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The effects of cheatgrass invasion on US Great Basin carbon storage depend on interactions between plant community composition, precipitation seasonality, and soil climate regime

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Abstract

1. Annual-grass invasions are transforming desert ecosystems in ways that affect ecosystem carbon (C) balance, but previous studies do not agree on the pattern, magnitude and direction of changes. A recent meta-analysis of 41 articles and 386 sites concludes that invasion by annual grasses such as cheatgrass (*Bromus tectorum* L) reduces C in biomass across the Great Basin (Nagy et al., 2021). Reanalysis reveals that whether cheatgrass affects biomass C stocks is not generalizable, but rather depends on the considerable variation in climate across the subject sites. Our analysis suggests that accurate Great Basin-scale estimates of cheatgrass effects on C balance are not yet possible.
2. Addition of climate variables to the meta-analysis reveals that cheatgrass invasion (a) reduced C in above-ground biomass in relatively summer-wet sites but not in summer-dry sites, (b) increased surface soil C in sites with intermediate resistance and resilience classifications (R&R) but not in low R&R sites—that is, mesic/aridic soil climates and (c) did not affect deep soil C.
3. Considering that cheatgrass has expanded most in relatively summer-dry sites and mesic/aridic sites, omission of climate factors leads to model overestimates of cheatgrass effects on C when extrapolating to larger areas. Estimates of cheatgrass effects on C would also be improved if the analysis considered that (a) perennial grasslands are a common community state in the Great Basin that have intermediary C relative to annual grasslands and sagebrush stands, that is the omission of perennial grasslands from analysis inflates the baseline C storage of uninvaded Great Basin ecosystems, and(b) cheatgrass does not often exist in stable monocultures and soil carbon can reflect current or recent presence of other species.
4. *Synthesis and applications*. Invasions often reveal heterogeneity in ecosystem structure and function that is not otherwise evident, and the heterogeneity can influence estimation of the net impacts of the invaders. For cheatgrass and

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other invaders, we propose that formally accounting for the spatial variability of invasion on ecosystem functions will improve the estimation of their net effect on ecosystem C, and thus improve prospects for adjusting management practices to optimize C sequestration.

KEYWORDS
carbon sequestration, cheatgrass, climate, fire, Great Basin, meta-analysis, soils

1 | INTRODUCTION

The processes that impact the flow of carbon (C) in arid and semi-arid ecosystems are affected by spatial variation in climate (Campos et al., 2017), geomorphic and edaphic setting (Ayala-Niño et al., 2020), biotic factors such as plant community (Bradley et al., 2006; Wilsey et al., 2020), disturbances such as wildfire (Nolan et al., 2018), and land management (Zamanian & Kuzyakov, 2019). Interactions between these factors and processes are often poorly characterized and can have complex outcomes on C flow and storage (Doetterl et al., 2015). Biological invasions that result in community state transitions, such as the vast conversion of perennial shrub-steppe to annual grasslands in the Western United States, have the potential to alter plant productivity in ways that impact C balance at both the local and continental scales (e.g. Bradley, 2009; Bradley et al., 2006). Further, quantification of annual-grass impacts on soil C is needed to justify and guide management interventions such as eradication of invaders and restoration after their removal (Germino et al., 2016).

Invasions by exotic annual grasses such as cheatgrass (*Bromus tectorum* L) into shrub-steppe is transformative because these shallow-rooted species that are active and green for only short periods each year replace a diverse blend of native deeper-rooted perennials that otherwise more reliably provide ecosystem structure and functioning, including productivity across drought cycles (Germino et al., 2016). Cheatgrass creates fine-textured wildfire fuels that are dry and combustible for much longer than fuels produced by perennials, and cheatgrass often fills interspaces between perennials and causes undesirable fuel connectivity (Brooks et al., 2004). The net outcome of these plant-canopy changes are more frequent wildfires and greater wildfire spread, which favour the continued increase of cheatgrass relative to perennials. This plant-environment feedback and corresponding plant-community conversion is expected to impact ecosystem C by reducing the annual time frame for autotrophic C assimilation, increasing heterotrophic C respiration, eliminating C storage in wood, reducing C accumulation in deeper soils, and redistributing C nearer to the soil surface (Germino et al., 2016). The net outcome is that C storage and fluxes are predicted to be less stable in time and space, and it is quite reasonable to expect that annual grass invasions would overall lead to less ecosystem C—particularly in standing biomass and in deeper soils in sites where shrubs are most abundant (Germino et al., 2016). Consistent with these expectations, a recent meta-analysis concluded that invasion by the exotic annual, cheatgrass (*Bromus tectorum* L), decreases above- and below-ground biomass C, increases topsoil C, and decreases deep soil C, with a net effect of substantial declines in ecosystem C. (Nagy et al., 2021). These authors analysed the reported changes in above- and below-ground carbon across a gradient of invasion from 41 studies of C storage across much of the domain of sagebrush ecosystems, extending beyond their stated focus on the Great Basin. The effort by Nagy et al. is the first major attempt to summarize the literature on this important topic, and they successfully highlight the complexity of the system and the need for further research by confirming the multi-directional shifts in C storage that are anticipated with cheatgrass invasion.

The analysis of Nagy et al., however, did not account for the large environmental gradients that exist across the Great Basin that are known to impact plant-community composition and associated resistance to cheatgrass invasion (i.e. resisting structural change in the ecosystem due to species replacement) and resilience to disturbances such as fire (i.e. ability to regain ecosystem structure after diturbance; hereafter, resistance and resilience are referred to as 'R&R'; Chambers, Bradley, et al., 2014; Chambers, Miller, et al., 2014; Chambers, Pyke, et al., 2014). Low R&R sites generally occur at relatively low-elevation sites that have mesic aridic soil temperature and moisture regimes, compared to the cooler and wetter conditions at mid- or high-R&R sites (cryic or frigid, xeric), that is sagebrush ecosystems spans a remarkable range of climates in the Great Basin. Nagy et al. did acknowledge the importance of climatic, geographic and edaphic variability across sites, but then suggested the broad geographic distribution of studies included in their analysis allowed for generalized conclusions with respect to C storage. However, the available dataset is highly skewed to low R&R sites (see our Section 3.2) and consideration of the diversity and distribution of climate regimes, soil types and plant communities across the Great Basin (see our Section 4) leads to a different estimation of the effect of cheatgrass on ecosystem C balance.

Areas of the Great Basin that receive relatively more summer precipitation tend to favour higher proportions of perennial grasses relative to shrubs, and substantial differences in C storage capacity exist between perennial grasses and shrubs (Hooker et al., 2008; Huber et al., 2019; McAbee et al., 2017). These differences relate to perennial bunchgrasses' shallower, fibrous root systems and completely deciduous habit, which, although perennial, is more similar to cheatgrass than the semi-evergreen, deep-rooted shrubs. Thus, the perennial grass community state likely

has intermediary C storage to cheatgrass- and shrub-dominated sites (McAbee et al., 2017). Additionally, perennial grasses are considered key to providing R&R because, unlike sagebrush, their greater overlap of fibrous root depths with cheatgrass and ability to resprout after disturbance provides both a greater ability to compete with cheatgrass and to recover after fire (Chambers, Bradley, et al., 2014; Chambers, Miller, et al., 2014; Chambers, Pyke, et al., 2014). Thus, we propose that perennial grasslands must be distinguished from shrublands in analyses of Great Basin C balance. Spatial variability in seasonal and soil climate are readily available in soil-survey maps and the variability is likely to influence the impact of cheatgrass on C balance.

Here, we demonstrate that Nagy et al.'s results and conclusions about cheatgrass effects on C would differ if a reanalysis considered that (1) climate, specifically seasonality of precipitation and soil climate, varies considerably across Great Basin and likely causes spatial variability in the impacts of cheatgrass invasion on C, (2) the effects of cheatgrass invasions on perennial grasslands of the Great Basin are very likely different from the effects on shrub-dominated areas, (3) variation in soil C could result from other species that co-occur with cheatgrass (often transiently) or species recently lost from sites that left a legacy impact on soil C, creating a risk of mis-attribution of impacts to cheatgrass and (4) some processes that strongly affect soil C are not well characterized in the literature and effects of these processes could also be misattributed to cheatgrass. We provide a reanalysis of the Nagy et al. dataset and a discussion on how including these factors changes and mostly lowers estimates of the negative impacts of cheatgrass effects on C in the Great Basin and the broader geographic domain of big sagebrush.

2 | MATERIALS AND METHODS

2.1 | Aproach

We tested for both direct and interactive effects between annual climate data, and intra-annual climate variability and the Nagy et al. final model variables by modifiyng their models for above- and below-ground biomass, soil organic carbon and total soil carbon (our Table 1, their Table 2). We re-created their mixed effects models using their categorical predictor variables of 'time since fire', 'vegetation class' and 'soil depth' (where relevant) with 'Article ID' as a random effect. Fire removes the standing crop and litter, and removes woody species at least temporarily, and so categories of 'time since fire' is a reasonable factor to include in the model. We then added our new variables (discussed below), removing them in order of least to most significant until a model with lowest AIC or BIC was identified. When our climate variables were co-varying, we kept the one with the greatest correlation coefficient between it and the response variable of interest for a particular model. Modelling was done using the package LME4 in the R statistical environment (Bates et al., 2015; R Team Core, 2019). Due to significant interactions between 'time since fire' (with classes of <5 years, 5–20 years and >20 years) 'vegetation class', 'soil depth' and 'resistance and resilience' (i.e. 'R&R') class, we distinguished all factors in our visualizations.

2.2 | Climate seasonality

We extracted mean annual precipitation and temperature, and bioclimatic variables from the Worldclim database for each study site

TABLE 1 Comparison of significance of response of soil or above-ground biomass carbon to predictor variables, according to chi square (df) and significance, where $^{*}p < 0.05$, $^{**}p < 0.01$, $^{***}p < 0.001$. For models with soil organic carbon as the response variable AIC/BIC were 1051/1106 and 1009/1145 for Nagy et al. and the revised model, respectively. For models with above-ground biomass carbon as the response variable, AIC/BIC were 1508/1556 and 1501/1553 for Nagy et al., and the revised model, respectively. Bold variables are newly introduced by our analysis. "R&R" refers to resistance and resilience classification.

Response variable	Predictor variable	Original Nagy et al. model (2021)	Revised model
Soil organic carbon	**Proportion of precipitation in summer**		13.7 (2)***
	Time since fire (Factor)	26.9 (2)***	80.8 (2)***
	Vegetation class	1.05 (2)NS	3.85 (2)NS
	Soil Depth (Factor)	1.97 (2)NS	17.8 (2)***
	R&R: Vegetation		44.0 (8)***
	Time since fire:Vegetation	4.08 (4)NS	28.7 (4)***
	R&R: Soil Depth		28.6 (4)***
	Time Since Fire:Soil Depth	4.90 (3)NS	
	Vegetation Class:Soil Depth	20.4 (4)***	17.9 (4)**
Above-ground biomass carbon	Time Since Fire:Vegetation:Soil Depth	4.50 (4)NS	
	Proportion of precipitation in summer		4.80 (1)*
	Time since fire (factor)	9.85 (2)**	10.1 (2)**
	Vegetation class	11.5 (2)**	11.5 (2)**
	Time since fire:Vegetation	41.3 (4)***	38.8 (3)***

location (coordinates) reported in the Nagy et al. dataset (Fick & Hijmans, 2017). Evaluation of Worldclim's bioclimatic variables in the Nagy et al. models did not reveal significant correlations with C data likely because seasons in the Great Basin are not easily divided into quarters of the year, or well defined by coefficients of variance based on monthly climate data (O'Donnell & Ignizio, 2012). Thus, we defined our own seasonal temperature and precipitation variables that more accurately represent the eco-hydrologic seasons of the Great Basin. We quantified the proportion of precipitation occurring in different seasons by dividing average spring (March–May), summer (June–September), fall (October–November) or winter (December–February) precipitation by mean annual precipitation, generating a continuous variable based on expert knowledge of the seasonality in this ecosystem. Seasonal temperatures were calculated by averaging monthly temperature means over the same time periods. These newly generated metrics of seasonality were added to our set of variables for model selection. Variable selection (as described in Section 2.1) revealed the proportion of precipitation occurring in summer as the most significant metric of seasonality.

For visualization and direct comparison of seasonality to all combinations of grouping variables (i.e. LSD means separation tests with 'plant community type' and 'time since fire') we categorized the hydroclimate of each study location as 'summer-wet' or 'summer-dry' by splitting the dataset in half, where sites that had greater than the median proportion of summer precipitation were categorized as summer-wet, while sites that had less than the median were categorized as summer-dry (Figure 1). Data were presented separately for each category when the continuous variable was significant.

2.3 | Soil climate

R&R classifications of 'High', 'Moderate', 'Low' or 'Wetlands' were extracted for each study location (coordinates) using the sagebrush conservation dataset from the Rangeland Analysis Platform's gridded data products (Figure 2, https://rangelands.app, Maestas et al., 2016). Sixteen sites from three articles were classified as 'Wetlands' and were removed for our analysis. The R&R classes

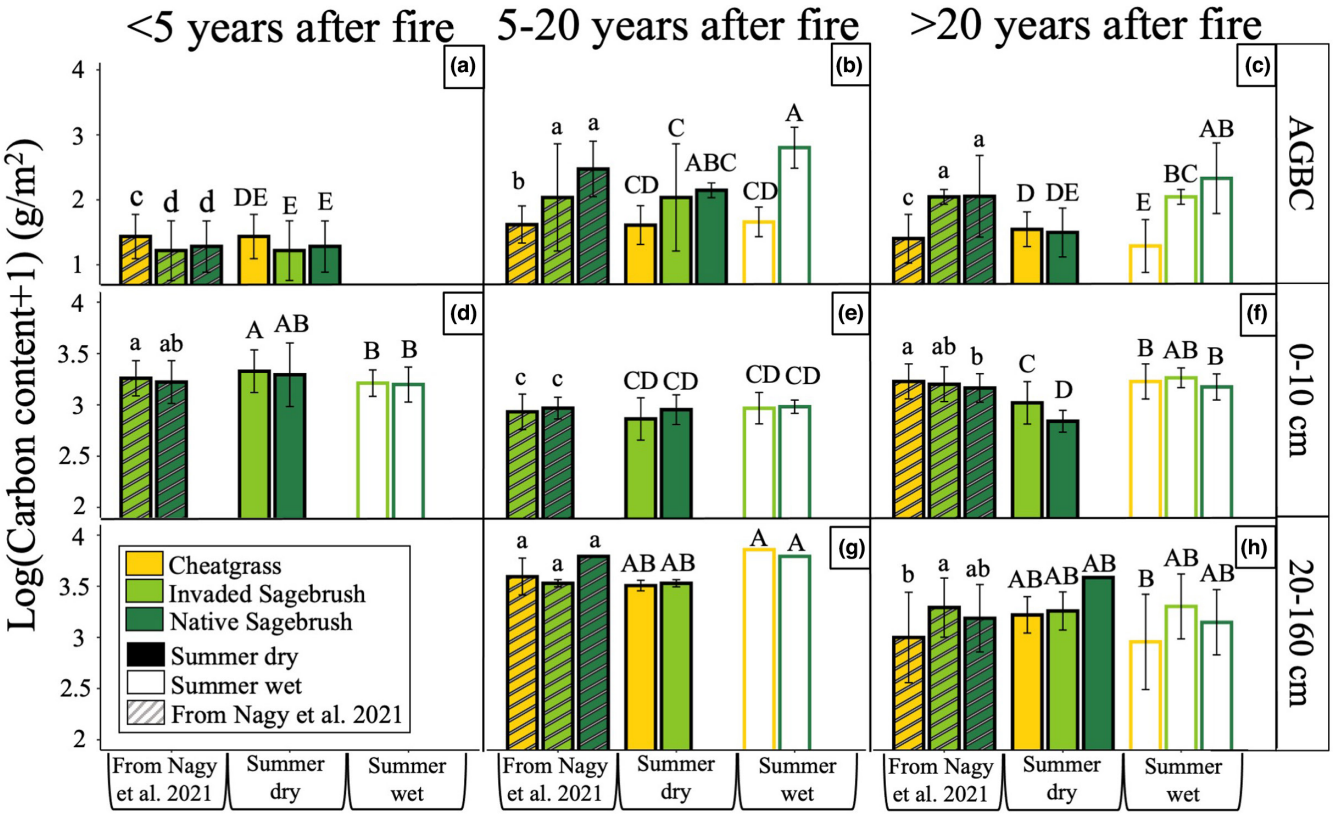

FIGURE 1 Above-ground biomass (AGBC) and soil carbon at two depths (0–10 cm, and 20–160 cm) as a function of time since fire (top panels) and plant community grouping, for the original analysis of Nagy et al. (2021) from their Figure 3e (striped), and for our revised analysis that distinguishes sites as summer dry (closed bars) or summer wet (open bars) for native sagebrush steppe (dark green), cheatgrass invaded sagebrush (light green) or cheatgrass sites (yellow). *Y* axis scales are different for soil and AGBC data to help visualize differences between variable combinations. All variable combinations were represented in the dataset, thus some areas are left blank on the plot, additionally some combinations had only one data point and are therefore lacking error bars. Significant differences are reported for LSD tests where striped bars are for Nagy et al. (2021) original data (lowercase lettering) and unfilled bars for the revised analysis (capital letters). Lowercase letters above striped bars are for comparison between all striped bars in that row and capital letters above filled or open bars are for comparison between all filled or open bars in that row.

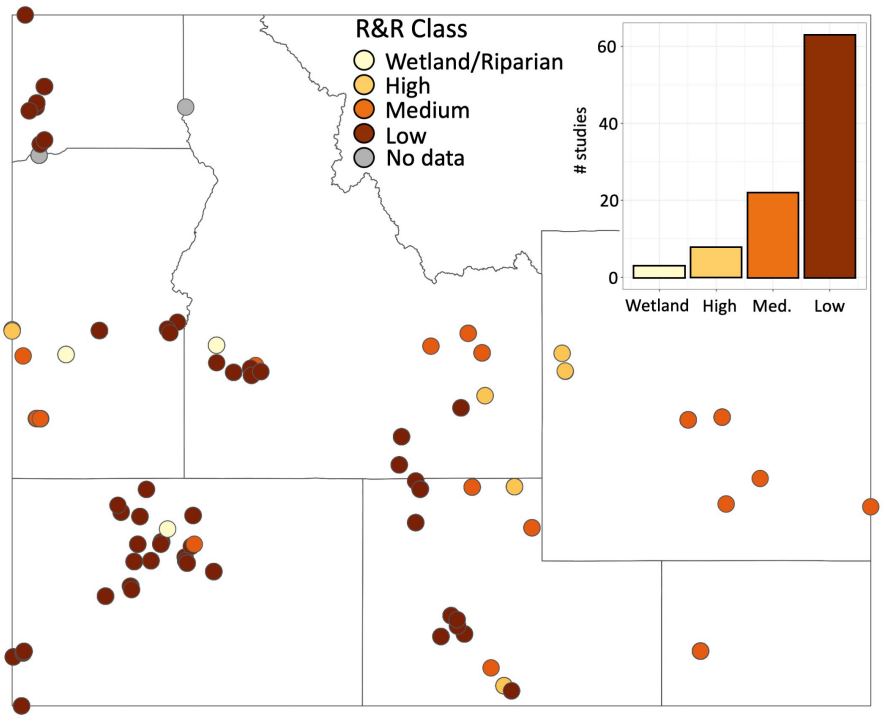

FIGURE 2 Map of studies in Nagy et al.'s (2021) metanalysis, along with annotation of the resistance and resilience (R&R) classification for each site (Rangeland Analysis Platform, Maestas et al., 2016).

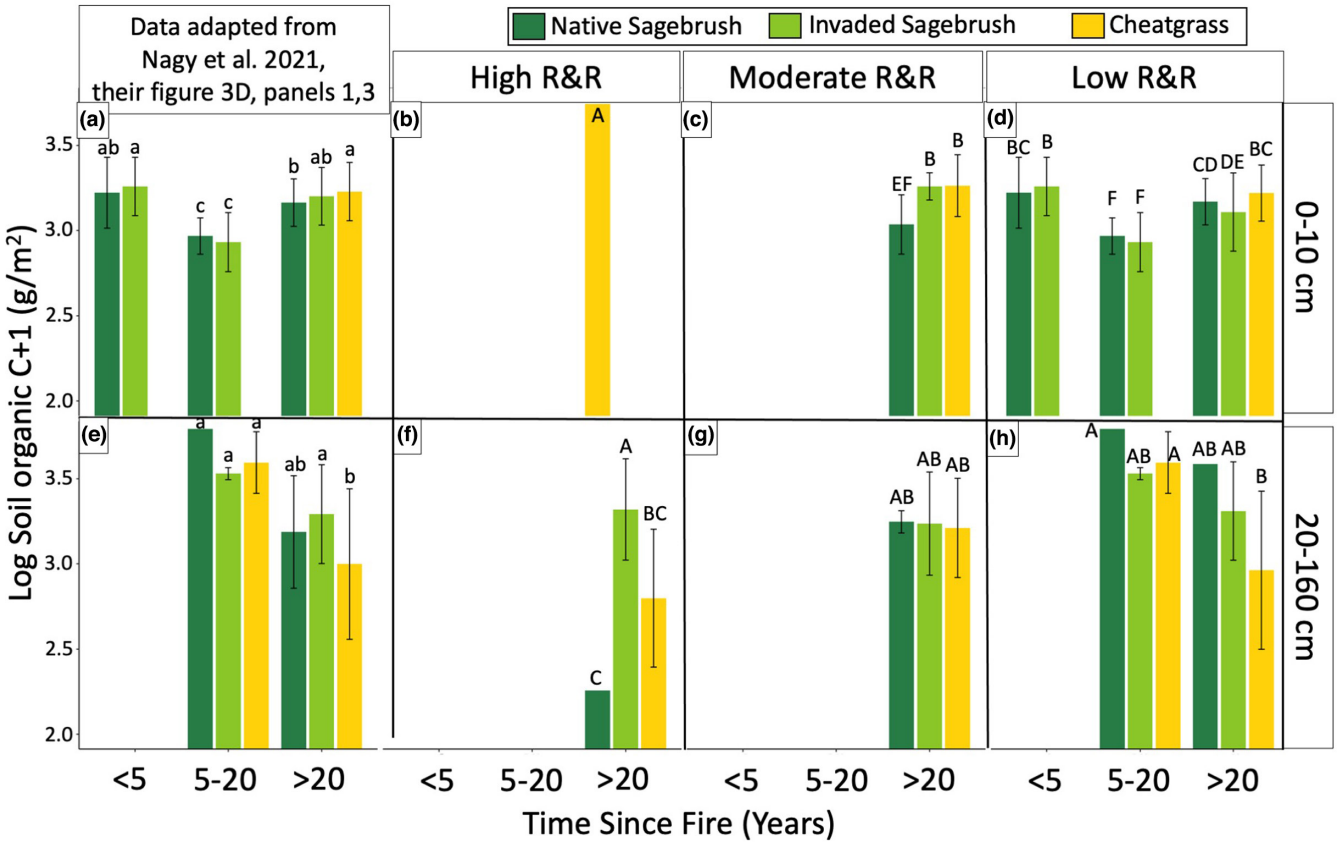

FIGURE 3 Organic carbon content of soil in topsoil (0–10 cm, top panels) and deep soil (20–160 cm, bottom panels) at different times since fire as reported by Nagy et al. (2021) (recreated in panels a, e). The original figure identity was Figure 3d. The same data are represented in the 6 panels on the right, now differentiated by R&R class. Note: Axes start at a value of 2, which is less than the minimum value across all data. Not all variable combinations were represented in the dataset, thus some areas are left blank on the plot. Significant differences are reported for LSD tests within each depth class and across R&R classes in our reanalysis.

were provided as a data product and had been derived from soil moisture and temperature regime classifications and developed specifically to aid land managers in resisting cheatgrass invasions in the sagebrush steppe (Chambers, Pyke, et al., 2014; Maestas et al., 2016).

2.4 | Plant communitiy composition in the Great Basin and Sagebrush domain

The Rangeland Analysis Platform provides annually resolved, gridded data products of foliar cover for key plant functional groups across the Western United States. We aggregated the 2019 cover data to 500m^2 grid cells, for annual herb, perennial herb and shrub content for each grid cell in the Great Basin (shapefile provided by the Conservation Biology Institute) and the broader Sagebrush domain (shapefile provided by the Rangeland Analysis platform). Gridded data was processed using google earth engine and summary statistics within each domain were calculated and visualized in the R statistical envrionment using the packages RASTER, RGDAL and TERNARY (R Team Core, 2019).

3 | CLIMATE EFFECTS

3.1 | Precipitation seasonality influences the effect of cheatgrass on above-ground carbon balance

Mean annual precipitation (MAP) varies from ~140 to ~400 mm/year among sagebrush ecosystems, which is the range of MAP in which productivity increases most per incremental increase in MAP across all biomes globally (Smith et al., 1997). Moreover, there is considerable variation in seasonality of precipitation, notably from nearly no precipitation during summer months in the western part of the range (e.g. Reno, NV) to relatively wetter summer conditions in the eastern part of the Great Basin (e.g. Salt Lake City, UT) and especially the eastern domain of big sagebrush (e.g. Cheyenne, WY). Several studies indicate that seasonality of precipitation and other temporal variations are pivotal factors (sometimes more important than MAP) affecting species composition such as relative abundances of sagebrush, perennial grasses, and also community resistance to cheatgrass (Bates et al., 2006; Bradley, 2009; Germino & Reinhardt, 2014). Bradley's (2009) bioclimate envelope modelling suggested that decreased summer precipitation would cause a 45% increase in area of the western US that would be suited to cheatgrass invasion, supporting the hypothesis that summer-wet sites will have greater resistance to cheatgrass due to enhanced competition from native bunchgrasses, which benefit from summer precipitation. Thus, we asked if the same gradients in precipitation seasonality that drive invasability by cheatgrass also impact cheatgrass effects on C among the field studies comprising the Nagy et al. analysis.

Adding precipitation seasonality to Nagy et al's analysis, specifically by grouping sites as either relatively summer-wet or summer-dry, revealed that (1) the post-fire declines in above-ground biomass C attributed to cheatgrass by Nagy et al. occur only in summer-wet sites >5 years after fire, with an average of 15.4-fold more biomass C in native compared to cheatgrass-dominated sites (effect sized determined from back-transforming data in Figure 1b,c), and (2) significant differences in soil C were evident only >20 years after fire in summer-dry sites, where cheatgrass-invaded plots had 1.5-fold more C in the soil surface compared to native plots (again, calculated from nontransformed data and not the log C shown in Figure 1f).

3.2 | Soil climate influences the effect of cheatgrass on below-ground carbon storage

Soil temperature regimes in sagebrush ecosystems generally vary from mesic to cryic (warm to cold), and soil moisture regimes vary from aridic to xeric or ustic (dry to seasonally wet). Mesic/aridic sites are generally classified as having low resistance and resilience, whereas frigid or cryic sites that are xeric or ustic generally have moderate to high resistance and resilience, though local factors can change these resistance and resilience (R&R) ratings (Chambers, Bradley, et al., 2014; Chambers, Miller, et al., 2014; Chambers et al., 2019; R&R maps available from US Department of Agriculture, Natural Resources Conservation Service, n.d.). It is important to note that soil climate (and thus R&R class) is distinct from metrics of climate seasonality because soil moisture and temperature regime characterizations are derived from models that account for processes occurring throughout the soil column (e.g. depth to restrictive layers, soil texture, and potential evapotranspiration) in addition to the local climate (Bonfante et al., 2011; Van Wambeke, 2000).

Reproducing the statistical models of soil organic carbon from Nagy et al. but including soil temperature and moisture regime (via R&R) and summer precipitation seasonality improved the model strength and changed the findings in several key ways. Nagy et al. found a 1.2-fold increase in surface soil C >20 years after fire (Figure 3a). The new analysis revealed that cheatgrass invasion increased organic C in topsoil (0–10 cm) only in moderate R&R sites and >20 years after fire by a larger, 1.7-fold factor, but had no such effect in low R&R sites (Figure 3c,d). There were no statistically significant declines in deep soil C (Figure 3e–h) in contrast to the conclusions of Nagy et al. Instead, the revised model suggested that, according to the one study available, cheatgrass increased deep soil C at high R&R sites (Figure 3f). Differences were also apparent between R&R classes, where native sagebrush communities in moderate R&R had less surface soil C than native sagebrush communities in low R&R sites. However, the opposite relationship existed in invaded sagebrush sites, which suggested that reported increases in surface soil C with invasion depended on soil processes.

3.3 | How robust is the set of constituent studies and what do the climate effects imply?

Significant spatial variation in climate across the domain of sagebrush ecosystems affected the impact that cheatgrass has on C. Thus, the original conclusions reported by Nagy et al. are conditional, not generalizable, and our re-analysis suggests that they likely overestimated the negative effect of cheatgrass on biomass and soil C loss within their dataset. This is based on our finding that invasion does not lead to a significant decline in biomass in summer-dry sites, or soil C at any site when the appropriate comparisons are made. Thus, their estimation for C loss due to cheatgrass in sagebrush ecosystems extrapolated cheatgrass-induced C loss to sagebrush-steppe community types that were (1) not actually parameterized and (2) may be less prone to C loses with invasion. Moreover, the distribution of constituent studies available for the meta-analysis was also skewed to low R&R sites which points to a need for additional studies of cheatgrass effects on C in moderate or high R&R (i.e. wetter and cooler) climates. According to our re-analysis, a dataset with better representation of moderate and high R&R sites would increase the 'average' effect of cheatgrass on biomass C or accumulation of surface-soil C due to the larger observed C in summer-wet or moderate R&R compared to summer-dry and/or low R&R sites. Given that a more balanced dataset is expected to display these opposing effects, the net effect of cheatgrass invasion on ecosystem C balance in sagebrush ecosystems is still quite uncertain.

Another consideration is whether the findings made across the collection of studies are tenable—they may be statistically significant, but are the effects reliable and ecologically meaningful? For example, cheatgrass rooting depths are much shallower and growing seasons much shorter than for nearly all of the native species considered (Germino et al., 2019; Schenk & Jackson, 2002), yet the data show that with invasion there was either no change, or increased soil organic C at depth, depending on soil climate. There are few straightforward explanations for this statistical meta-result. One possible explanation is that neither the original nor reanalysed studies considered the potential residual root biomass effects that likely persisted for years if not decades after perennials were lost from cheatgrass-invaded sites (Andersen et al., 2016). This slowly decomposing residual below-ground biomass could cause soil C to be 'artifically' elevated in cheatgrass sites.

It is also unclear why cheatgrass would reduce biomass C only in summer-wet sites, considering that intact summer-dry sites might be expected to have a relatively greater proportion of woody shrub biomass lost to invasion. Summer-wet sites typically have a greater abundance of perennial herbs such as bunchgrasses that are functionally more similar to cheatgrass, such that one would assume that cheatgrass invasion would have a lesser effect on soil C dynamics in these sites (Chambers et al., 2019; Rau et al., 2014; Schenk & Jackson, 2002). Regardless, differences in precipitation seasonality indicate that sites with a greater tendency to not be invaded stand to lose more C if they do get invaded. In other words, while the most resistant and resilient sites are highly productive and support a diverse shrub-bunchgrass community, when the right conditions for stand replacement by cheatgrass do occur, these sites may lose the most C. The impacts of soil climate were more complex, where interactions between R&R class, plant community and soil sampling depth indicated that the effects of cheatgrass invasion on soil C are variable. Importantly, the data do not show that cheatgrass will always enhance surface soil C accumulation as is often suggested. Overall, our analyses point to the need for more studies that specifically target soil C monitoring in different plant communities, different fire histories and R&R classes, as there is a relative scarcity of data <20 post-fire in moderate and high R&R sites.

We suggest that by using precipitation seasonality and soil climate (i.e. R&R) to distinguish between sites, we can improve the assessment of cheatgrass effects on C and make geographically weighted estimations that inform land managers on where restoration of sagebrush would be the most impactful for maintaining or enhancing C sequestration.

4 | VARIABILITY IN THE COMPOSITION OF NATIVE AND CHEATGRASS-DOMINATED COMMUNITIES OBSCURES THE EFFECTS OF INVASION

The relative cover of shrubs, species richness and plant diversity are all highly variable over the space and time frames reported on by Nagy et al. (Figures 4 and 5, Miller et al., 2011, 2013). One source of variability is the community response to press or pulse disturbances (e.g. grazing or wildfire, respectively) and the subsequent 'successional' recovery following the disturbance (Chambers, Miller, et al., 2014). Thus, predictions of changing above-ground biomass C associated with disturbance must account for varying community composition that may lead to changes in ecosystem structure and function (e.g. plant biomass, root architecture or land use).

Notably, large areas that were once sagebrush steppe are dominated persistently by perennial plant communities. Currently, an estimated 40% of the Great Basin and and 58% of the full geographic range of big sagebrush are mapped as being in a perennial grassland state, respectively, which compares to 18% and 26% being dominated by shrubs and 21% and 14% in annual grassland (Figure 4; dominant is defined as a pixel with >20% absolute cover; USDA Rangeland Assessment Platform; RAP, https://rangelands.app/, Maestas et al., 2016). Nagy et al. did not consider the perennial grassland state, which at present covers more area of the Great Basin mapped as sagebrush ecosystems than do shrub and annual dominated communites combined (Figures 4 and 5). Instead, the Nagy et al. analysis focuses on only three community states of the Great Basin: intact sagebrush steppe, sagebrush overstory with cheatgrass understory or cheatgrass grassland.

Visual comparison of the most common plant communities across the Great Basin according to the RAP vegetation maps (Figure 5)

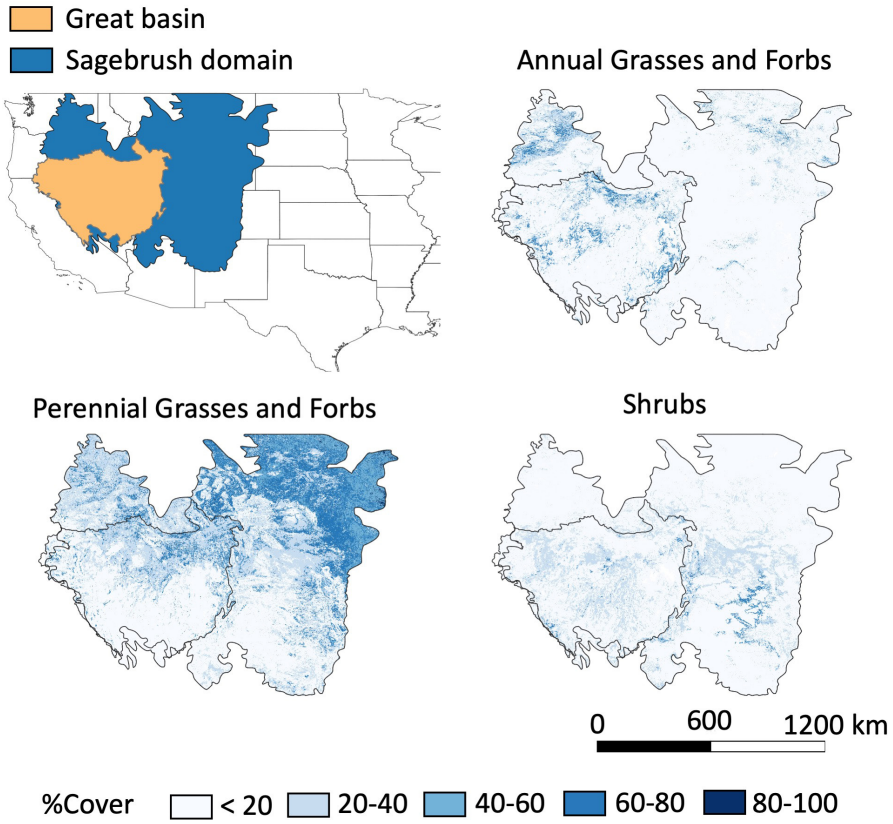

FIGURE 4 Maps of the potential geographic range of big sagebrush (Rangelands.app; Maestas et al., 2016), with the Great Basin nested within (boundary obtained from Great Basin Landscape Conservation Cooperative Boundary, n.d., upper left), and absolute cover of annual herbs (upper right), perennial herbs (lower left), and shrubs (lower right) within those areas. Data acquired from the rangeland analysis platform from 2019 data, aggregated to 500 m^2 resolution (Rangelands.App; Maestas et al., 2016).

reveals that (1) partially invaded plots are not identifiable as a single community type, that is there is large variability in the composition of intermediate plant communities (Figure 5a–c), (2) heavily invaded plots with approximately 60% annual herbs also tend to have 30%–40% perennial herbs and few (<5%–10%) shrubs, and (3) there is substantial variation in community composition within annual- and perennial-dominated communities across the entire range of big sagebrush, the Great Basin, and also within the studies comprising the Nagy et al. dataset (Figures 4 and 5). In fact, according to the RAP data, the most common species' blends within the regions encompassed in Nagy et al.'s analysis often do not fit into the designated community groupings (Figure 5a,c), although these remotely sensed data (aggregated to 500 m^2 resolution) are not intended to accurately represent small study sites.

The concern about omission of native or naturalized perennial-grass-dominated community states in the assessment of cheatgrass effects on C is that the omission likely leads to a substantive overestimate of the cheatgrass effect. Generally, perennial grasslands in sagebrush steppe assimilate and store less carbon than sites populated by big sagebrush (Hooker et al., 2008; Huber et al., 2019; McAbee et al., 2017). In other words, C fluxes and storage are likely more similar between cheatgrass annual grasslands and perennial grasslands than between cheatgrass and sagebrush-dominated perennials. A Great Basin-wide (or big sagebrush-domain) estimate of cheatgrass effects on C that does not account for perennial grasslands, such as in Nagy et al. (2021), would estimate overestimate shifts in C balance because the baseline C balance is inflated if based only on shrub-dominated communities, which actually only comprise 18% of the land area.

5 | PROCESSES CO-OCCURRING WITH CHEATGRASS INVASION CONFOUND INTERPRETATION OF ITS EFFECT ON CARBON CYCLING

Another uncertainty in quantifying the true effect of cheatgrass invasion is the lack of long-term studies, especially ones with pre-invasion carbon storage measurements. Even observational studies of natural (nonexperimental) cheatgrass invasion that include paired control plots may not be able to account for processes that co-occur with cheatgrass invasion. For example, large wind events common to the Great Basin can redistribute or entirely remove centimetres of C-rich topsoil after wildfires, which are closely related to the cheatgrass invasion patterns (Hasselquist et al., 2011). The factors controlling this flux are poorly characterized; however, these events commonly occur, transporting substantial amounts of C and leaving a nutritive deficit (Hasselquist et al., 2011). As cheatgrass often invades after wildfire, it is possible that other variables such as these erosion events have independently impacted both the driver and response (i.e. cheatgrass invasion and C storage), complicating attribution of C losses to cheatgrass invasion. This is just one example of how cause-and-effect inferences can be marginal. To avoid conflation of the effects of cheatgrass invasion compared to fire and

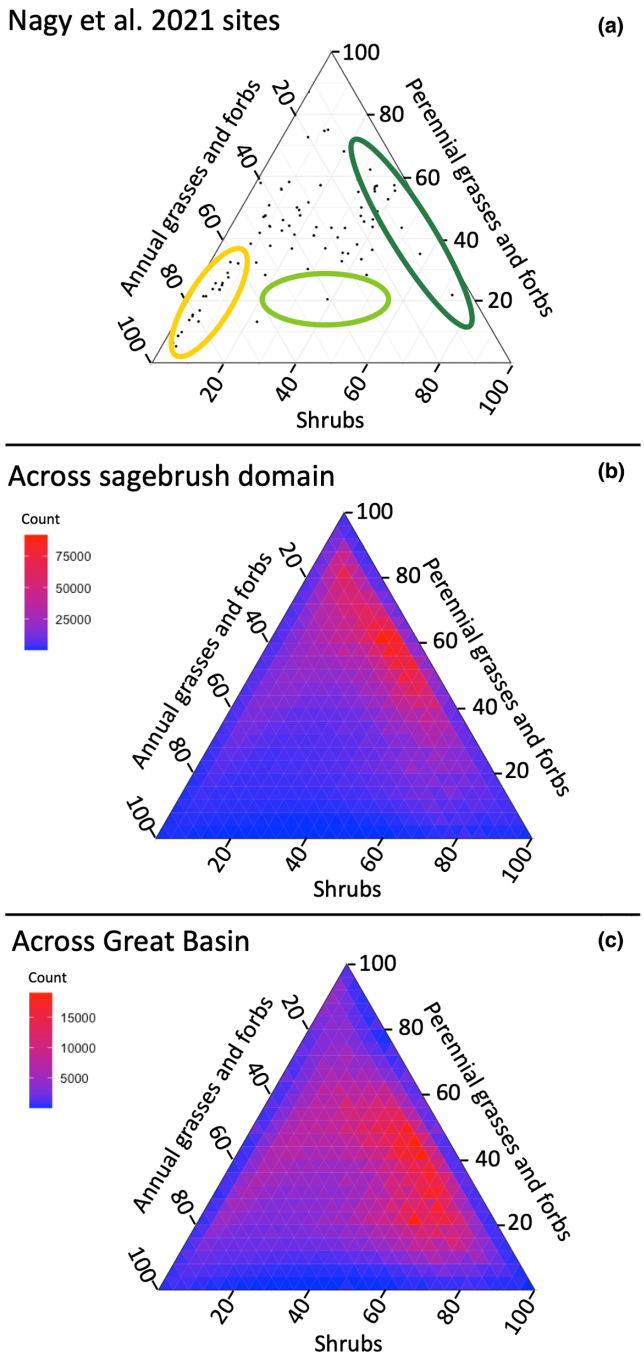

FIGURE 5 Relative abundances of shrubs, perennial herbs and annual herbs within the Nagy et al. (2021) dataset (a), and throughout the geographic range of sagebrush (b), or within the Great Basin (c) for each pixel in Figure 4. Community composition is shown for individual sites from the meta-analysis of Nagy et al. (2021) (a) with yellow, light green and dark green circles representing approximations of 'cheatgrass' (60%–100% annuals), 'invaded sagebrush' (20%–60% shrubs and 20%–60% annuals) and 'native sagebrush' (20%–80% sagebrush, 20%–80% perennials, and <10%annuals) communities used in their paper, respectively. Colours of the heatmaps (b, c) represent the total count (as in a histogram) of raster cells contributing to a cell in the ternary diagram, where warmer colours reflect more commonly occurring plant community mixtures. The legends indicate the pixel count (from Figure 4) for each cell in the corresponding ternary heatmap.

other disturbance related effects on C balance, there is a need for more detailed studies (i.e. across all common plant communities and environmental conditions) and studies that isolate cheatgrass presence or absence as an experimental factor (e.g. by planting or removing cheatgrass).

6 | CONCLUSIONS

Reanalyzing the meta-dataset of Nagy et al. (2021) to account for regional climate differences, specifically, including seasonality of precipitation and soil climate as R&R, altered the conclusions about cheatgrass effects on C. For example, reanalysis suggests summer-wet sites stand to lose substantial above-ground biomass C if invaded by cheatgrass, while summer-dry sites may be unaffected. Thus, to maximize C sequestration in post-fire restoration efforts, our analysis suggests that maintenance of summer-wet native plant communities should be prioritized. However, soil C has complex responses to cheatgrass invasion where increases in surface soil C were observed in moderate, but not low R&R sites, with little data in high R&R sites. We suggest that there is a need for further research that relates soil C storage and plant community composition across a broader range of site qualities and fire histories.

While cheatgrass has many well-documented undesirable effects on ecosystem processes (e.g. more frequent wildfires and the endangerment of endemic flora and fauna), its impact on C cycling is more complex. Our analysis shows that changes in C storage resulting from plant invasions likely depend on whether an invader replaces a functionally similar species (e.g. in summer-wet sites where perennial bunchgrasses are known to dominate). Further, the many interacting processes associated with cheatgrass invasion make attribution of its effect on C balance difficult. We suggest that the many studies to date were not designed to comprehensively assess the net influence of cheatgrass invasion on C cycling in the Great Basin and domain of big sagebrush. While our reanalysis revealed results that more accurately represent the 41-study meta-dataset, our revised conclusions were also suspect, as they conflict with established theory (i.e. replacement of woody perennial shrubs with annual grasses should decrease above-ground biomass and deep soil C). The implication is that the available data may not be adequate to support estimates of C cycling responses to cheatgrass invasion in sagebrush ecosystems or the Great Basin specifically.

Cheatgrass is the most well-studied plant invader of natural habitats (Hulme et al. 2013) that is addressed in tens of thousands of publications in Google Scholar (accessed 4th April 2022) including the 41 studies alone on its C effects (Nagy et al., 2021). Of all invaders and ecosystem contexts, we might expect to be better able to understand and predict cheatgrass effects on C in sagebrush steppe from existing literature better than for other invaders and contexts. However, our reanalyses reveals that the available studies on cheatgrass effects on C do not provide a completely coherent and compelling comparison with theory as we might expect.

One way to more accurately estimate the impacts of cheatgrass invasion may be to experimentally convert plots containing a variety native plant communities to cheatgrass, avoiding conflation of the impacts of disturbance (and its secondary effects) with cheatgrass invasion, and then observe the C responses over the long-term. Experiments of this sort are not trivial to accomplish in terms of time, effort, ethics, and cost, but yet may well be worth the investment. For now, accounting for heterogeneity in climate offers a more accurate assesment of what the existing scientific literature indicates are the effects of cheatgrass invasion on C storage in sagebrush ecosystems or the Great Basin. The revised reanalysis also improves our ability to prioritize restoration in a way that maintains or improves C sequestration across the vast domain of sagebrush in North America.

AUTHOR CONTRIBUTIONS

Matthew Germino conceived of the paper, Toby Maxwell and Matthew Germino designed the analyses, Toby Maxwell analysed the data, and Matthew Germino and Toby Maxwell wrote the paper.

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CONFLICT OF INTEREST

The authors declare no conflict of interest.

DATA AVAILABILITY STATEMENT

Climate and Resistance and Resislience data were extracted from publically available platforms provided by Worldclim (https://www.worldclim.org/) and Rangeland Analysis Platform (https://rangelands.app/), respectively. All other data were from the original manuscript which and are available via the Dryad Digital Repository at https://doi.org/10.5061/dryad.4mw6m9082 (Nagy et al., 2021).

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