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Annual grass invasions and wildfire deplete ecosystem carbon storage by >50% to resistant base levels

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Ecological disturbance can affect carbon storage and stability and is a key consideration for managing lands to preserve or increase ecosystem carbon to ameliorate the global greenhouse gas problem. Dryland soils are massive carbon reservoirs that are increasingly impacted by species invasions and altered fire regimes, including the exotic-grass-fire cycle in the extensive sagebrush steppe of North America. Direct measurement of total carbon in 1174 samples from landscapes of this region that differed in invasion and wildfire history revealed that their impacts depleted soil carbon by 42–49%, primarily in deep horizons, which could amount to 17.1–20.0 Tg carbon lost across the ~400,000 ha affected annually. Disturbance effects on soil carbon stocks were not synergistic, suggesting that soil carbon was lowered to a floor—i.e. a resistant base-level—beneath which further loss was unlikely. Restoration and maintenance of resilient dryland shrublands/rangelands could stabilize soil carbon at magnitudes relevant to the global carbon cycle.

A key strategy for managing earth's carbon may be increasing sequestration of carbon into soil, but avoiding losses of ecosystem carbon to the atmosphere may be equally important. Conserving current soil-carbon stocks, i.e., the amount of carbon stored per unit land area, should contribute meaningfully to enhancing carbon sequestration where management or conservation efforts affect vast land areas. One such region is the Intermountain Western U.S., which is vulnerable to carbon loss due to widespread impacts of disturbances such as wildfires and exotic plant invasions, both of which are exacerbated by climate change^{1–4}. Further loss of carbon to the atmosphere could feed back to intensify these disturbances, causing the region to shift from a net carbon sink to a source by 2050^{5,6}.

Cold desert-shrublands, and specifically sagebrush steppe, are thought to have the greatest relative potential to gain carbon stock among ecoregions in the Intermountain Western U.S.⁵. Carbon-loss threats to sagebrush steppe are substantial and result specifically from exotic annual grass (EAG) invasions and the increased wildfire, which they benefit from and promote (i.e., the “grass-fire cycle”)^{1,4,7,8}. The net impact of the feedback is the conversion of diverse, deep-rooted perennial plant communities to shallow-rooted annual grasslands, which has impacted >50,000,000 ha already and is occurring at a rate of ~400,000 ha annually⁹. The exotic annual grasses include species such as cheatgrass (*Bromus tectorum* L.) that have short and early growing seasons of weeks to a few months, that otherwise leave fire-prone mats of senesced, dry, and fine-textured foliar litter¹. This contrasts with the potential for nearly year-round photosynthesis from native

evergreen perennials such as sagebrush, and a correspondingly more positive annual ratio of ecosystem photosynthesis:respiration¹⁰. Importantly, while the grass-fire cycle is best studied in the arid and semi-arid Western US, the introduction of exotic grasses to perennial ecosystems and subsequent conversion to grasslands is globally relevant, impacting fire behavior in Central and South America, Hawaii, and Australia, among other places, with unknown consequences to carbon stocks¹⁷.

Decreases in above- and belowground productivity and biomass resulting from plant-community shifts from perennial woody and herbaceous communities to annual grasslands should impact soil carbon stocks^{11–13}. Wildfire, which is promoted by EAG invasion, is also expected to locally degrade soil carbon stocks both directly by volatilizing biomass carbon and indirectly by eliminating deep-rooted woody perennials and through the loss of carbon-rich topsoil by erosion^{4,8,14}. Detecting changes in soil carbon in response to disturbance or land management actions is challenging because there is substantial vertical, horizontal, and temporal heterogeneity in dry shrubland plant community structure, and soil water and biogeochemical cycling that must be considered^{12,15–17}. Further, the effects of disturbance or management on soil carbon are not likely to be uniform, whether due to heterogeneity in disturbance severity or because of variation in the capacity of soils to store and stabilize carbon^{18–24}. Conservation, management, or sequestration of soil carbon in dry shrublands can be improved with an understanding of how carbon and its sensitivity to disturbance are distributed across

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the mosaic of plant communities and soil types that dominate these ecosystems^{4,10,23,25–27}.

A recent review revealed that neither the direct nor the synergistic effects of wildfire and EAG invasions on soil carbon stocks are well understood because the two disturbances often co-occur, and their separate effects are not trivial to identify⁴. Studies on exotic annual grass effects on soil carbon have not together considered the effects of wildfire, the strong lateral heterogeneity—i.e. plant-soil microsites—that typifies the dominant plant community types in sagebrush steppe, the duration of invasion, and the soil depths where impacts are likely evident^{4,13}. To make more accurate assessments of the distribution of carbon stocks and their disturbance responses, we designed and implemented a benchmark sampling plan that addressed (1) the statistical power needed to detect changes in soil carbon across variable landscapes²⁸, (2) variation in plant-community states and the different soil microsites within them⁴ (Fig. 1), and (3) both the commonly sampled shallow soils (< 40 cm) as well horizons up to 1 m depth that are rarely sampled^{13,29}. Our sampling regime also removed sampling biases that result from non-systematic errors in the measurement of bulk density and corresponding up-scaling error³⁰ or incomplete removal of fine roots that can be misconstrued as shallow-soil carbon under annual grasses.

Specifically, we assessed the impact of EAGs and wildfire on soil carbon stocks from 0–100 cm depth in three cold-desert ecoregions in the vast sagebrush-steppe landscape of the Western U.S.: the Northern Great Basin, the Snake River Plain, and the Idaho Batholith. We sampled sites with all combinations of burned/unburned and invaded/uninvaded disturbance history and accounted for spatial heterogeneity within and between plant-community types by sampling soils and weighting carbon stocks according to the abundance of key, representative microsites (Fig. 1, *methods: carbon stocks*). Our results revealed that wildfire and EAGs threaten soil carbon stocks, stabilization, and sequestration in the vast sagebrush-steppe rangelands, which are a relatively well-studied model system for the vast cold-desert shrub steppes of the world.

Results and discussion

Overview—impact of invasion and burning on carbon stocks

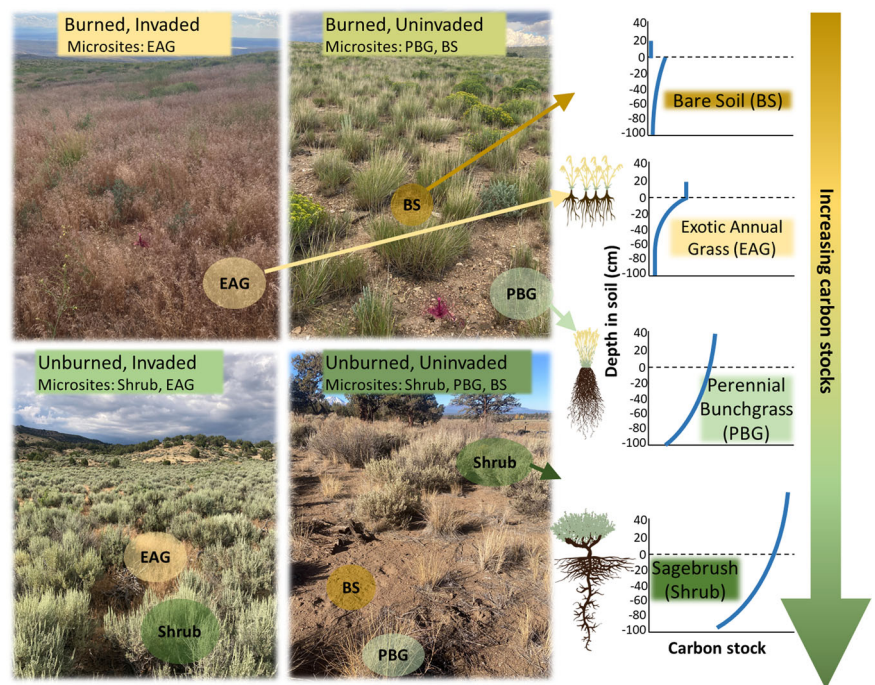
Landscapes that had been invaded or burned had 55% and 93% less aboveground biomass, respectively, and approximately half the soil carbon stocks of areas that were not burned and not invaded (Figs. 1 and 2). Across

all ecoregions, 66% of the soil carbon occurred in ‘deep’ soils—i.e., from 40 cm–1 m, which was the maximum depth sampled—despite greater carbon concentrations near the surface (Fig. 3), which is common for semi-arid soils where inorganic mineral carbon can be redistributed to- or formed in deeper soils^{31,32}. Carbon stocks from 60–100 cm depth in unburned or burned landscapes that were invaded were 73% or 43% less than uninvaded shrublands or grasslands that were unburned and burned, respectively (Fig. 3). The significant reductions in soil carbon below 60 cm in invaded/unburned areas was surprising because invaded shrublands had substantial (18–49%) canopy cover of deep-rooted native perennial shrubs (Table S2) that should have conferred root and carbon inputs to deep soils^{11,12}. In addition to revealing the sensitivity of deep soil carbon to invasion, our findings of reduced deep soil carbon under EAGs in both burned and unburned areas indicate that EAG invasion impacts likely involve alteration of both organic and inorganic carbon processes³². Also, the similarity of carbon stocks across disturbed areas may indicate that there is a limit to how much carbon can be lost from soils following disturbances to the biotic regulators of carbon flow, which we propose as a “soil-carbon floor hypothesis”. Despite this putative soil-carbon floor, the effects of invasion and wildfire were substantial (Fig. 2). Our results implicate 20.0 Tg/year of carbon loss from the top meter of soil over the ~400,000 ha of sagebrush shrublands are estimated to be degraded primarily by wildfire and plant invasions annually, amounting to the loss of ~1% of all carbon stored in Western U.S. cold desert soils, annually (Fig. 2)^{5,9}. Maintaining intact sagebrush-steppe by protecting against the annual grass-fire cycle thus appears to be a highly effective “nature-based” solution to the global greenhouse gas problem.

Plant community and biomass relationships to invasion, fire, and soil carbon

Areas that were burned and/or invaded had distinct plant communities in terms of growth habit, lifespan, species richness, and root architecture (Fig. 1 and Table S2), which we expected, but did not observe, to be proportional to differences in soil carbon storage (Fig. 2 and Table 1). This result implies that interspecific competition and plant community functional diversity were not a direct factor affecting the observed soil carbon loss, as might be expected³³, but instead that indirect and/or abiotic effects, that were associated with the plant community shift may explain the lesser soil carbon

Fig. 1 | Photographs of representative sites, the primary microsites comprising each site, and generalized predictions for relative differences in carbon stock above ground and by depth in the soil for each microsite. Over all soil depths, the relative ranking of carbon stock by microsite was predicted to be Shrub>PBG > EAG > BS, where PBG is perennial bunchgrass, EAG is an exotic annual grass, and BS is bare soil. Photo credit: Toby Maxwell.



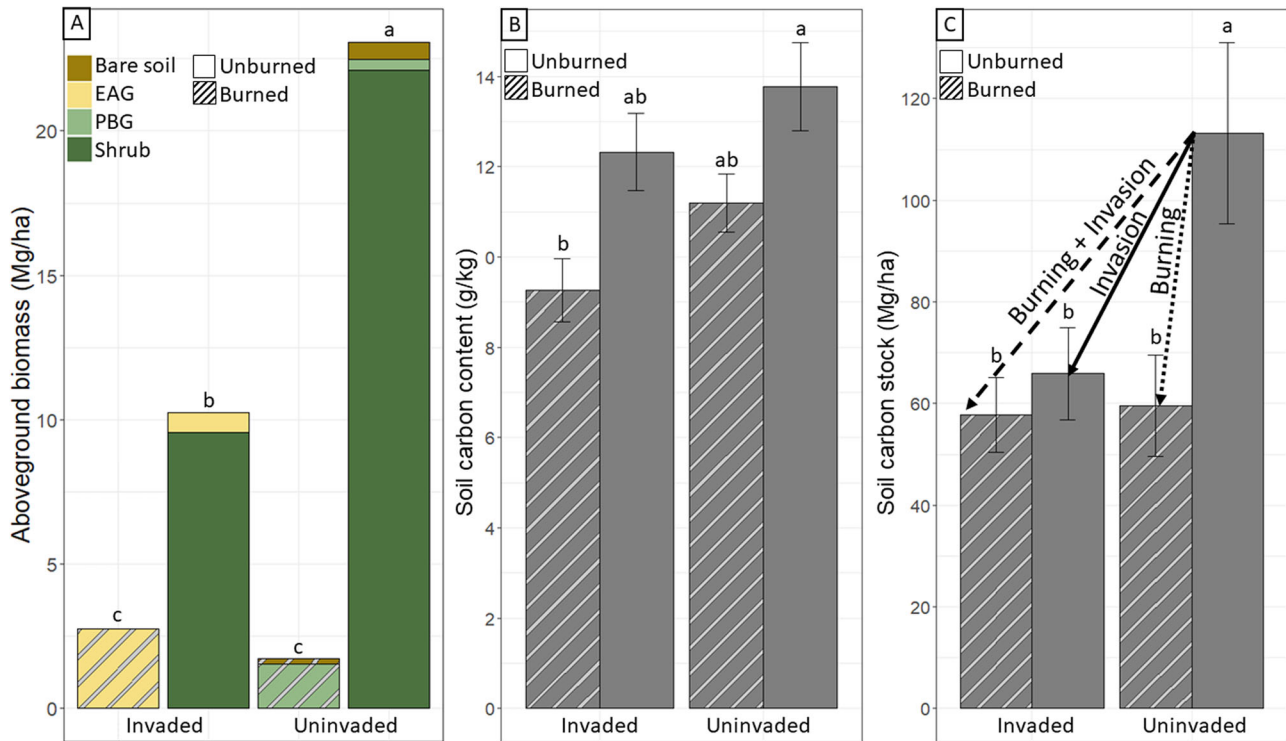


Fig. 2 | Aboveground biomass, carbon content, and carbon stock in invaded or uninvaded and burned or unburned areas. Brown, Yellow, light green and dark green portions of the bars represent the contribution of bare soil, exotic annual grass (EAG), perennial bunchgrass (PBG), and shrub biomass to the total aboveground biomass stock (A). The carbon effects of annual grass invasion and wildfires are shown in C for burning (dotted arrow), invasion (solid arrow), and burning with

invasion (dashed arrow). Bars represent average carbon content (B) or total carbon stocks (C) for 0–100 cm depth for each landscape condition. Significant differences (Tukey’s HSD test, $p < 0.05$) between bars within each panel are represented by lowercase letters at the top of each bar where a shared letter indicated no significant difference. Error bars represent standard error. Note the varying scale and units for each panel.

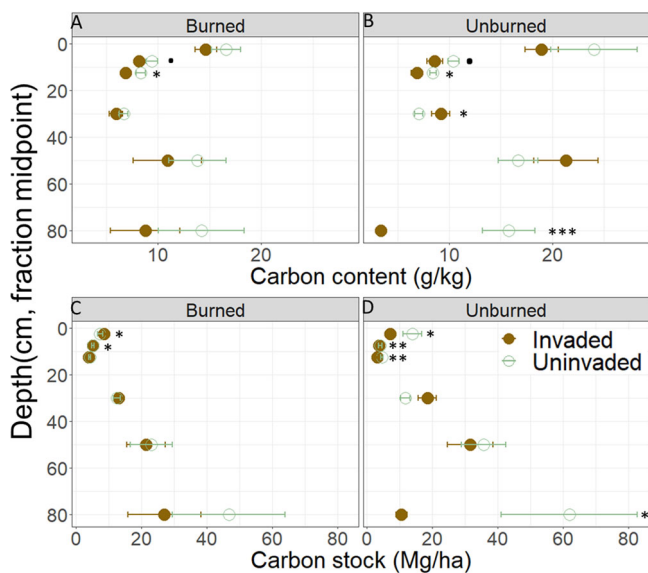


Fig. 3 | Variation in carbon with soil depth among the plot types. Carbon content (A, B) and carbon stocks (C, D), aggregated across ecoregions and microsites for different depth ranges for burned (left) and unburned (right) as well as invaded (brown, filled points) and uninvaded (green, empty points) plots \pm SE. Significant differences are indicated where: $p < 0.1$, $*p < 0.05$, $**p < 0.001$, $***p < 0.0001$ for paired t -tests between invaded and uninvaded plots within a single depth fraction and burned and invaded treatment combination. No symbol is displayed for $p > 0.10$.

in burned or invaded areas. Burning reduced biomass by 93%, but post-fire invasion increased aboveground biomass of burned areas by 22% (Tukey HSD, $p < 0.05$, Fig. 2A). Invaded plots also had greater live herbaceous biomass (by 2.5- and 1.5-fold) and herbaceous litter (by 1.1- and 2.0-fold) in unburned and burned plots, respectively, compared to their uninvaded analogs, which corresponded to greater foliar canopy cover and a lack of bare soil (Fig. 1 and S2; Tables 1 and 2). In unburned areas, differences in biomass were mainly due to 2.5-fold greater shrub biomass in uninvaded compared to invaded sites (Fig. 2A and S2).

Mean soil carbon was enriched to 60 cm depth underneath the crowns of perennials (although the enrichment was not significant, Tukey HSD, $p > 0.05$, Fig. S3), similar to previous reports (Fig. 1)¹⁵. Somewhat surprisingly, the greatest microsite-horizon for carbon stock was the deepest soils under bare soil—i.e., only found in uninvaded sites—and the least carbon storage at 60–100 cm depth was under EAGs (Fig. S3). Possibly the greater amount of carbon in bare-soil—compared to EAG microsites was due to differences in acidic root exudates between the microsites that could have impacted inorganic carbon formation and permanence, which could be evaluated with measurements of root density in relation to organic and inorganic carbon.

Deep soil carbon in drylands should be dominated by inorganic carbon, which is redistributed within soil profiles by water^{31,32}. Thus, the well-documented greater water-content of bare-soil microsites in dryshrublands³⁴ could drive their greater-than-expected deep soil carbon storage (Fig. S3). Unsurprisingly, the loss of fertile-island microsites created and maintained by shrubs is a common effect of wildfire, which leads to the loss of soil-carbon hotspots and thus is a key mechanism by which carbon storage is reduced with invasion¹⁰ (Fig. 1 and S3). Where fertile-island microsites persist after wildfire, they compound their benefit to carbon

Table 1 | Mixed effects model results. Model structure and parameter results for carbon content (g/kg soil), carbon stocks, and aboveground biomass for two different models of each parameter, varying in their fixed and random effects. Estimates are reported relative to the intercept case for each model. Nesting of random effects is represented by parentheses, independent sets of random effects are separated by a comma, and interactions are represented by a colon

Response	Random Intercept (s)	Parameter	Estimate (SE)	$p \geq z $
Soil carbon content (g/kg) ^a	Site (transect position (depth class)), microsite	Intercept (burned, invaded)	2.02 (0.20)	<0.0001
		Uninvaded	0.22 (0.085)	0.0104
		Unburned	0.22 (0.060)	0.0002
		Burning:invasion interaction	-0.21 (0.075)	0.0048
Soil carbon stocks (Mg/ha) ^a	Site (transect position)	Intercept (burned, invaded)	4.82 (0.26)	<0.0001
		Uninvaded	-0.085 (0.10)	0.39
		Unburned	0.76 (0.26)	0.0032
		Aboveground biomass carbon	-0.089 (0.028)	0.0017
		Species richness	-0.14 (0.037)	0.0002
Soil carbon stocks (Mg/ha) ^a	Site (transect position), Burning: Invasion interaction	Intercept	4.07 (0.23)	<0.0001
		Aboveground biomass carbon	0.021 (0.0056)	0.0002
		Species richness	-0.048 (0.034)	0.15
Aboveground biomass (Mg/ha) ^a	Site (replicate ID), microsite	Intercept (burned, invaded)	6.27 (0.86)	<0.0001
		Unburned	-1.21 (0.29)	<0.0001
		Uninvaded	1.36 (0.48)	0.0042
		Burning:invasion interaction	1.38 (0.39)	0.0004
Aboveground biomass (Mg/ha) ^a	Site (replicate ID), Burning:invasion interaction	Intercept (bare soil)	4.51 (0.60)	<0.0001
		EAG microsite	3.42 (0.41)	<0.0001
		Perennial bunchgrass microsite	1.43 (0.26)	<0.0001
		Shrub microsite	3.92 (0.26)	<0.0001

^aModel coefficients estimated using a Gaussian distribution of the log response.

retention by facilitating establishment of deep-rooted perennials³⁵, which confers greater net ecosystem carbon gain compared to areas that are invaded after fire¹⁰ (Fig. S3).

Our finding that invasion and wildfire led to greater differences in carbon stocks at depth compared to the surface contradicted the prevailing expectation that near-surface soil carbon is most sensitive to disturbance on short time scales due to relatively faster cycling near the soil surface^{29,36,37} (Fig. 3 and S3). However, this paradigm stems from a conceptual model of carbon cycling developed for agriculture and forests^{29,33,37–39} that may not apply well to drylands and other low-productivity ecosystems where ratios of above:below-ground inputs are lower^{12,40,41}. For example, 72% of biomass is estimated to be underground in drylands, compared to 9% for croplands or 19% for temperate evergreen forests¹². More than half of the belowground biomass in deserts is below 20 cm depth, which helps to explain our finding that deep soil carbon was sensitive to disturbances that altered the plant community and reduced aboveground productivity¹² (Fig. 3 and S3). Relatively little research has been done to evaluate the impact of disturbances on deep soil carbon cycling. In one notable study in which shallow and deep soil carbon cycling were assessed after a forest-to-grassland pasture transition, gains in topsoil carbon were balanced by equivalent and sometimes greater losses of deep soil carbon, indicating an active carbon pool with ~10 year turnover in deep soils¹¹. While deep soil carbon is generally considered to be older and more stable than surface soil carbon³⁶, our data are consistent with the hypothesis that seasonal patterns of root growth and shedding may lead to meaningful quantities of actively cycled deep soil carbon in ecosystems where plant productivity is dependent on deep-soil resources^{11,42,43}. Our work adds to a small, but growing body of evidence showing that disturbances that lead to shallower rooted plant communities with shorter growing seasons are expected to affect deep soil carbon on shorter time scales than is typically thought^{11,41,42,44}. Importantly, in drylands, slow decomposition rates and the heterogeneous distribution of

roots in the soil make detection and attribution of changes in deep soil carbon particularly challenging⁴.

Evidence for a soil carbon ‘floor’

Burning and invasion led to somewhat similar reductions in both soil carbon stocks and content (Fig. 2B, C), despite their unique impacts on vegetation, litter, and other aspects of the ecosystem that affect carbon flow and storage¹⁰. It is possible that most of the readily mineralizable, labile soil carbon was lost from either burning or invasion, thereby decreasing soil carbon stocks to a minimal and base “floor” level, at which remaining carbon was strongly bound or chemically recalcitrant. By analogy, the remaining carbon could be referred to as the soil-carbon “basement”. In support of the soil-carbon floor hypothesis, a soil-carbon “ceiling” has been recognized that helps explain why soil carbon does not always increase following organic inputs^{19,36,45–47}. Awareness of soil-carbon floors and ceilings is important in evaluating or predicting stability of soil carbon, specifically where or when it may be unresponsive to perturbation.

All soil resources exist in a gradient of forms or matrices that affect reactivity and availability to transformation or transport, and thus a similar trend should be identifiable for soil carbon. For example, soil water can be freely available or tightly bound at the same gravimetric water content, depending on the texture and structure of a soil⁴⁸. Similarly, phosphorus content in soil can be weakly related to its bioavailability because it is often most abundant as phosphate or as organic phosphorous, both of which tend to strongly sorb to soil minerals, rendering them relatively unavailable for plant uptake⁴⁹. Soil nitrogen can also be soluble, mobile, and bioavailable when oxidized to nitrate, or plant-available yet relatively immobile when reduced to ammonium, or relatively unavailable as organic nitrogen⁵⁰.

The form of basement soil carbon could vary with the processes that formed it^{51–53}. Inorganic carbon tends to be 10–17-fold greater than organic carbon stocks in dryland soils and, moreover, concentrated at ~30 cm depth

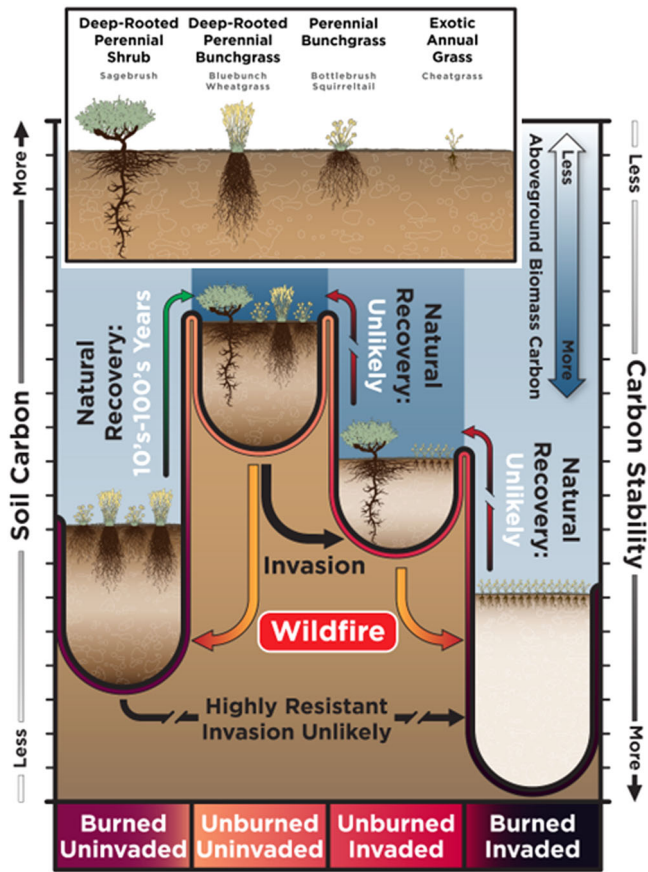


Fig. 4 | Ball-and-cup diagram conceptualizing results on changes in soil carbon resulting from plant community state transitions associated with exotic annual grass invasion and wildfire. Relative soil carbon stocks (left axis) and ecological stability of the carbon (right axis) are represented by the four “ground levels” of soil on the y-axis for each ecosystem state (x-axis) in this study. The plant community for each ecosystem state is represented within each cup (also see Fig. 1), as is the relative aboveground biomass (intensity of blue coloring) and soil carbon with depth (intensity of brown shading), where darker shading represents more carbon. Arrows show perturbations that cause state transitions among plant communities to a new state where wildfire is represented by shaded orange/red, invasion in black, and state transitions to states that have more or less carbon in green (natural recovery likely) or red (natural recovery unlikely), respectively. Red arrows represent the ecosystem states where intervention/restoration would be most appropriate. The height of the hill between states is proportional to the severity of a disturbance (or restoration intervention) that would be required to shift the ecosystem from one state to another. For example, a more intense restoration/disturbance would be required to stimulate recovery to the greatest carbon state for the burned/invaded compared to the unburned/invaded state. This original image was made for exclusive use by the authors by Mason Otis.

or deeper^{31,54}. Soil inorganic carbon tends to accumulate in dryland soils because hydrologic events that leach and remove minerals out of the soil profile are rare, leading to an accumulation of eluviated or precipitated carbonate minerals at the depth of the wetting front^{31,55}. Mineral carbon is fully oxidized and does not function as an electron acceptor for microbial respiration, or as a nutrient, in the way that mineral nitrogen can, for example. Thus, while much of soil inorganic carbon is derived from photosynthesis, its fate and transport are mostly abiotically and particularly hydraulically determined^{31,56}. In drylands soil inorganic carbon may provide a substantial and stable basement compared to ecosystems where soil carbon is predominantly organic and/or meteoric water is more abundant, and soil properties conducive to redistribution of the carbon outside the ecosystem by leaching or respiration. However, while soil inorganic carbon is often disregarded as recalcitrant, altered soil pH, hydrology or the cycling of

nitrogen that occurs with EAG invasions could conceivably and rapidly affect soil inorganic carbon stocks that formed over long timeframes (1 K to >1 M years)^{10,16,57,58}.

Disturbance effects on soil carbon stability

Carbon tends to be more abundant and stable in finer-textured soils, and therefore, more reliably stored, thus changes in soil texture due to invasion or burning could impact carbon stability and storage^{59–62}. Model estimates from our data revealed the counter-intuitive result that for each percentage-point reduction in fine particles (silt+clay content), soil carbon stocks would be expected to be 1.0 Mg/ha greater (generalized linear mixed effects model; Table S3). Thus, burning or invasion could have secondary effects that impacted the observed carbon-texture relationship. EAGs can reduce soil erosion, and because they can germinate in the first fall rains that follow a fire, sites that were invaded could have avoided aeolian or alluvial erosion, particularly in burned sites through the first growing season^{8,63,64}. Alternatively, soil texture may simply be a confounding factor because EAG invasion is facilitated by finer soil textures in semi-arid landscapes^{57,65,66}. Were it not for the finer soil texture in invaded, lower carbon, sites, we would expect to have seen stronger negative effects of invasion on soil carbon stocks because EAG selection effects should have a benefit of greater storage and stabilization properties of silt and clay particles that cannot be conferred by native vegetation (Fig. S5).

As our data revealed, biogeochemical measures of soil carbon stability —i.e., physical protection by association with fine soil particles, or chemical recalcitrance^{47,62}—may only partially explain soil carbon stability, particularly where disturbances are frequent, overlapping, or widespread. For example, biogeochemical carbon-stability metrics have complex responses to wildfire that are poorly described in dry shrublands²³ and an unknown relationship to EAG invasion¹⁰. While the effect of disturbances on micro-scale soil carbon stability is a topic that deserves more study, our data suggest that two additional forms of carbon stabilization at the ecosystem scale that should be considered. First, ecogeomorphic stability, which can be thought of as the effect of plant-community composition and soil surface structure on erosion and soil hydrology^{8,56,67}. Aeolian erosion can amount to centimeters of topsoil loss annually after fire, and could selectively affect soil particles that store biogeochemically stable carbon—i.e. silt, clay, and microaggregates^{8,62,68,69}. Plant communities that rapidly regrow after wildfire can resist this erosion, preventing substantial carbon losses from these ecosystems^{8,63}. Second, ecological stability refers to the resilience, or the tendency of a plant community to return to its previous state following disturbance⁷⁰, and therefore the likelihood that plant-soil interactions that affect soil carbon storage are stable over long periods of time (Fig. 4). For example, sites that are not burned or invaded that effectively turn into low diversity shrublands due to overgrazing and the depletion of native resprouting perennials, as has occurred across much of the western U.S.⁷¹, may maintain a substantial carbon stock, but are also the most vulnerable to carbon loss, because, when they burn, natural recovery of native perennials is unlikely (Fig. 4)⁷². Lack of perennial recovery portends further loss in carbon gain due to a positive shift in annual net ecosystem carbon fluxes (i.e. to a source from a sink⁵), and the greater wind erosion losses expected from shrub microsites after wildfire⁶⁹. The effect of plant community composition on carbon stabilization can be direct—through altered magnitude, chemistry, and vertical distribution of carbon inputs^{11,53}, or indirect by affecting soil hydrology or nitrogen cycling in ways that could impact soil resource availability and water infiltration^{56,57,73} and thus primary productivity. Therefore, restoration and maintenance of native-perennial shrublands that are resistant to EAG invasions and resilient to wildfire should confer stability to soil carbon stocks and be more responsive to restoration to the greater-carbon-storing shrubland state (Figs. 2 and 4)^{35,74}.

Improvements on inference

Here, to the best of our knowledge, we provide the first comprehensive, robust sampling to evaluate the relationship of soil carbon to EAG invasion and wildfire—extensive disturbances that are closely linked to millions of

acres of land management in dry shrublands^{3,4}. Few studies have measured soil carbon beyond 30 cm depth and even fewer accounted for heterogeneity within and between plant-communities by sampling the relevant plant-soil microsites that are common to dryland ecosystems^{4,13}. Studies have also lacked a statistically defensible sampling design that paired invaded and uninvaded sites with adequate assurance about the longevity of the exotics with and without their covarying burn effects⁴. Our results corroborated the hypothesized negative overall effects of EAGs on soil carbon that were previously developed in studies that compared invaded and uninvaded sites between studies without consideration of the effect of soil type, climate, and disturbances on soil carbon stocks^{4,13}. In contrast, we did not observe greater surface-soil carbon in invaded areas. The available related studies typically did not describe in adequate detail whether their soil processing methods did the onerous sifting that would have removed the fine roots of EAGs, and thus may have had included coarse organics as soil carbon, making accurate meta-analysis or inter-study comparison of carbon stocks challenging and sometimes impossible⁴.

Soil carbon is generally considered to be greater in areas that receive more moisture, especially along precipitation gradients in drylands where primary productivity is moisture limited⁷⁵. However, we found that wildfire and EAG invasions disrupted the established positive climate-biomass-soil carbon relationship (Fig. 2 and Table 1)^{33,76}. For example, we observed that the Idaho Batholith had 40–49% greater precipitation and, accordingly, 28% greater biomass in intact native perennial communities that had not been burned or invaded compared to undisturbed areas of the Northern Basin and Range or Snake River Plain. However, in disturbed areas of the Idaho Batholith, biomass ranged from 16% to 42% less, and soil carbon was 62% less than in areas that were similar in terms of burning and invasion in the other drier ecoregions (Fig. 2; S2 and S4). Across all sites we found that differences in species richness were not intuitive (i.e. negatively related to soil carbon) and aboveground biomass was not proportional to changes in soil carbon in response to disturbance. These observations were contrarian to previous studies, and were due to the disruptive effects of EAG invasion and wildfire (Table 1)^{33,39,76}.

Modeled estimates of carbon stocks are often restricted to shallow soils^{37,38,77,78}. Our data confirmed observations from other studies that disturbances can affect deep soils just as strongly as shallow soils (Figs. 2–4 and Table 1)^{11,36}. Thus, while sampling deeper soils is more challenging, our data show that models that do not incorporate deep soils may underestimate the carbon losses due to disturbances, especially perennial-to-annual, or forest-to-pasture conversions that may have a lesser net effect on the total carbon in surface soils (Figs. 3A and 4)^{11,41}. There are still significant barriers to modeling soil carbon at high resolution for single time-points, even in the top 30–40 cm of soil^{78,79}, and little data is available to validate or parameterize deep soil carbon responses to disturbances^{13,36}. Therefore, more research describing how wildfire and plant community composition interact to affect carbon cycling throughout the soil column would be beneficial.

This research provides robust evidence for significant and substantial effects of wildfire and plant invasions on soil carbon and shows that those effects were contrary to theoretical expectations based on differences in aboveground biomass, species richness, and soil texture between plots. However, critical questions remain about the mechanisms driving differences in soil carbon. Specifically, more study is needed to improve understanding of how the different forms of carbon are affected by plant invasions due to any differences in organic or inorganic C, rather than total carbon or, further, due to any differences in particulate or mineral associated organic carbon pools which have important implications for the long-term stability of carbon⁴⁷. Similarly, differences in fire frequency that occur in grasslands could lead to growth of the pyrogenic carbon-pool which could take millennia to accumulate⁸⁰, but could eventually offset some of the short-term carbon losses. The primary land use in this ecosystem is grazing, and thus it will also be important to test whether there are any interactions between grazing, wildfire, and plant invasions⁸¹. Additionally, to understand the empirical mechanisms that govern changes in carbon is an important part of

improving the capacity of earth system models to represent our findings. Specifically, it is not well understood if and whether there are differences in soil hydrology, evapotranspiration, root architecture, or plant functional type due to invasion or wildfire that may be impacting the flow and chemical and biological processing of both organic and inorganic carbon. Finally, state-of-the-art ecosystem carbon models⁷⁷ account for microbial community structure and function, and among many microbial processes that represent the processing of carbon in the soil, it could significantly improve both empirical understanding and also modeling capabilities to know whether the carbon-use efficiency of the microbial community is altered by these disturbances.

Conclusions

By experimentally isolating the effects of wildfire and EAG invasion, we showed that soil carbon stocks and stability in semi-arid landscapes are threatened by EAG invasions and associated wildfire. Surprisingly, there was no synergistic or even additive effect of invasion and wildfire on the loss of soil carbon stocks, which indicated that soil carbon may have been lowered to a ‘floor’, beneath which further carbon loss would be unlikely. Biogeochemical and soil physical processes are often cited as the main factors affecting soil carbon stability, but here we show that exotic plant invasion and wildfire are ecological forces that strongly and rapidly destabilize carbon accumulated over times scales ranging from decades to millennia, or more. While there are increasing calls to sequester carbon in soils as a ‘natural climate solution’, and it may be possible to increase carbon stocks in dryland/shrub steppe soils through careful management, a related and more achievable goal may be to invest in the ecological stabilization of current soil carbon stocks by restoration and management of intact native perennial communities that are resilient to wildfire and resistant to invasion that are known to be net carbon sinks, and thus could at least partially offset the potential loss of 20 Tg carbon annually in western North America alone.

Methods

Approach

We measured plant community composition and soil carbon stocks in dominant microsite types within sites that were: (1) burned and invaded—Annual grass dominated near monocultures of cheatgrass (*Bromus tectorum* L.), and in one case, medusahead (*Taeniatherum caput-medusae*), (2) burned and uninvaded—perennial bunchgrass stands of Bluebunch wheatgrass (*Pseudoroegneria spicata*), Siberian Wheatgrass (*Agropyron fragile*), squirreltail (*Elymus elymoides* and *Elymus multisetus*), and/or Idaho Fescue (*Festuca idahoensis*), (3) unburned and invaded—cheatgrass and big sagebrush (*Artemisia tridentata*) and (4) unburned and uninvaded—intact shrub-steppe dominated by big sagebrush often with perennial bunchgrasses (Fig. 1 and Table S2), in each of three cold-desert ecoregions: The Snake River Plain, Northern Basin and Range, and the Idaho Batholith⁸². All sites have been grazed to some extent over the last 100+ years and are best described as wildlands disturbed by pastoral grazing that created an inroad for exotic annual grass invasion and associated wildfire (as described for the region by Mack 1986).

Site classification as (un)burned or (un)invaded

Sites were defined as burned if there had been a wildfire 20–50 years prior to sampling according to the historical wildfire maps from the U.S. National Interagency Fire Center⁸³. A site was defined as unburned if it had not burned for at least 50 years, which is the minimum recovery time for Wyoming big sagebrush communities which have historical fire return intervals of 171–342 years, while perennial grasslands are thought to burn every 35–100 years^{84,85}. Invasion history was determined by a combination of on-the-ground knowledge from local Bureau of Land Management agency staff and by using Rangeland Analysis Platform to assess the extent and duration of EAG invasions. Specifically, maps of herbaceous annual cover were obtained for the areas of interest for years 1998–2001 and 2018–2021 (rangeland analysis platform—RAP⁸⁶). A plot was considered invaded if it had >50% herbaceous annual cover for the 20 years prior to our

sampling and uninvaded if it had <20% herbaceous annual cover for 20 years. This was determined by a combination of communications with local land managers and by quantifying maximum cover values of herbaceous annuals for each plot from RAP data (see above) for years 1998–2001 (i.e., a 4-year window 20 years prior to sampling) and 2018–2021 (i.e., for the 4 years prior to sampling). At the time of sampling all burned or unburned invaded plots had 100% or 51–82% canopy cover of EAGs, respectively (Table S2). The accuracy of RAP products is variable at the ~1 km² scales of our plots^{87,88}. While our application of RAP was at a smaller scale than the most accurate applications of RAP (12 km²), our interest was not to quantitatively assess EAG cover at a specific time, but rather to classify annual grass cover as either extremely high or low over multiple years, and thus we believe our application of the data to be appropriate^{87,88}.

Ecoregion, site, and plot descriptions

The Snake River Plain ecoregion is xeric with lacustrine and alluvial parent materials deposited by Pleistocene Lake Idaho and the Snake River. The natural potential vegetation is sagebrush steppe, with greasewood-saltbrush in more arid subregions⁸⁹. Unburned plots were located at 870 meters above sea level at approximately 43.328312 N, 116.382486 W within the Birds of Prey National Conservation Area and have no recorded burn history. The burned sites were located approximately 14 km NW of the unburned sites on Kuna Butte, a small volcanic butte located on the Snake River Plain at approximately 43.448739 N, 116.462508 W. Burned plots were at an elevation of 935 m above sea level within the boundary of the 1957, 1983 and 1987 'Kuna Butte' fires and the 1996 Coyote Butte fire. Burned-uninvaded plots were located within a 1983 drill seed that established the current stand of bluebunch wheatgrass. All plots were flat, soils lacked restrictive horizons and had silt loam texture. Mean annual temperature and precipitation were 11.0 °C and 253 mm, respectively (Table S1). Long-term mean annual temperature and precipitation data were extracted from 800 m gridded climate data provided by the PRISM climate group (Table S1)⁹⁰.

The Northern Basin and Range ecoregion is characterized by dissected lava plains, rolling hills, alluvial fans, valleys, and scattered mountains. It is generally higher in elevation and cooler than the Snake River Plain. The natural potential vegetation is sagebrush grasslands or saltbush greasewood, with cool season grasses. Higher elevations support mountain sagebrush and juniper woodlands⁸⁹. All plots were in the Owyhee Mountains Southwest of Boise, Idaho, USA and were all co-located at approximately 43.492878 N, 116.992677 W at 1115 meters above sea level. Unburned plots were preserved 'islands' of sagebrush shrubs that, while inside documented fire perimeters, did not burn. Burned plots were burned in the 2001 Trimble creek fire and the 2015 Soda fire while burned uninvaded plots were located within the bounds of a successful drill seed of Siberian Wheatgrass that occurred immediately after the fire. All plots were flat and had a highly developed restrictive horizon at approximately 25–30 cm depth and gravelly loam soil texture. Mean annual temperature and precipitation were 10 °C and 269 mm, respectively (Table S1)⁹⁰.

The Idaho Batholith ecoregion is mountainous, deeply dissected, underlain by granitic rocks, and characterized by limited fertility and water-holding capacity. Much of the Idaho Batholith is montane, but lower elevations support sagebrush shrublands and perennial grasslands⁸⁹. Our burned plots were established at approximately 43.55986 N, 116.07119 W at 1114 meters above sea level within the bounds of the 1957 Rocky Canyon fire and the 2003 High Crow fire, and our unburned plots at 43.57403, -116.06201 at 1278 meters above sea level, all within the Boise River Wildlife Management Area. The last recorded burn at the 'unburned' sites was the 1959 Oberbillig fire, and all sites burned in the 1957 Rocky Canyon fire. EAG establishment in the Boise Foothills subregion of the Idaho Batholith is aspect dependent and therefore our invaded plots were located on NW aspects and uninvaded plots on S/SE aspects. Plots ranged from 18–24° slopes and were loamy sand to sandy loam in texture. Long-term average mean annual temperature and precipitation were 10.5 °C and 377 mm, respectively (Table S1)⁹⁰.

Vegetation monitoring

Canopy cover was measured at each plot by line point intercept. A 50 m transect was randomly established within the bounds of the appropriate treatment combinations (of burning and invasion). At every 50 cm along the transect, plant species that intercepted a pin flag were recorded at all levels of the canopy for a total of 100 points. In a second pass of the same transect, canopy gaps between identified microsite types that were present at the site were determined and their length represented along the transect recorded (Fig. 1 and Table S2). Short statured perennial grasses such as *Poa secunda* that occasionally occupied interspaces was not considered as a perennial for the purposes of the canopy gap assessment. Microsite composition was determined by continuous lengths of canopy cover for each microsite type along the transect, and considered continuous when breaks in that microsite type were <20 cm length. If an EAG or perennial bunchgrass was present below a sagebrush canopy, that microsite was listed as sagebrush canopy. Bunchgrass microsites were considered to extend beyond their basal area, i.e., any location underneath the canopy of a bunchgrass was recorded as a perennial bunchgrass microsite.

Soil sampling

At 5, 15, 25, 35, and 45 m locations along the transect, soils were sampled from the closest example of each type of microsite found in the canopy gap measurement described above. Soils were sampled using a slide hammer soil core sampler (AMS 3" x 6" steel soil core sampler, American Falls, ID) for the top 40 cm of soil (2 cores) which were then separated into depth fractions by hand. When possible, a gas-powered drill was then used to drill deeper, and soils sampled from 5 cm depth increments within the 40–60 and 60–100 depth ranges. Soils could not always be sampled at the exact same depth even within a transect due to the variable depth and presence of impenetrable calcic hardpans, and thus analyses were done on 'binned' groups of soil samples within depth ranges that reflected the horizonation of each soil (see below). To assess the bulk density of the soils, soil pits were dug at 5, 25, and 45 m along the transect and soil cores extracted using thin walled, 5 cm diameter steel cylinders to carefully remove a known volume of soil from 0–5 cm, 5–10 cm, 10–15 cm, 20–40 cm, 40–60 cm and 60–100 cm depth ranges. For soils down to 15 cm, 2 cylinders of approximately 60 cm³ volume were removed and combined as an aggregate sample. For samples below 20 cm depth, 3 samples were taken evenly across the depth range and aggregated. The number of samples taken was determined by applying an a priori test of statistical power based on soil carbon concentrations and variation from a study in sagebrush steppe at the Idaho National Lab on the eastern Snake River Plain that had measured soil carbon concentrations under perennial canopies and in bare soil microsite locations⁹¹. The sampling campaign resulted in 1174 soil samples. The number of replicates per treatment combination can be found in the data release for this manuscript published on the dryad digital repository.

Soil processing and analysis

Soils were oven dried at 60 °C for 48 h, or until the weight of the samples had stabilized. Surface soils that had been stored in plastic sleeves used in the slide hammer-soil corer were separated into 0–5, 5–10, and 10–15 cm depths by careful removal from the cores with a spoon. Depth ranges were adjusted for compaction when the depth of sampling did not match the core height. Soils were sieved to 2 mm, coarse and fine roots removed, ground to a powder, and analyzed for total carbon with a Costech ECS 4010 elemental analyzer (Costech Analytical Technologies, Inc., Valencia, CA). A duplicate sample was included every 10 samples, and an entire sample run of ~40 samples re-run if any duplicate was >10% different, including for internally validated soil standards.

Texture of mineral soil

Soil texture was measured in a representative subset of 793 samples using the micro pipette method⁹². Approximately 5 g of soil was added to 40 mL 0.5% (w/v) sodium hexametaphosphate and shaken overnight to separate aggregate particles. After shaking, a 5 mL micropipette was used to extract

2.5 mL soil solution from 2.5 cm depth in the tubes at approximately 11 s (sand particles had settled) and 1 h 46 min (sand and silt particles had settled) after shaking was stopped. Settling times were calculated from Stokes law assuming spherical soil particles of density 2.60 g/cm³ settling at 24 °C (the measured lab temperature) and that sand particles were >50 μm and clay <2 μm diameter.

Bulk density

Bulk density was measured using the pit method⁹³—i.e., by digging soil pits with flat vertical faces and extracting intact cores by inserting thin-walled 5 cm diameter steel pipe that was cut to 5 cm lengths, excavating the cylinder from the soil, and bringing the soil to the lab for measurement. Soil from each core was dried at 105 °C for 48 h, or until the weight stabilized. Soil was sieved to 2 mm and fine roots separated. Rock volume was measured by displacement of water in graduated cylinders. Bulk density was calculated according to the fine earth method³⁰ where coarse fragment volume was subtracted from core volume to calculate bulk density of the mineral soil (<2 mm) fraction only.

Carbon stocks

Carbon stocks for each sample were calculated as a function of bulk density, sample depth range, and carbon content on a per mass basis. (Eq. 1)

$$\text{Carbon stock} = \text{soil carbon content} \left(\frac{\text{g carbon}}{\text{g soil}} \right) \times \text{bulk density} \left(\frac{\text{g soil}}{\text{cm}^3 \text{ soil}} \right) \times \text{sample depth (cm)} \frac{1 \text{ Mg}}{1,000,000 \text{ g}} \times \frac{100,000,000 \text{ cm}^2}{\text{ha}} \quad (1)$$

Carbon stocks for each plot type (i.e. each combination of burning/invasion within the site) were reported as microsite-weighted carbon stocks by weighting the carbon stock for each microsite by the relative canopy cover for each microsite that was present at a plot (see vegetation monitoring above, and Fig. 1 and Table S2) and then summing the average weighted values for each microsite at an individual transect location (Eq. 2). The sum of relative cover for all microsities at a site was always 100 and standard carbon stocks are calculated as in Eq. 1.

$$\begin{aligned} &\text{Microsite – weighted carbon stocks} = \\ &\text{Standard carbon stock}_{\text{microsite A}} \times \text{relative cover}_{\text{microsite A}} + \\ &\text{Standard carbon stock}_{\text{microsite B}} \times \text{relative cover}_{\text{microsite B}} + \\ &\text{Standard carbon stock}_{\text{microsite C}} \times \text{relative cover}_{\text{microsite C}} \end{aligned} \quad (2)$$

Reported total carbon stocks for all site types within an ecoregion were the sum of all measurable carbon stocks from 0–100 cm depth. Soil samples were binned into depth categories of 0–5 cm, 5–10 cm, 10–15 cm, 15–40 cm, 40–60 cm, and 60–100 cm (Figs. 2 and 3). Carbon content measurements of each sample within a depth range for an individual soil pit were averaged and converted into stocks representing the entire depth range. For some sites, soil was <100 cm deep and our pits ended at either bedrock or consolidated bedrock which was not always possible to sample, and also contained no mineral soil. The result was that the same depth ranges are not represented at all plots, however, our carbon stock measurements represent the total measurable carbon stocks in mineral soil from 0–100 cm in each site type. To estimate the effect of burning and invasion on carbon stocks across the region, carbon stocks were averaged across ecoregions (Figs. 2 and 3). Similarly, to estimate the microsite and ecoregion effect on carbon stocks, carbon stocks were averaged across burning, invasion and ecoregion or microsite effects (Figs. 3 and S4) To estimate EAG invasion impacts on soil carbon stocks across the 526,100 ha of sagebrush steppe that is degraded annually (as reported in the abstract), differences in total carbon stocks between burned/invaded and unburned/uninvaded sites (Fig. 2) were multiplied by that area and scaled by 69%, which is the portion of that degradation that was attributed to annual grass invasion⁹. Specifically, we report the observed range of loss of 47.1–55.2 Mg/ha carbon at our

sites which amounts to 42–49% compared to 113 Mg/ha in unburned uninvaded communities (Fig. 2). This loss was multiplied by 526,100 ha, or the area of sagebrush that are estimated to be degraded each year and then again multiplied by 69%, which is the portion of the degradation that has been attributed to annual grass invasion, generating the range of 17.1–20 Tg carbon that could be lost across the area of intact sagebrush steppe that is disappearing annually.

Biomass

Herbaceous biomass and litter were collected from a within 1 m² frame placed at randomly determined distances from the transect (but less than 5 m) at 5, 25, and 45 m transect locations. Within the frame, each microsite type that was identified on a transect was independently sampled, and from within each microsite type, the following biomass classes were collected separately: herbaceous, EAG, woody litter, and herbaceous litter. Shrub biomass in Mg/ha was estimated by combining shrub density measurements made at our plots with allometric equations developed specifically for sagebrush shrubs⁹⁴. Shrub density was estimated using a frequency-density approach, by counting shrubs within a 5, 9, or 13 m radius until at least 5 mature shrubs were included in the area. Three counts were made per transect within a 5 m radius at 5, 25, 45 m transect locations. Shrub biomass was estimated using Eq. 3 below, where diameter 1 was the largest diameter of the shrub canopy, diameter 2 was perpendicular to diameter 1, and the shrub volume was calculated as the volume of an elliptical cylinder based on diameter 1 and 2, and the shrub height (Pyke et al.⁹⁴). All measurements were in cm or cm³.

$$\begin{aligned} \text{Biomass (kg)} = &0.0462 - 0.00294 * \text{Diameter1} + 0.00422 * \text{Diameter2} \\ &+ 0.00000112 * \text{Shrub volume} \end{aligned} \quad (3)$$

Statistics

Significant differences in carbon content or stocks between invaded and uninvaded plots for all depth ranges of the soil were determined by paired *t*-tests (Fig. 3, *p* < 0.05). All data from all ecoregions and microsities were averaged and tests were conducted individually for each set of invaded and uninvaded sites that were either burned or unburned. The error of carbon stock measurements (Figs. 2 and 3; S4) was the standard error of the mean for all replicates of carbon stocks across all plots that were used to calculate a reported value. The net effect of invasion and burning on soil carbon content (% carbon by mass), and carbon stocks was assessed with generalized linear mixed effects models using the package glmmTMB in R^{95,96}. Model structures are detailed in Table 1. Model residuals were normally distributed (Shapiro–wilks test, *p* > 0.05), and there was no correlation between model predicted values and residuals. Post-hoc Tukey HSD tests were conducted on soil carbon stock data using *HSD.test* function from the *agricolae* package (Fig. 2; S3 and S4)⁹⁷.

Reporting summary

Further information on research design is available in the Nature Portfolio Reporting Summary linked to this article.

Data availability

Data are available in the Dryad digital data repository <https://doi.org/10.5061/dryad.d2547d88k>.

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Author contributions

M.J.G and H.E.Q. conceived the idea. T.M.M., S.J.P., and M.J.G. designed the experiment. T.M.M. and S.J.P. led the field sampling campaign. S.J.P. performed the geospatial analysis. T.M.M. wrote the first draft and co-led the writing of the manuscript with M.J.G., analyzed the data, and performed the

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Competing interests

H.E.Q. is employed by Environmental Science US LLC, a solutions provider for rangeland protection.

Additional information

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