

Letters to the Editor

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Comment on: Grazing disturbance promotes exotic annual grasses by degrading soil biocrust communities

To the Editor:

Biological soil crusts (hereafter, biocrusts) are a critical component of many semiarid ecosystems because they seriously affect seed germination, soil stability, fertility, and hydrology (Belnap 2003). These factors are central to ecosystem recovery following soil–plant disturbances such as increased wildfire or livestock grazing. Livestock grazing is the primary land use of semiarid landscapes globally, and the impacts of hooved animals on both soils and plant community condition, including exotic plant invasions, have been recognized for over a century (Samson and Weyl 1918, Daubenmire 1940). Invasion by exotic annual grasses greatly increases wildfire occurrence in many semiarid ecosystems, causing a loss of native perennial species and resulting in an annual-grass–fire cycle (Brooks et al. 2004). Livestock grazing practices that are not matched to the adaptive capacity of native perennials have caused a decline of herbaceous perennials in desert rangelands of the United States. There are many lines of evidence that depletion of perennial herbs, particularly the perennial grasses that tend to best compete with annual grasses, is a key mechanism by which livestock grazing causes invasion by exotic annual grasses such as cheatgrass (*Bromus tectorum*, L.; reviewed by Chambers et al. 2016, Pyke et al. 2016). In turn, population growth of annual grasses is favored in the post fire environment, particularly where grazing has depleted perennial grasses, further increasing production of fine-textured wildfire fuel and fire occurrence (Brooks et al. 2004, Chambers et al. 2016).

While biocrusts are a driver of ecosystem recovery, they are also sensitive to plant–soil disturbances and associated exotic plant invasions (e.g., Dettweiler-Robinson et al. 2013). Mutual interactions between biocrusts, disturbances, and plant community condition can greatly affect disturbance–recovery cycles. The reciprocal nature of these interactions and the tendency of the factors to covary in time and space also complicate our ability to infer causal relationships between biocrusts and their environment. As a result, it is difficult to identify the relationships between any two factors without experimental means for separating them (e.g., Hoover

and Germino 2012, for physical crusts). Unfortunately, biocrusts are relatively slow growing, and inferences on biocrust relationships with their environment are often derived from observations of natural variation. Thus, a mechanistic understanding of biocrust–environment interactions and underlying evidence is still in development, especially regarding how biocrust management could be incorporated into conservation and restoration practice (Bowker 2007, Young et al. 2019).

In the first 2020 issue of *Ecological Applications*, Root et al. (2020) evaluated the relationships of biocrusts, exotic annual-grass abundance, and indicators of livestock grazing, using a snapshot of their natural variation across a $\sim 50 \times 50$ km managed landscape in the sagebrush steppe of the Snake River Plain, Southwest Idaho, USA. These rangelands have experienced some the largest increases in wildfire activity and associated annual-grass invasion in recent decades as any landscape in the United States or elsewhere around the globe, as shown by satellite imagery (e.g., Boyte et al. 2019). The invasive annual grasses were primarily *Bromus tectorum*, but also included *Eremopyrum triticeum* and *Taeniatherum caput-medusae* (Root et al. 2020). Root et al. (2020) used a general linear model (GLM) to compare biocrusts and plant-community composition among 26 plots located in patches that had low, medium, or high abundances of livestock dung. Structural equation modeling (SEM) and multivariate analyses were used to further identify the possible causal relationships and key functional group relationships, and the resulting data set offers insight on how diversity within biocrust communities relates to disturbances and exotic grass abundances.

Root et al. (2020) concluded that greater abundances of annual grasses were due to livestock-induced reductions in biocrust, with no effect of changes in perennial grasses. However, nearly half of the plots (11 plots) had burned in recent decades, some up to four times in the last 40 yr (Fig. 1 and Appendix S1: Table S1), and the strong impacts of fire on biocrusts and annual grasses are well known (e.g., Root et al. 2017 and our comments here). Fire history was not considered in Root et al.'s (2020) analysis. Here, we show that including fire in the analysis affects the inference in how abundances of annual and perennial grasses and biocrusts relate to livestock grazing. We demonstrate this with a reanalysis of Root et al.'s (2020) data, adding fire history of plots added as either a random or a fixed effect in two different models (R Core Team 2019; lme4 package, Bates et al. 2015 for inclusion as a random effect; data *available online*).² The number of recorded past fires per plot were levels of the fire factor in our mixed-effects model, whereas fire was parameterized as a binary variable

² <https://doi.org/10.5061/dryad.2s7g00v>

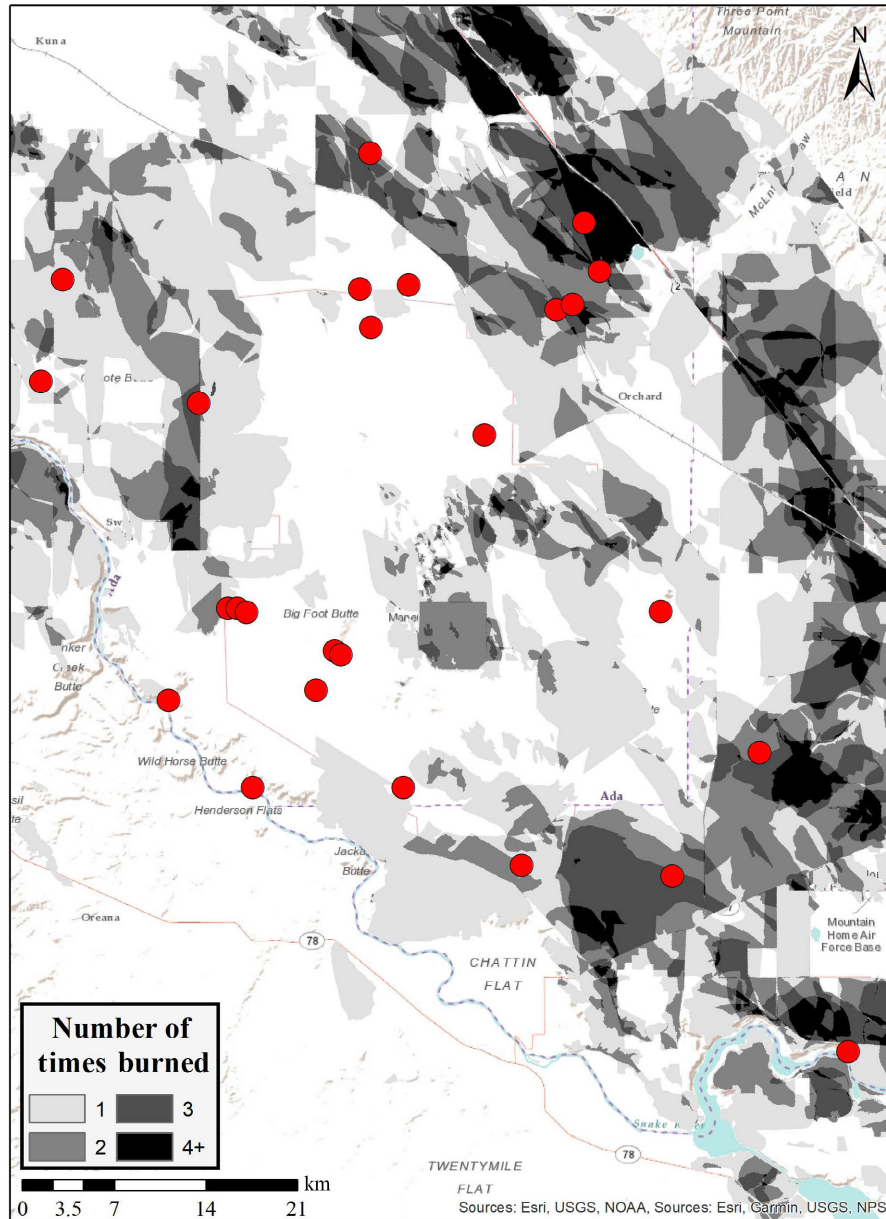


FIG. 1. Spatial distribution of the 26 plots sampled by Root et al. (2020; red circles) in southwestern Idaho, USA and corresponding fire history (from Welty and Jeffries 2020).

(burned, unburned) in our fixed-effect GLM of fire, grazing, and fire \times grazing effects. There was insufficient replication at each burn frequency level to include the number of times burned as a fixed effect with factor levels.

Adding the random effect of fire history to the fixed effect of grazing in the linear mixed model explained 30% more variation in cover of biocrusts and annual grasses ($r^2 = 0.62$ and 0.56 , respectively) compared to

Root et al.'s (2020) model that did not include fire ($r^2 = 0.56$ for biocrusts and 0.43 for annual grasses, respectively; the percent increase was calculated as change in r^2 divided by the original r^2). The addition of fire history as a random effect also improved model fit for all response variables (Tables 1 and 2). For example, AIC_c values for biocrust cover decreased from 214.97 to 202.71 with the inclusion of fire history as a random effect (Table 1). Also, whereas models omitting fire

TABLE 1. Model AIC_c values for the cover or richness of soil biocrusts, cover of annual grasses, or cover of perennial grasses based on the incorporation of fire in the statistical models as a random effect, fixed effect, or no inclusion of a fire (Root et al.'s [2020] original model).

Response variable	AIC_c values		
	Fire, random effect	Fire, binary fixed effect	Fire not included
Biocrust cover	202.70	217.67	214.97
Biocrust species richness	185.89	204.65	194.84
Annual-grass cover	97.59	102.17	97.91
Perennial grass cover	223.03	239.23	243.68

Notes: AIC_c is the Akaike information criterion corrected for sample size. The smaller the AIC_c value, the better the model fit.

TABLE 2. Relationship of cover or richness of soil biocrusts, cover of annual grasses, or cover of perennial grasses to livestock grazing level, as determined by a mixed-effects linear model to include “number of previous fires” as a random effect.

Response variable and grazing level (abundance of dung piles)	Estimate	SE	<i>P</i>
Biocrust cover			
Low	42.391	5.271	<0.001
Medium	-18.191	6.054	0.006
High	-36.772	6.188	<0.001
Biocrust species richness			
Low	30.44	3.01	<0.001
Medium	-6.56	4.25	0.137
High	-20.07	4.38	<0.001
Annual-grass cover			
Low	0.9019	0.8162	0.310
Medium	0.7919	0.8318	0.346
High	18.3966	0.8513	<0.001
Perennial grass cover			
Low	37.268	10.995	0.010
Medium	-6.222	8.877	0.491
High	-21.108	8.974	0.029

Notes: Annual-grass cover results are back transformed from natural log. Boldface type indicates significant variables ($P \leq 0.05$). “Low grazing” level is the model intercept.

found no grazing effects on perennial grass cover, perennial grass cover was less in burned compared to unburned areas (Table 3) and adding fire to the mixed model led to the new insight that perennial grasses were scarcer in areas with high grazing (Table 2). Including fire in the fixed-effects model also increased the *F* statistics for biocrust and annual-grass cover in the fixed-effect model and revealed biocrust cover to be sensitive to fire (Table 3). These new findings indicate that adding historic fire to the SEM might result in the SEM suggesting perennial grasses to be a mediating factor

TABLE 3. Comparison of GLMs of the response of crusts, annual grasses, and perennial grasses to the fixed effects of grazing and fire (left) or the fixed effects of grazing alone (right columns, as reported in Root et al. 2020).

Response variable and factor	GLM including fire			GLM not including fire, from Root et al. (2020)		
	df	<i>F</i>	<i>P</i>	df	<i>F</i>	<i>P</i>
Biocrust cover						
Grazing	2	20.7	<0.00001	2	17.77	
Fire	1	5	0.0373			<0.0001
Grazing × fire	2	0.9	0.41			
Residual Error	20			23		
Biocrust species richness						
Grazing	2	9.6	0.001	2	10.8	<0.0005
Fire	1	0	0.94			
Grazing × fire	2	0.2	0.82			
Residual Error	20			23		
Annual-grass cover						
Grazing	2	13.3	0.0002	2	12.14	0.0003
Fire	1	4.2	0.05			
Grazing × fire	2	0.5	0.6			
Residual Error	20			23		
Perennial grass cover						
Grazing	2	2	0.15	2	1.13	0.28
Fire	1	9.2	<0.01			
Grazing × fire	2	3	0.07			
Residual Error	20			23		

Notes: Boldface type indicates significant variables ($P \leq 0.05$).

between grazing and annual grasses. Perennial grasses were an expected yet surprisingly small effect in the original SEM of Root et al. (2020). Unfortunately, with only 26 plots measured, adding a sixth variable (wildfire) would cause the ratio of variables to samples to fall below 5:1, which Kline et al. (2015) stated is insufficient for SEM.

Our analysis combines with Root et al.'s (2020) to demonstrate that heterogeneities in grazing and fire over space and time are important to incorporate into analyses of the interactions of perennial and annual grasses, and biocrusts. The unaccounted heterogeneity in time and space in grazing and fire likely contributed to the unexplained variance in the models. Grazing and fire can occur patchily within an area mapped as being disturbed by them, with patches sometimes completely undisturbed or having different levels of disturbance intensity (Fuhlendorf et al. 2009, Clark et al. 2016). The patchiness can result from livestock preference for certain vegetation community conditions, or historic disturbances, or fencing and water placement. Livestock may use burned areas more intensively because they lack unpalatable shrubs that impede animal movements, and

annual grasses are more palatable in spring, when trampling might most impact biocrusts. There are also many different ways grazing is applied to a landscape, such as in different seasons or with different stocking rates and duration (Davies and Boyd 2020). Unfortunately, records of grazing history are relatively poor, likely leading to Root et al.'s reliance on recent dung to measure livestock use. The heterogeneity in grazing effects could conceivably link to fire in ways that would potentially confuse cause-and-effect relationships.

All combined, these considerations indicate that recorded wildfire activity is an important variable to consider in the relationships among grazing, biocrusts, perennial and annual grasses in Root et al. (2020). Notably, numerous publications by the authors of Root et al. (2020) and others have demonstrated that fire reduces biocrust cover and alters biocrust community composition, specifically in sagebrush steppe (e.g., Dettweiler-Robinson et al. 2013, Condon and Pyke 2018a, b, Aanderud et al. 2019). Some of these prior studies even used a similar SEM approach as Root et al. (2020) to evaluate fire and similar factors (Condon and Pyke 2018a). Fire impacts on biocrusts have also been reported for other ecosystem types (e.g., Ford and Johnson 2006). Wildfire can combust biocrust biomass, and the wind erosion that is common for months or years after fire in flat sagebrush-steppe landscapes (i.e., subject Snake River Plain area; Sankey et al. 2009) can cause appreciable mechanical damage to biocrusts (Belnap and Gillette 1998, Aanderud et al. 2019). Biocrusts can be relatively slow growing, and how their recovery after fire and related disturbances can be hastened by restoration is an important focal question for current research (e.g., Chaudhary et al. 2019, Condon and Gray 2020).

The considerations presented here are important because livestock grazing is a primary way that vegetation is managed in sagebrush steppe and other rangelands, and management should be based on an accurate knowledge of ecosystem vulnerabilities. Our note is not intended as a criticism to Root et al., but to build upon that initial paper that domestic grazing, or activity of any hooved or burrowing animal, is likely to disturb biocrusts. In fact, it is hard to imagine how trampling by hooved animals would not disturb biocrusts, as has been reported previously (e.g., Belnap 2003, Dettweiler-Robinson et al. 2013). Additionally, it is reasonable to expect that annual-grass establishment would be greater under conditions of reduced biocrusts, which has also been reported previously (e.g., Condon and Pyke 2018a, b). However, we contend that the path by which livestock promote exotic annual grasses is likely more complex and diverse than Root et al.'s (2020) suggestion that the relationship is mediated primarily by livestock-induced degradation of biocrusts. Fire is another key variable explaining the abundance of exotic annual grasses and

biocrust condition, as well as the perennial herbs they interact with in sagebrush-steppe landscapes.

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SUPPORTING INFORMATION

Additional supporting information may be found online at: <http://onlinelibrary.wiley.com/doi/10.1002/eap.2277/full>

DATA AVAILABILITY

Data are available from the Dryad Digital Repository (Root et al. 2019) at <https://doi.org/10.5061/dryad.2s7g00v> and USGS ScienceBase (Welty and Jeffries 2020) at <https://doi.org/10.5066/P9Z2VVRT>.