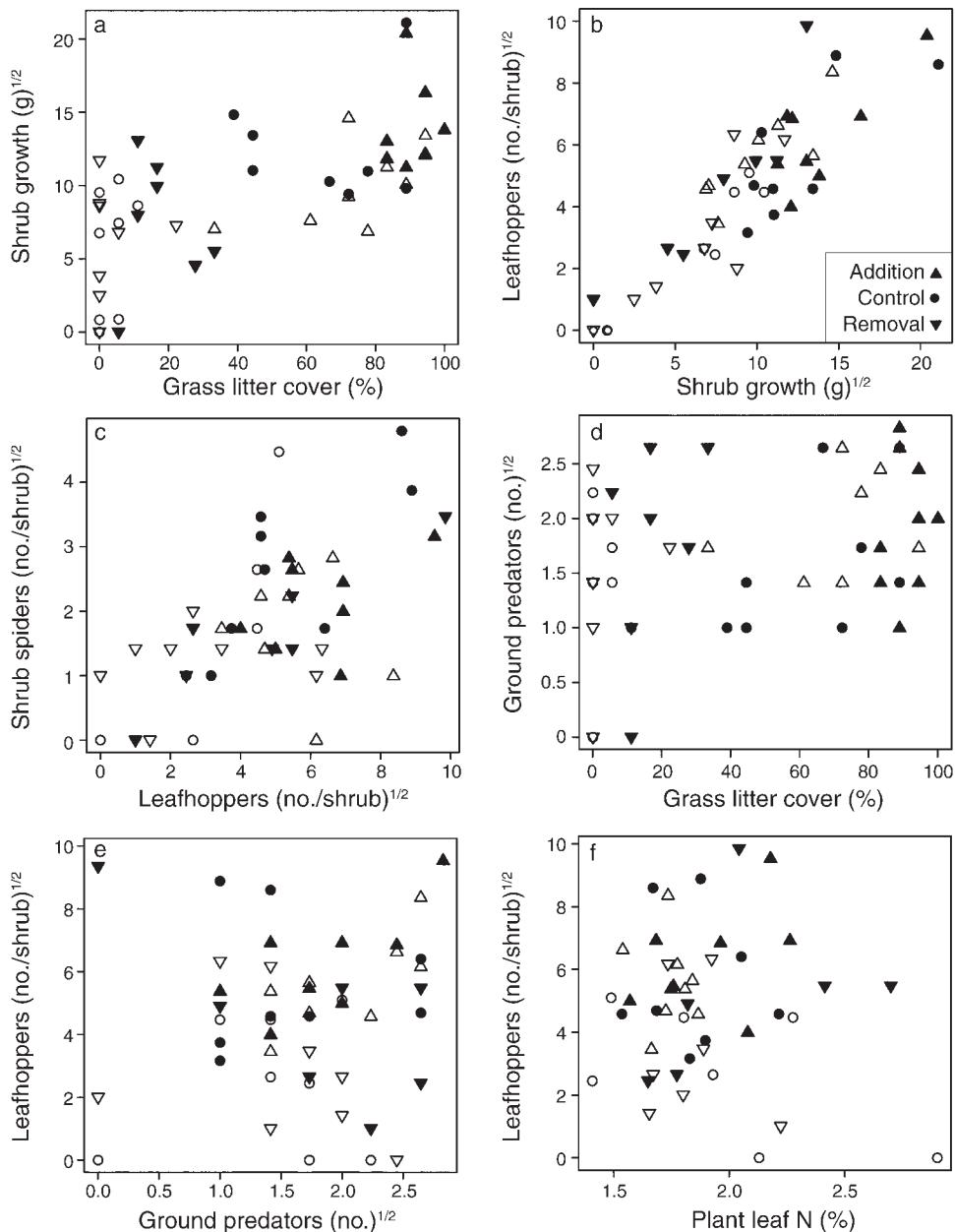
FIG. 3. Bivariate relationships among shrub-specific variables in 2007, two years after the first manipulation of nonnative grass litter. The superscript 1/2 on the axis units indicates square root.

support the top-down (resource shunt) or plant quality (bottom-up) hypotheses for decreased grazing-web abundance when plants invade. Instead, grass litter increased soil moisture and led to a large increase in growth of the native dominant coastal sage scrub (CSS) shrub *A. californica* (Wolkovich et al. 2009*a*), which increased shrub herbivores and predators.

Results argued against the resource-shunt hypothesis (where ground predators may suppress shrub arthropods), and suggested the role of detritus in controlling ecosystem properties is key in this xeric ecosystem. As in many Mediterranean climate systems (Vila and Sardans

1999), moisture is a major limiting resource in CSS; litter's abiotic effect on soil moisture and related increased shrub growth (Wolkovich et al. 2009*a*) appeared to be the main pathway through which litter affected shrub arthropod communities. Previous detrital-manipulation studies have generally been limited to crops, forests, and grasslands adjoining forests (Settle et al. 1996, Chen and Wise 1999, Halaj and Wise 2002, Miyashita and Niwa 2006)—systems where the effects of litter on soil moisture would presumably not be as dramatic as in CSS. Additionally, studies of arthropod communities in plant-invasion systems have been
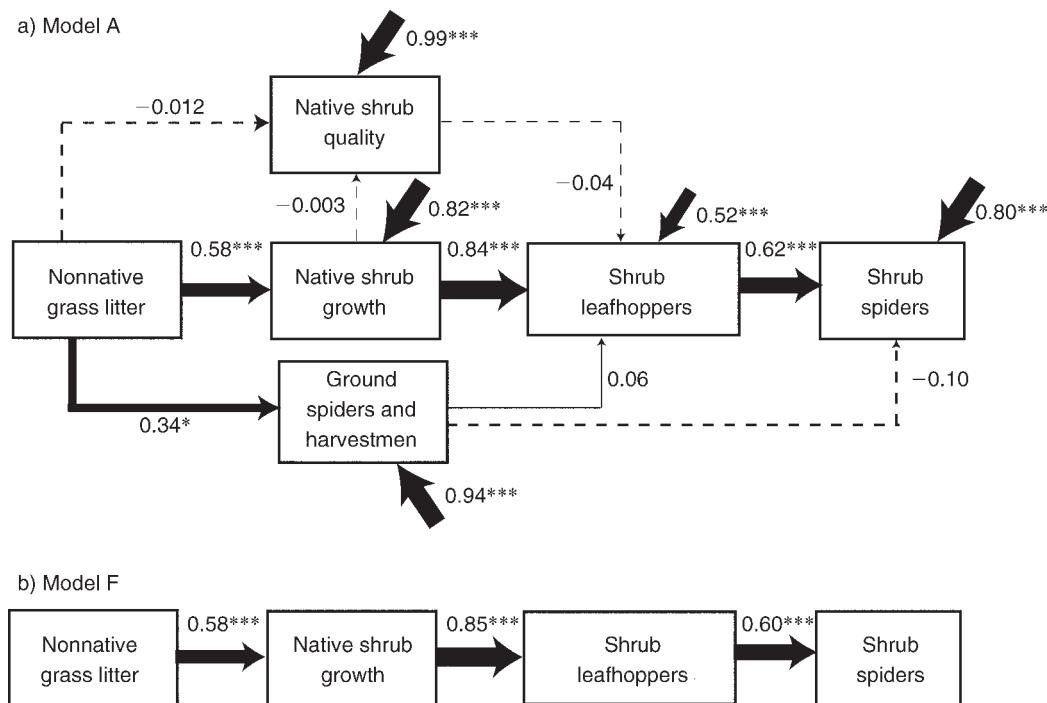
a) Model A

b) Model F

Fig. 4. (a) Path-analysis diagrams of Model A (model with the most links and all predictor variables) and (b) Model F (best-fitting and simplest model). Leafhoppers were the dominant herbivore group on the native shrub, while spiders were the dominant predator group. Plant quality was operationally defined as N percentage of shrub leaf tissue. Arrows represent positive (solid) and negative (dashed) path coefficients, which are indicated and also represented by arrow thickness. Path coefficients changed little across models; thus I show only two models and give unexplained-variation values (arrows not linking variables) only in panel (a). See Table 1 for description of the other four models and their fit statistics.

  * $P < 0.05$; *** $P < 0.0005$.

focused in marshes and mesic habitats, where water limitations are also greatly reduced (Ernst and Cappuccino 2005, Flanders et al. 2006, Gratton and Denno 2006). Most of these invasion studies also lacked experimental manipulations or measurements of litter and thus have not resolved mechanistic relationships between nonnative litter and arthropod communities.

Moreover, the lack of a resource shunt may be due to a separation of predators and prey between brown and green webs in this system. While studies have found omnivorous predators in several terrestrial systems (Wise et al. 2006, Oelbermann et al. 2008), results reported here suggest a distinct separation indicated by path analysis and the lack of correlation between ground and shrub arthropod food webs. Although the dominant spider families (Scytodidae) on the ground and on shrubs (Linyphiidae) have habits that should enable them to exploit both detrital and grazing prey (Uetz et al. 1999), there were different species in the two communities, indicating that individual species are not active across webs. Finally, Diptera, which have been noted previously as key prey for brown–green web connections (Miyashita and Takada 2007), are relatively rare in this system (Bolger et al. 2000, Appendix C).

Plant quality (percentage nitrogen of leaf tissue) did not affect shrub arthropods, suggesting even high

variation among shrubs is not sufficient to affect shrub arthropods in this system. I expected that lower-quality shrub tissue would decrease the abundance of shrub herbivores, but found no association. However, I did document a twofold variation in tissue quality, which is relatively high for a single species (Reich et al. 1996, Wright et al. 2004). Additionally this variation covered the observed range of *A. californica* quality across years and sites (E. Wolkovich and M. Nathan, *unpublished data*), and large, rapid changes in soil nitrogen (Wolkovich et al. 2009b), but these were unrelated to tissue quality. The importance of variation in tissue quality to trophic structure may thus occur across larger scales, such as among plant species (Cebrian and Lartigue 2004, Borer et al. 2005) or soil types. Alternatively, tissue quality may have generally been above critical levels required by shrub leafhoppers.

Although the study did not document dramatic changes in morphospecies composition with grass invasion, community variability among shrubs appeared to decrease with the addition of invasive litter. While shrubs in high-litter plots shared similar, numerically abundant, morphospecies-rich arthropod communities dominated by several herbivore and predator morphospecies, shrubs in low-litter plots had consistently smaller, more variable communities, often containing a

PLATE 1. Leafhoppers and spiders were the most common arthropod herbivores and predators, respectively, in the shrub arthropod communities studied. The (left) leafhopper *Ballana* sp. (*sera* or *cerea* DeLong) and (right) Salticid spider were collected from *A. californica* shrubs in San Diego, California, USA. Photo credits: Mayda Nathan.

relatively high proportion of less common morphospecies. This could be due to a simple sampling effect (Herben 2005), where smaller shrubs in low-litter areas inadequately sampled the larger community. However, if shrubs act as moderately isolated communities the lower variance in invaded areas could be important to structuring total arthropod diversity in CSS. Reduced variance following disturbance has been linked to decreased stochastic community assembly (Chase 2007), where disturbed systems appear to include a repeating set of species, resulting in lower regional diversity. Applied to CSS, if invasion leads to decreased variance among arthropod communities on shrubs, as indicated here, it could cause long-term reductions in uncommon species. Such a reduction in extremely rare arthropod species was suggested by a restoration study examining planted *A. californica* shrubs, which authors noted were surrounded by invasive grasses (Burger et al. 2001).

Results here demonstrate that resource shunts may not be ubiquitous across all systems. While studies in aquatic systems (Vadeboncoeur et al. 2003), and terrestrial systems have found strong connections by predators between brown and green webs, research on resource shunts is still relatively novel (Pringle and Fox-Dobbs 2008) and limited. This study represents the first in a semiarid system, and one of the few lasting more than one season, which may have allowed time for effects on nutrient cycling and soil moisture (Wolkovich et al. 2009*b*) to propagate through to shrubs and their arthropod communities. In addition, this study used grass litter, which generally produces slower decomposition via quality and microclimate effects (Austin and Vivanco 2006, Cornwell et al. 2008) than higher-quality litters, as have been used in other studies (e.g., Halaj and Wise 2002, Wise et al. 2006). However, teasing apart the causes of differing results across studies requires further research in this field. Additional community ecology

studies that consider detritus as both a food resource and modulator of ecosystem processes may eventually provide a more general paradigm for the role of detritus in structuring food webs.

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APPENDIX A

A table of comparisons of removal control and control treatments (*Ecological Archives* E091-055-A1).

APPENDIX B

A figure showing results of parametric MANOVA tests (*Ecological Archives* E091-055-A2).

APPENDIX C

A complete list of the collected shrub arthropod taxa (*Ecological Archives* E091-055-A3).

APPENDIX D

Two figures depicting additional path-analysis results (*Ecological Archives* E091-055-A4).