

Short communication

Type conversion from native California sage scrub to non-native grassland accelerates decomposition processes

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ABSTRACT

Predicting how plant invasions influence decomposition processes is difficult, as multiple factors change with plant community alteration. Here, we examined the importance of various abiotic and biotic factors (litter quality (C:N), UV radiation, and macroinvertebrate access) in driving early decomposition processes in native California sage scrub (CSS) and in adjacent non-native grassland habitats. Many findings from our experiment were consistent with studies from semi-arid regions (e.g., UV radiation drove decomposition processes and high quality litter decayed more rapidly). However, the acceleration of litter decomposition in the non-native grassland relative to native California sage scrub (CSS) was unexpected and contrasts with studies of partially invaded CSS systems. Our results highlight that studies of invaded systems that still retain native species diversity should not be extrapolated to type-converted systems. We hypothesize that high grass cover in the type-converted grassland created conditions that enhanced soil moisture, bacterial abundance, and macroinvertebrate influence relative to the CSS, accelerating decomposition and reducing regional C storage.

Invasive plant species have the potential to drive global environmental change through their effects on productivity, microbial communities, and nutrient pools (Vitousek et al., 1997; Ehrenfeld, 2003). Since multiple factors that drive ecosystem function change with alteration of plant community composition, it is difficult to forecast how landscape transformations associated with invasions influence important ecosystem processes (Hooper and Vitousek, 1998; Kourtev et al., 2002). For example, many key drivers of litter decomposition [e.g., litter quality (Cornwell et al., 2008), UV radiation exposure (Austin and Vivanco, 2006), invertebrate community (Hättenschwiler et al., 2005)], an important ecosystem process responsible for substantial fluxes of carbon dioxide to the atmosphere, often differ between native and invaded habitats (Mayer et al., 2005; Wolkovich et al., 2010).

A notable example of widespread invasion is the expansion of annual Eurasian grasses, such as *Bromus* and *Avena* spp., into the shrublands of southern California. These non-native annual grasses represent a distinctly different functional type than the shrub species (e.g., *Artemisia californica* and *Salvia* spp.) that typify the native California sage scrub (hereafter, CSS) ecosystem (Rundel, 2007). CSS has been reduced to < 10% of its original distribution (Noss et al., 1995), and many natural areas have been type-converted to non-native grasslands (Cox et al., 2014; Riordan and Rundel, 2014; Talluto and Suding, 2008).

Complicating our understanding of how grass invasions influence ecosystem function in CSS, previous studies comparing decomposition and carbon storage in intact CSS to either CSS with non-native grass incursion or type-converted grasslands found different patterns. For example, Wolkovich et al. (2010) found that invasion of non-native grasses into CSS slows litter decomposition rates and enhances C storage. However, conclusions stem from an experimental design that doubled the amount of naturally occurring grass litter into experimental plots. Conversely, comparative studies by Wheeler et al. (2016) and Caspi et al. (2018, 2019) found that type-converted grasslands store less C than CSS habitats. To examine how type conversion of CSS to a non-native grassland influences decomposition, we manipulated three factors in both habitats—leaf litter type, UV radiation, and macroinvertebrate access—and measured decay for seven months.

This study was conducted at the Robert J. Bernard Biological Field Station (BFS) in Claremont, California (N 34.1°, W -117.7°), which harbors intact CSS (~25 ha) and a non-native grassland (~3.5 ha) consisting predominantly (> 95% cover) of annual European grasses (*Bromus* spp.). Soil abiotic properties, excluding pH which is lower in CSS, do not differ among habitat types (Wheeler et al., 2016; Caspi et al., 2019). Leaf samples from eight common plant species were analyzed for C and N content. *Bromus diandrus*, the dominant non-native grass species, had higher C:N values than the seven native CSS

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Table 1
C:N ratios for the most abundant plant species at the BFS in the CSS and grassland habitat types. Species used in this study are in **bold**.

Litter type	C:N (± SEM)
<i>R. aureum</i> (golden currant)^a	13.02 ± 0.51^a
<i>Bromus</i> spp. (European grasses)^a	60.88 ± 4.79^a
<i>A. californica</i> (California sagebrush)	18.31 ± 1.05
<i>E. crassifolium</i> (yerba santa)	21.32 ± 2.56
<i>E. fasciculatum</i> (buckwheat)	33.93 ± 3.74
<i>S. apiana</i> (white sage)	25.56 ± 1.31
<i>E. pinifolia</i> (pinebush)	22.14 ± 2.15
<i>S. mexicana</i> (blue elderberry)	10.42 ± 0.74

^a Selected for decomposition experiment. Litter used to construct the litter boxes differed slightly in C:N content.

plants sampled (Table 1). Based on assessment of C:N and consideration of the feasibility of retaining litter within the mesh of litterbags, *Ribes aureum* was selected to typify CSS in the decomposition experiment.

To examine decomposition processes in the two habitats, 768 litter boxes were constructed using 2.0-mm mesh and plastic produce boxes (11.4 × 9.5 × 6.6 cm) for 3-dimensional structure (Fig. 1). Litter boxes were assigned to treatments in a 2 × 2 × 2 factorial design. Litter treatments consisted of *R. aureum* and *B. diandrus* leaves, our high and low litter quality treatments, respectively (Table 1). UV treatments consisted of a UV allowed treatment, and a UV blocked treatment with a Gila® UV-blocking window screening covering that blocked 97% of the UV in the 250 to 400 nm range. Conditions within UV treatments varied by < 1 °C and 1% relative humidity with large fluctuations due to microhabitat. Macroinvertebrate treatments consisted of a macroinvertebrate excluded and a macroinvertebrate allowed treatment, with two 2 × 2 cm holes in the screening to allow access (see Meyer et al., 2011; Fig. 1).

Litter boxes (64 at each site; 8 replicates per treatment type) were deployed on the natural litter layer ~0.1 m apart at six undisturbed sites in CSS, and six in the grassland in July 2014. CSS sites were separated by at least 50 m to maintain heterogeneity in both plant community composition and abiotic conditions among the sites. Non-native grassland sites were systematically placed (~40 m apart) across grassland portion of the BFS. In the grassland, litter boxes were placed in systematic rows, and in the CSS, they were placed randomly throughout the site to minimize impact but make sure the bags were contacted the soil surface, which involved placement in interspaces and below existing shrubs. Two litter boxes of each treatment were collected at all sites in October (late summer) and December 2014 (fall), and the remaining four were collected in February 2015 (winter) (due to concerns that grasses growing through the boxes would begin to decompose and be indistinguishable from experimental litter samples). Following collection, litter samples were dried (50 °C, 72 h), weighed to the nearest 0.01 g, and ground on a Wiley Mill™. Subsamples were ashed in a muffle furnace (500 °C, 4 h) to determine ash-free dry mass, and others were analyzed in the Elementar varioCUBE Elemental Analyzer to

obtain C and N concentrations. Decomposition data was fitted to a linear decay model ($M_t = M_0 - kt$, where M_t is the litter mass at time t and M_0 is the initial litter mass) to calculate decomposition rate constants (k , y^{-1}). To identify differences in litter decomposition rates, a four factorial PERMANOVA was run using PRIMER-E with the PERMANOVA+ add on (Anderson et al., 2008) that included the factors litter type, UV treatment, invertebrate treatment, and site nested within habitat. A PERMANOVA is a permutation based analysis that does not require assumptions of equal variance or a normal distribution (Anderson et al., 2008). All PERMANOVA tests used a resemblance matrix constructed using Euclidean distances.

Our study underscores the difficulty associated with predicting how invasions impact key ecosystem processes. Many of our findings were consistent with studies from semi-arid regions (Fig. 2; Supplementary File 1): (1) UV radiation was the primary determinant of decomposition rates, with treatments that allowed UV penetration increasing decomposition rates by an average of 32% (Austin and Vivanco, 2006; Brandt et al., 2010); (2) high quality (low C:N) *R. aureum* litter decayed 5% more rapidly than the low quality grass litter, *B. diandrus* (Cornwell et al., 2008); and (3) macroinvertebrates did not significantly alter overall decomposition rates (Wall et al., 2010). However, significant litter × invertebrate and invertebrate × habitat interactions do suggest that the impact of invertebrates depends on ecological context (high nutrient litter and grasslands support invertebrate decomposer communities). Also, Meyer et al. (2011) highlights that invertebrates play a larger role later (after 6 mo.) in the decomposition process. However, accelerated litter decomposition by 26% in the non-native grassland relative to the CSS was unexpected and modified by a strong habitat × UV interaction (Figs. 2; 3a). Leaf litter is expected to decompose more rapidly in more nutrient-rich soils and litter (Vitousek, 2004), but studies at regional sites, including ours, have found that native sage scrub soils contain more C and N than non-native *Bromus*-dominated grasslands (Wheeler et al., 2016; Caspi et al., 2019). In addition, Wolkovich et al. (2010) suggest that incursion of grasses with lower litter quality into CSS slows decomposition.

By testing multiple factors that influence decomposition processes across seasonal periods, our study provides insights into what may be driving the differences between habitats. The influence of UV was related to habitat (Supplementary File 1), and blocking UV radiation slowed decomposition to a greater degree in CSS than in the non-native grassland (Fig. 3a). UV radiation is less likely to penetrate dense live grasses in late fall and winter. Therefore, the positive UV effect seen in the grassland is less likely the result of direct organic matter mineralization by photodegradation in the summer (Lin and King, 2014). Instead, it may be due to photoprimering, whereby UV makes recalcitrant litter more susceptible to microbial breakdown under cooler and wetter conditions in winter and spring (Foereid et al., 2010; Baker and Allison, 2015). In CSS, UV radiation exposure is still high in the fall and winter, as cover of annuals is minimal relative to the grassland. As such, we hypothesize that thick grass cover in the grassland in the fall and winter increases soil surface moisture (Wolkovich et al., 2009) and enhances decomposer activity by diminishing UV exposure (Duguay and

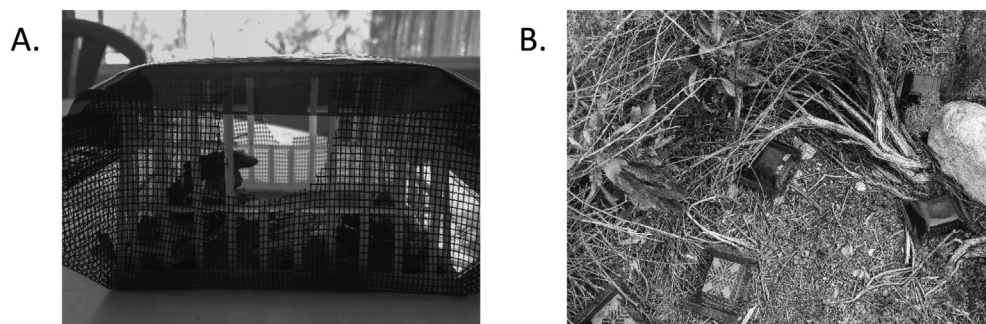


Fig. 1. Pictures of litter boxes: (a) a litterbox with *Ribes aureum* litter, holes for macroinvertebrate access, and Gila® UV-blocking window screening to reduce UV radiation exposure; and (b) part of a CSS site with 2 litterboxes that allow UV radiation to penetrate (mesh only) and 3 litterboxes from the UV-blocked treatment (mesh + black covers). (Photos by M. Dipman). Strawberry boxes were used to provide 3-dimensional structure and were covered with 2.0-mm mesh, allowing air-flow and providing opportunities for invertebrate access.

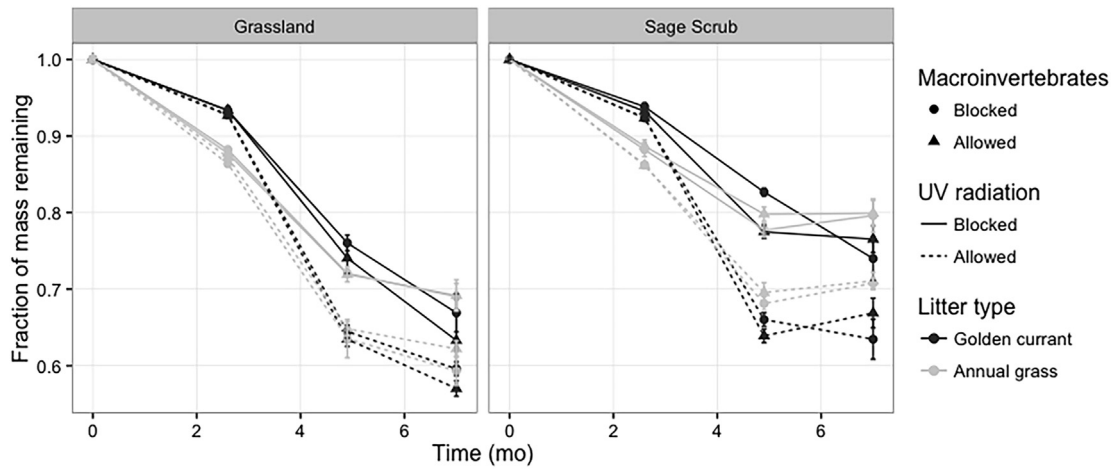


Fig. 2. Average fraction of leaf litter mass remaining for the eight treatments placed in the grassland and sage scrub habitat types. Bars represent standard error of the mean.

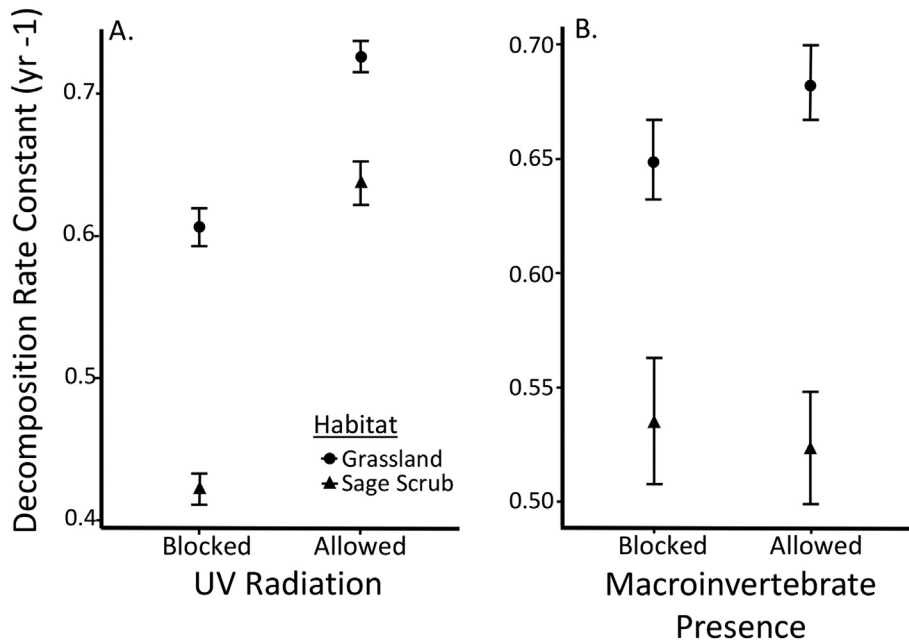


Fig. 3. Interaction of (a) habitat type and UV radiation and (b) habitat type and macroinvertebrates for overall decomposition rates. Bars represent standard error of the mean.

Table 2

Microbial analyses ($\mu\text{g/g}$ of biomass) of soil from CSS and grassland habitats. Soil samples were collected in March 2015 by taking cores at study sites in the grassland and CSS. Samples were homogenized and sent to Earthfort Labs (Corvallis, OR) for direct count microscopy. Significant ($p < 0.05$) differences are in **bold**.

Measure	Grassland (\pm SEM)	CSS (\pm SEM)	t	p
Active bacteria	30.0 \pm 2.23	16.7 \pm 2.92	3.68	0.005
Total bacteria	175 \pm 19.9	207 \pm 24.1	-1.02	0.334
Active fungi	2.74 \pm 0.46	1.95 \pm 0.43	1.21	0.257
Total fungi	290 \pm 30.1	308 \pm 31.3	-0.40	0.698
Total fungi: total bacteria	1.69 \pm 0.15	1.66 \pm 0.39	0.08	0.937
Active bacteria: total bacteria	0.18 \pm 0.022	0.084 \pm 0.016	3.47	0.007
Active fungi: total fungi	0.01 \pm 0.002	0.006 \pm 0.002	1.15	0.279
Active fungi: active bacteria	0.09 \pm 0.02	0.1 \pm 0.04	-0.90	0.391

Klironomos, 2000; Johnson, 2003; King et al., 2012), accelerating decomposition processes relative to the drier, more exposed CSS. Higher concentrations of active bacteria in the grassland (Table 2) and a greater impact of macroinvertebrates on decomposition in the grassland (Fig. 3b) are congruent with this hypothesis.

Predicting how plant invasions influence decomposition processes is difficult, as multiple factors change with plant community alteration and stage of invasion. For example, CSS invaded by non-native grasses and type-converted grasslands function differently (Wheeler et al., 2016), and results from studies of partially invaded systems should not be extrapolated to type-converted systems. Here, we found that decomposition rates increased in the non-native grassland, despite the fact that the invader produced lower quality (higher C:N) litter. We think the high grass cover created conditions that enhanced soil moisture, bacterial abundance, and macroinvertebrate influence, accelerating decomposition. This study was conducted in 2014 and 2015 in the middle of an extreme drought. As such, decomposition rates in these habitats during high rainfall years are untested, though we hypothesize that decomposition would remain enhanced in the grassland habitat

relative to CSS, as grasses would grow taller increasing moisture retention. Since habitat type modified the impact of these individual factors through various interactions, type conversion may have complex, unexpected ramifications for nutrient cycling. Type conversion of CSS to non-native grasslands is expected to become more pervasive with climate change and continued disturbance (Talluto and Suding, 2008), which, in accordance with our findings, has the potential to reduce regional C storage (Supplementary File 2).

Supplementary data to this article can be found online at <https://doi.org/10.1016/j.apsoil.2019.07.005>.

Declaration of Competing Interest

None.

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