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Is *Pyrenophora semeniperda* the Cause of Downy Brome (*Bromus tectorum*) Die-offs?

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Downy brome (cheatgrass) is a highly successful, exotic, winter annual invader in semi-arid western North America, forming near-monocultures across many landscapes. A frequent but poorly understood phenomenon in these heavily invaded areas is periodic 'die-off' or complete stand failure. The fungal pathogen *Pyrenophora semeniperda* is abundant in cheatgrass seed banks and causes high mortality. To determine whether this pathogen could be responsible for stand failure, we quantified late spring seed banks in die-off areas and adjacent cheatgrass stands at nine sites. Seed bank analysis showed that this pathogen was not a die-off causal agent at those sites. We determined that seed bank sampling and litter data could be used to estimate time since die-off. Seed bank patterns in our recent die-offs indicated that the die-off causal agent does not significantly impact seeds in the persistent seed bank.

Nomenclature: Downy brome, *Bromus tectorum* L.; black fingers of death, *Pyrenophora semeniperda* (Brittleb. & D.B. Adam) Shoemaker.

Key words: Cheatgrass, Great Basin, seed bank, seed pathogen, stand failure.

Bromus tectorum L. (cheatgrass or downy brome) is an invasive winter annual grass that was introduced from Eurasia into interior western North America at the end of the nineteenth century. It quickly colonized cold desert shrubland and shrub steppe communities in the wake of massive disturbance caused by unsustainable livestock grazing practices, reaching its modern distribution in about 30 yr (Mack 1981). It has become the most common vascular plant in this region, infesting tens of millions of acres (Knapp 1996). In highly invaded areas, indigenous plant species often become locally scarce or even extirpated (Stewart and Hull 1949). This type conversion from shrubland to annual grassland is largely because of the fact that *B. tectorum* invasion is associated with greatly increased frequency of fire (Brooks et al. 2004). Repeated burning results in near-monocultures of *B. tectorum* that range in size from tens of square meters to thousands of hectares.

Bromus tectorum stands produce prodigious quantities of seeds, which disperse in early to midsummer. Early autumn *B. tectorum* seed bank densities from 10,000 to 30,000 seeds m^{-2} (1,000 to 3,000 seeds ft^{-2}) are commonly encountered (Beckstead et al. 2010, Meyer et al., 2007). The majority of these seeds germinate with the first germination-triggering rains, which can occur any time from early autumn to early spring, depending on the site and year. Seeds that fail to germinate but remain viable in the seed bank (usually 7 to 15% of seeds produced) can form a persistent seed bank that carries over to the next year in a state of secondary dormancy (Meyer et al., 2007; Smith et al., 2008). Exponentially decreasing percentages sometimes persist into the second and third years (Smith et al., 2008).

One reason that *B. tectorum* seed bank persistence tends to be limited is the ubiquitous presence of the ascomycete pathogen *Pyrenophora semeniperda,* which infects and kills large numbers of dormant and slow-germinating *B. tectorum* seeds in field seed banks (Beckstead et al., 2007; Meyer et al., 2007). Densities of seeds killed by this pathogen may be as high as 20,000 seeds m^{-2}, which represents a sizeable fraction of seed production from the previous year (Beckstead et al. 2007; Meyer et al. 2007). Seeds that germinate rapidly in response to the first germination-triggering storm usually escape mortality, while remaining ungerminated seeds are the primary target of the pathogen. Infection by the fungus produces distinctive, macroscopic black stromata that protrude from killed seeds. Examination of seed bank samples in late spring after germination is complete, but before any dispersal of current-year seed production, can yield estimates of the size of the potential persistent seed bank

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Management Implications

Cheatgrass is the most abundant exotic plant species in the natural landscapes of the western United States, occurring in near-monocultures over very large areas. Cheatgrass die-off occurs when a discrete area that is highly dominated by cheatgrass shows complete stand failure for one or more growing seasons. From a distance, these areas are most visible in late spring, when the matted, gray litter in failed stands contrasts sharply with the green of adjacent established stands. Die-offs have both positive and negative implications. In the short term, they present a rare situation in which formerly infested areas present much reduced cheatgrass competition for at least a year, suggesting that they may represent restoration opportunities. However, these sudden and unpredictable events also represent loss of spring forage for livestock and wildlife. In the longer term, areas experiencing prolonged or repeated die-offs may suffer increased erosion, resulting in soil loss and continued site degradation. Our study represents the first organized investigation of cheatgrass die-offs. Its goal was to determine whether the pathogen *Pyrenophora semeniperda* (also known as "black fingers of death") played a role in nine die-offs in Nevada, Utah and Washington. This pathogen is omnipresent in cheatgrass seed banks and can kill large quantities of slow-germinating seeds. We found no evidence that this pathogen was a die-off causal agent at the studied sites, but we developed a greater understanding of the die-off process. Our seed bank data suggested that die-off mortality does not impact the persistent seed bank directly. Areas that have experienced die-off often show stand failure for multiple years, but most eventually revert back to cheatgrass dominance. Appropriate management of the sometimes large areas affected by cheatgrass die-off depends on a continuing research effort aimed at elucidating both causes and consequences of die-off events.

(i.e., seeds that did not germinate) as well as what fraction of that seed bank successfully carried over as viable seeds or was killed by *P. semeniperda* or some other agent of mortality.

A relatively frequent but poorly studied phenomenon in communities heavily invaded by *B. tectorum* is die-off or stand failure. Die-offs occur in areas that recently supported dense stands, but where, for unknown reasons, the in situ seed bank from the previous year completely failed to emerge, establish, or produce a new generation of seeds. Areas that supported hundreds of *B. tectorum* plants per square meter the year previous to the die-off event have been observed to lack even a single *B. tectorum* plant. The *B. tectorum* die-off phenomenon is important from a land management perspective for several reasons. While die-offs may present opportunities for ecological restoration and/or the development of biological control agents, sudden and unpredictable losses of *B. tectorum* cover can lead to increased wind erosion and soil loss, and can be a significant localized reduction of important spring forage.

Die-offs become visible as dead areas covered with gray litter in mid and late spring, when adjacent, healthy *B. tectorum* stands are thick and green. These die-offs are not associated with drought conditions that may severely reduce *B. tectorum* stands in years of below-average precipitation, and their patchy pattern of occurrence on the landscape suggests a biotic cause. Several agents have been implicated at least anecdotally in the die-off phenomenon. These include heavy insect herbivory, epidemics of fungal, bacterial, or viral pathogens, and disturbance-related changes in soil chemistry. To our knowledge there are no published investigations of *B. tectorum* die-off other than a few meeting abstracts (Baughman and Meyer 2009, Baughman et al. 2012, Meyer 2012, Morgan et al. 2011, Salo and Zielinski 2004).

While *P. semeniperda* is generally regarded as a weak pathogen with a limited ability to kill rapidly germinating seeds (Beckstead et al. 2007, Campbell and Medd 2003, Medd et al. 2003), we speculated that there might be scenarios under which this pathogen could act as a die-off causal agent and completely prevent *B. tectorum* stand establishment. For example, high seed mortality could result from recently-evolved hypervirulent pathogen strains (Meyer et al. 2010), or from extended periods at water potentials high enough for pathogen activity but too low for seed germination (H. Finch, personal communication).

Research Objectives and Hypotheses. Our study had two principal objectives. The first objective was to confirm the recency of apparent current-year die-offs by comparing litter characteristics in die-off and control areas. We hypothesized that current-year die-offs should have litter loads similar to adjacent control areas, whereas older die-offs that have not received litter for at least an additional year should have reduced loads relative to control areas. We also predicted based on earlier work (Beckstead et al. 2007, Meyer et al. 2007) that persistent seed bank size would be reduced relative to controls in older die-offs that had not received seed input for at least an additional year relative to controls.

The second objective was to use the subset of die-offs determined to be current-year die-offs according to litter and seed bank characteristics to investigate whether *P. semeniperda* could be the die-off causal organism. Our hypothesis was that a recent (current year) die-off caused primarily by *P. semeniperda* would show a significantly higher density of *P. semeniperda*-killed seeds in the seed banks of die-off plots as compared to the seed banks of adjacent control plots with current-year stands of cheatgrass.

Materials and Methods

Site Selection. Nine die-off sites in northern Nevada, western Utah, and eastern Washington were selected and sampled in late May 2008 (Table 1). We selected sites to represent a range of potential vegetation types and a wide geographic area, in an effort to test the generality of our results over a range of die-off scenarios and conditions. A die-off was defined as an area with no living *B. tectorum*

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Table 1. Site information for nine die-off sites sampled in 2008.

Site name	Code	Location	Latitude/longitude	Elevation	Precipitation[a]	Associated species[b]
				m	mm	
Dry Creek	DRC	Northern Nevada	41°14.631′N 117°23.017′W	1435	256	*Poa secunda,* *Sisymbrium altissimum*
Stewart Gap	STG	Northern Nevada	41°16.953′N 117°22.679′W	1452	301	*Lepidium perfoliatum,* *Ceratocephala testiculata*
Curlew	CUR	Northern Nevada	41°21.203′N 117°37.371′W	1482	217	*Erodium cicutarium,* *Sisymbrium altissimum*
Dun Glen	DGL	Northern Nevada	40°41.421′N 117°57.314′W	1384	243	*Lepidium perfoliatum,* *Sisymbrium altissimum*
Pronghorn	PRH	Western Utah	40°11.507′ N 112°42.052′W	1496	264	*Bassia scoparia,* *Erodium cicutarium*
Pronghorn South	PRS	Western Utah	40°08.695′N 112°41.571′W	1542	319	none
White Rocks Road	WRR	Western Utah	40°19.729′N 112°53.347′W	1567	297	*Ceratocephala testiculata*
Lost Dog	LDG	Western Utah	40°23.584′N 112°56.818′W	1584	347	*Sisymbrium altissimum,* *Elymus elymoides*
Wagner	WAG	Eastern Washington	47°06.338′N 117°49.018′W	550	423	*Sisymbrium altissimum,* *Taeniatherum caput-medusae*

[a] Annual precipitation is 2000 to 2010 average annual precipitation estimates from PRISM (PRISM Climate Group, Oregon State University, http://prism.oregonstate.edu, created 13 Apr 2012).

[b] Associated species are species that were encountered within sampling frames at the site, and are listed by descending cover. All but *Poa secunda* and *Elymus elymoides* are exotic weeds.

which had apparently supported a dense stand in the recent past. Sites were selected based on three main criteria. The sites had to have a die-off area which: (1) was located within or immediately adjacent to a healthy stand of *B. tectorum* (control area), (2) contained apparently recent *B. tectorum* litter, and (3) was not distinguishable from its respective control area by differences in slope, aspect, elevation, or known disturbance history.

Experimental Design and Sampling Protocol. Within each of the nine sites, five blocks that each spanned both conditions (die-off and control) were located such that each block contained a pair of plots, with one in each condition. When possible, plots were located several meters or more from the edge between conditions, in order to avoid potential edge effects. Within each plot, one point was sampled at random along a 40 m (131 ft) transect in each of the cardinal directions from the plot center. This created a total of 40 samples in 5 paired-plot blocks per site.

Bromus tectorum tiller density as well as organic litter percent cover and depth were recorded within a 9.3-dm^2 (1-foot^2) Daubenmire frame at each sample point. Seed bank samples were collected immediately adjacent to the frame at each sample point using a 6 cm diam by 4 cm deep (2.4 by 1.6 in.) soil can.

Seed bank samples were air-dried for several weeks, sieved to remove loose soil, then hand-processed to remove all ungerminated *B. tectorum* seeds (Meyer et al. 2007). Killed seeds with protruding *P. semeniperda* stromata were quantified. The stromata of *P. semeniperda* generally do not remain apparent in the seed bank for more than a year except under exceptionally dry conditions (S. Meyer, unpublished data). Therefore, killed seeds in late spring samples were likely to represent pathogen-caused seed mortality within the last year.

The remaining filled and apparently viable seeds were placed on wetted germination paper in Petri dishes at 20 C (68 F) for 14 d. Germinated seeds were counted and removed, and remaining seeds were scored as viable and dormant, killed by *P. semeniperda*, or apparently killed by an unknown pathogen. Because the seeds were allowed to lose dormancy in dry storage prior to seed bank processing, there were no viable, dormant seeds present at the end of incubation (Bauer et al. 1998); germination percentage was therefore equivalent to viability percentage. Because these viable seeds germinated rapidly, only seeds pre-infected by *P. semeniperda* in the field exhibited stromatal development during incubation. These killed seeds were summed with field-killed seeds obtained directly from the samples to obtain a total estimate of *P. semeniperda*-caused mortality.

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It is not known if seeds apparently killed by other pathogens during incubation were pre-infected in the field. Seeds killed by other pathogens or factors in the field and no longer apparently filled and viable could not be quantified.

Statistical Analysis. The experimental data were analyzed using mixed model ANOVA (Proc Mixed, SAS V. 8.1, SAS Institute, Cary NC, 2000). Condition (die-off vs. control) was treated as a fixed model variable, while site and site by condition interaction were treated as random model variables, and plot nested within site was treated as a random blocking variable with four samples per plot and a total of $n = 20$ samples (with minor exceptions) for each condition at each site. To test the significance of the site by condition interaction for each response variable, we used a Contrast statement in Proc Mixed based on best linear unbiased predictions (BLUPs). Significance tests for the difference between die-off and control conditions for each response variable at each site were then obtained from BLUP estimates using Estimate statements in the Proc Mixed analysis for each response variable (Littell et al. 1996). We also used a Contrast statement based on BLUPs to perform a post hoc analysis to test for the significance of the difference in each response variable between the group of six sites thought to represent older die-offs and the group of three sites thought to represent recent die-offs (Littell et al. 1996). These groups were defined by inspection of differences and their significance levels between die-off and control areas on a site-by-site basis. We interpreted the results of this post hoc test with caution, as alpha values tend to be inflated in such post hoc tests (Littell et al. 1996).

Response variables in the Proc Mixed analysis included site attributes (live tiller density, litter cover percentage, litter depth), and seed bank attributes (total seed density, viable seed density, total *Pyrenophora*-killed seed density, and density of seeds apparently killed by unknown pathogens). Density and depth variables were log transformed and litter cover percentage (proportion) was arcsine-square root transformed prior to analysis to improve homogeneity of variance. Untransformed data are presented in the figures.

Results and Discussion

Site Characteristics and Die-Off Age. Because die-off areas were selected based upon their lack of current-year growth, sampled tiller density was essentially nil in all die-off areas. Tiller density in control areas ranged from 350 to 1150 tillers m^{-2} (Figure 1A).

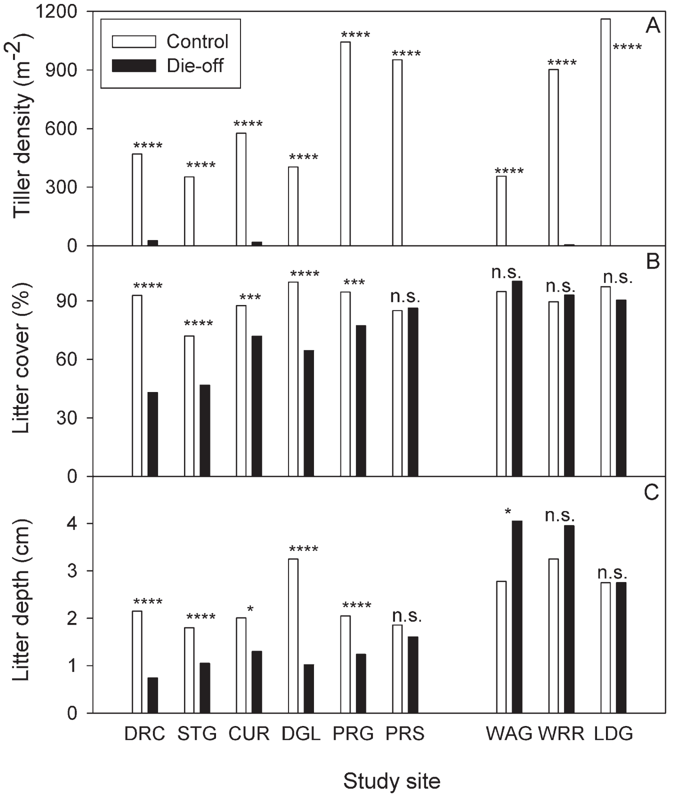

Figure 1. Mean *B. tectorum* tiller density (A), litter cover (B), and litter depth (C) measured in the field in die-off areas and adjacent control areas where die-off had not occurred for nine *B. tectorum* die-off sites in 2008. (Significance tests are based on best linear unbiased predictors from mixed model analysis of variance; n. s. $P > 0.05$; * $P < 0.05$; ** $P < 0.01$; ***$P < 0.001$; ****$P < 0.0001$. See Table 1 for site information).

The litter data generally supported the hypothesis that the nine die-off sites included in the study differed in time since die-off. As mentioned earlier, in the absence of litter input from a successful stand, litter cover and depth are expected to decrease through time. Five of the sites had significantly lower values for both litter cover and depth in die-off than in control areas, indicating that they probably represent die-offs at least a year old (Figure 1B, 1C). In contrast, four sites (PRS, WRR, LDG, and WAG) did not have significantly higher litter values in control areas, and one site, WAG, had significantly deeper litter in the die-off area (Figure 1B, 1C). This suggests that both control and die-off areas likely received litter from a successful stand the previous year, indicating that the die-off probably took place earlier in the current year at these sites and only affected the live tiller density.

Seed Bank Characteristics and Die-off Age. At six of the nine sites, there was a trend for lower total seed densities in die-off areas relative to control areas (significant for four sites; Figure 2A). At the other three sites (WRR, LDG, and WAG) this trend was absent; total seed densities were similar in die-off and control areas. Similar patterns were

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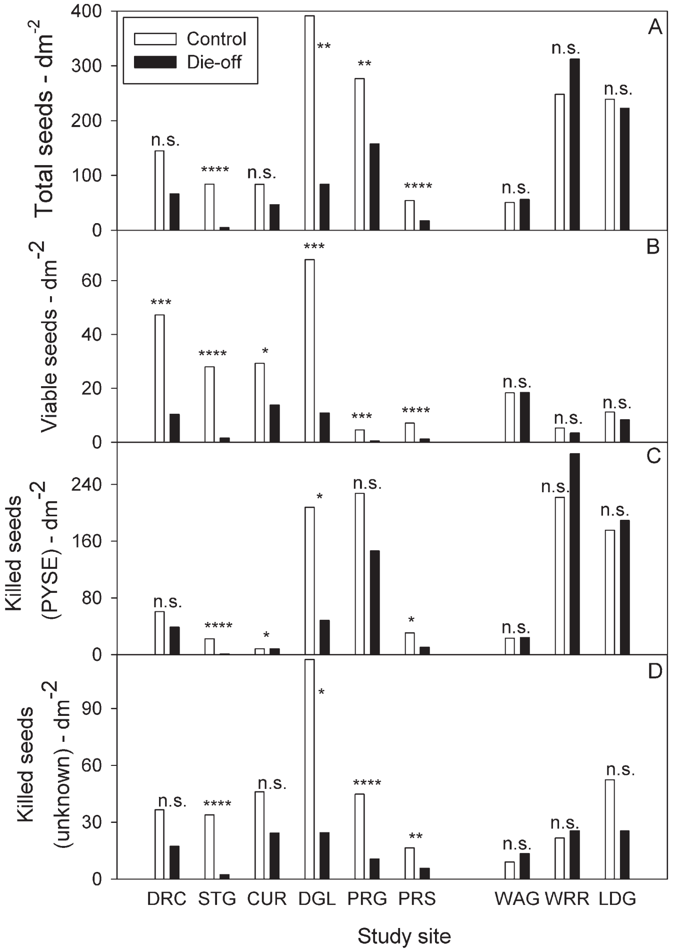

Figure 2. Mean cheatgrass carryover seed bank densities measured in soil samples collected in May in the field in die-off areas and adjacent control areas where die-off had not occurred for nine *B. tectorum* die-off sites in 2008: (A) Total seed density, (B) Viable seed density, (C) Density of seeds killed by *Pyrenophora semeniperda*, (D) Density of seeds killed by unknown pathogens. (Significance tests are based on best linear unbiased predictors from mixed model analysis of variance; n. s. $P > 0.05$; * $P < 0.05$; ** $P < 0.01$; ***$P < 0.001$; ***$P < 0.0001$. See Table 1 for site information).

observed for all three components of the potential carryover seed bank. Differences between die-offs and controls were generally evident and often significant for these variables at the first six sites, where die-offs had significantly lower seed densities than controls in most cases (Figure 2B, C, D; Table 2). In contrast, WRR, LDG, and WAG exhibited values for these three variables that were not significantly different and generally very similar between die-offs and controls (Figure 2B, C, D; Table 2).

The sites DRC, STG, CUR, DGL, and PRG present both litter and seed bank differences between die-off and control areas that strongly support the idea that they represent older die-offs. The sites WAG, WRR, and LDG present a lack of difference between die-off and control areas that strongly supports the idea that they are current-year die-offs. The site PRS presents the only anomaly in the data set. It clearly had the seed bank attributes of an older die-off, but there was no significant difference in litter characteristics between die-off and control areas.

We used post hoc contrasts to test which of the two age groupings (i.e., with PRS included as an older die-off vs. PRS included as a current-year die-off) is best supported by the data. When PRS is considered an older die-off, the two age groups are significantly different at $P < 0.01$ for every response variable and at $P < 0.0001$ for five of the seven response variables (Table 2). When PRS is considered a recent die-off, all F values decrease, and between-group differences for three of the four seed bank variables are no longer significant (data not shown). We therefore conclude that PRS is an older die-off, and that our grouping of six older die-offs and three recent die-offs is best supported by the data. A possible explanation for the relatively low litter cover and depth in the control area at PRS is that this area itself represents an older but recovering die-off that has not yet acquired the litter load of a fully recovered stand.

Killed Seed Densities in Recent Die-offs. *Pyrenophora semeniperda*-killed seed densities were not significantly higher in die-offs than in controls at any site, current or otherwise. Current-year die-offs showed no significant differences in *P. semeniperda*-killed seed densities in die-offs relative to controls. Because the evidence of *P. semeniperda* activity does not dependably last more than a year, we are limited to current year die-offs in making conclusions about our hypotheses. Nonetheless, putatively older die-offs showed either no differences in *P. semeniperda*-killed seeds between conditions, or significantly more killed seeds in controls, neither of which supports the hypothesis that this pathogen is causal. These findings provide no support for *P. semeniperda* as a primary causal agent of *B. tectorum* die-offs examined in this study.

The pattern of seed mortality from unknown pathogens was similar to the pattern we saw with *P. semeniperda*, with no difference in density between die-offs and controls in the current year sites and generally lower density in die-offs at sites with older die-offs. This suggests that none of these pathogens represent the die-off causal organism. However, the case for this claim is not as strong as our conclusion regarding *P. semeniperda* for several reasons. First, we did not identify the other pathogens, and we do not know the dormancy status of the killed seeds when infection took place. Also, we do not know if seeds killed by one or more of these pathogens during or shortly after the first germination-triggering precipitation event would remain detectable in the spring seed bank. Nonetheless, the fact that viable seed densities in carryover seed banks were similar between current year die-offs and controls suggests the die-off agent

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Table 2. Post hoc contrasts for seven response variables based on best linear unbiased predictors from mixed model analysis of variance for the interaction between condition (die-off vs. control) and putative die-off age (current-year vs. older die-offs).

				Means			
	Condition by age interaction			Current-year (n = 3)		Older (n = 6)	
Response variable	d. f.	F	P	Control	Die-off	Control	Die-off
Seed bank variables (seeds-dm^{-2})							
Viable seed density	1, 61	8.14	0.0059	11.4	10.0	27.7	6.1
Killed seed density (PYSE [a])	1, 225	7.89	0.0054	144.1	165.9	83.9	42.1
Killed seed density (unknown)	1, 165	17.54	< 0.0001	28.3	21.5	43.4	13.4
Total seed density	1, 280	43.25	< 0.0001	183.8	197.4	154.9	61.5
Site variables							
Tillers – m^{-2}	1, 299	18.13	< 0.0001	822	3.2	660	21
Litter cover percentage	1, 268	44.45	< 0.0001	0.948	0.954	0.887	0.661
Litter depth (cm)	1, 250	49.05	< 0.0001	2.93	3.56	2.11	1.17

[a] *Pyrenophora semeniperda*.

did not impact potential carryover seeds in the persistent seed bank, either because it did not impact the seed stage at all or because it did not impact dormant seeds likely to carry over.

We obtained some evidence that heavy litter from the previous year may itself predispose a site to die-off. There was a trend for thicker litter in the die-off areas than in the controls at two recent die-off sites, WAG and WRR (significant for WAG; Figure 2C; Table 2). Even older die-offs still had litter loads that made them superficially appear to be recent. It may be that seed bed micro-environmental conditions associated with heavy litter facilitate epidemic disease or otherwise favour an unknown die-off agent.

Bromus tectorum die-offs appear to be transient features of the landscape. Without active management, these areas almost always return to near-monoculture condition within a few years by recruiting from a viable seed bank that was unaffected by the causal agent. We have shown that *P. semeniperda* was not a causal factor of the sampled *B. tectorum* die-offs, though it is likely to have an impact on the post-die-off successional trajectory through its continuing effect on the seed bank. At this point we still have no clear understanding of the causes of *B. tectorum* die-off, but active research on this phenomenon is underway on several fronts. These include a more critical examination of the role of other soilborne pathogens, an intensive effort to understand spatiotemporal die-off patterns on the landscape using remote sensing approaches, and experimental seeding studies to determine whether die-offs represent restoration opportunities.

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