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A synthesis of the effects of cheatgrass invasion on US Great Basin carbon storage

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Abstract

1. Non-native, invasive *Bromus tectorum* (cheatgrass) is pervasive in sagebrush ecosystems in the Great Basin ecoregion of the western United States, competing with native plants and promoting more frequent fires. As a result, cheatgrass invasion likely alters carbon (C) storage in the region. Many studies have measured C pools in one or more common vegetation types: native sagebrush, invaded sagebrush and cheatgrass-dominated (often burned) sites, but these results have yet to be synthesized.
2. We performed a literature review to identify studies assessing the consequences of invasion on C storage in above-ground biomass (AGB), below-ground biomass (BGB), litter, organic soil and total soil. We identified 41 articles containing 386 unique studies and estimated C storage across pools and vegetation types. We used linear mixed models to identify the main predictors of C storage.
3. We found consistent declines in biomass C with invasion: AGB C was 55% lower in cheatgrass (40 ± 4 g C/m^2) than native sagebrush (89 ± 27 g C/m^2) and BGB C was 62% lower in cheatgrass (90 ± 17 g C/m^2) than native sagebrush (238 ± 60 g C/m^2). In contrast, litter C was >4× higher in cheatgrass (154 ± 12 g C/m^2) than native sagebrush (32 ± 12 g C/m^2). Soil organic C (SOC) in the top 10 cm was significantly higher in cheatgrass than in native or invaded sagebrush. SOC below 20 cm was significantly related to the time since most recent fire and losses were observed in deep SOC in cheatgrass >5 years after a fire. There were no significant changes in total soil C across vegetation types.
4. *Synthesis and applications*. Cheatgrass invasion decreases biodiversity and rangeland productivity and alters fire regimes. Our findings indicate cheatgrass invasion also results in persistent biomass carbon (C) losses that occur with sagebrush replacement. We estimate that conversion from native sagebrush to cheatgrass leads to a net reduction of C storage in biomass and litter of 76 g C/m^2, or 16 Tg C across the Great Basin without management practices like native sagebrush restoration or cheatgrass removal.

KEYWORDS
biomass, carbon, cheatgrass, grass-fire cycle, invasion, litter, sagebrush, soil

1 | INTRODUCTION

Globally, ecosystems are experiencing state changes in vegetation as a result of human activity (e.g. propagation of invasive species, land use change and management practices (e.g. grazing, fire), and anthropogenic climate change). Parts of South Africa, the Mediterranean and the western United States are experiencing woody encroachment (Knapp et al., 2008; Maestre et al., 2009; Stevens et al., 2016), while the southern Amazon, northern Australia, Hawaii and the Great Basin ecoregion of the United States are experiencing grassification or savannization (Bradley et al., 2006; Hoffmann et al., 2004; Litton et al., 2006; Setterfield et al., 2010). These vegetation state changes may be accompanied by changes in ecosystem function including altered C storage and fluxes, energy balance, hydrology, nutrient cycling and biodiversity (Davidson et al., 2012; Ehrenfeld, 2010; Pearson et al., 2013). For example, non-native plants have been linked to increased net primary productivity and faster decomposition relative to their native communities (Ehrenfeld, 2003, 2010; Liao et al., 2008). In this study, we synthesize the dozens of individual studies on the effects of *Bromus tectorum* L. (cheatgrass) invasion in sagebrush systems on C storage to provide valuable information for resource management in the Great Basin, as restoration of native vegetation provides an opportunity for C sequestration and climate change mitigation (Bastin et al., 2019).

Likely, the most successful plant invasion in North America (Chambers et al., 2007), the extent of cheatgrass invasion across the Great Basin is prolific (Germino et al., 2016; Mack, 1981) and estimated to cover 210,000 km^2 of semi-arid shrubland (Bradley et al., 2018). Native Great Basin shrubland species are predominantly sagebrush (*Artemisia* spp.) and some drier species (e.g. salt desert scrub; *Atriplex* spp.). Cheatgrass invasion can change many aspects of ecosystem structure and function including reducing species diversity (Germino et al., 2016; Mahood & Balch, 2019; Pellant, 1996) and altering nutrient cycling and soil water availability (Chambers et al., 2014; Rau et al., 2011; Wilcox et al., 2012), but is most notable for altering fire regimes (Balch et al., 2013; Pilliod et al., 2017; Whisenant, 1989).

Cheatgrass is one of the best known examples of promoting a 'grass-fire cycle' (Brooks et al., 2004; D'Antonio & Vitousek, 1992; Germino et al., 2016) and may require an integrated approach for managing both the change in vegetation and wildfire. Cheatgrass adds fine fuels and increases horizontal fuel continuity (Davies & Nafus, 2013), leading to fire return intervals that are twice as frequent as in native shrubland: 50–78 years for cheatgrass (Balch et al., 2013) versus 100–240 years for native sagebrush (Baker, 2006). Moreover, cheatgrass increases fire frequency even at low cover (<5%; Bradley et al., 2018), making fire a concern throughout the invaded range. Following fire, there is often complete loss of shrub cover and conversion to near monocultures of cheatgrass (Germino et al., 2016). Given this pronounced change, it is likely that the loss of woody biomass and conversion to cheatgrass-dominated grassland also substantially reduces C storage.

Following initial cheatgrass invasion, changes in C storage and fluxes have been observed as a result of differences in plant phenology and physiology, C allocation, litter quality and the resulting microclimate (Stark & Norton, 2015). AGB C may increase as cheatgrass fills in sagebrush interspaces and subcanopies (Zouhar, 2003). Litter C may also accumulate following cheatgrass invasion with higher cheatgrass productivity (Zouhar, 2003). Surface soils may display an increase in soil organic C (SOC) with cheatgrass invasion due to greater litter production and root turnover (Hooker et al., 2008). For example, Hooker et al. (2008) found significantly higher SOC in invaded sagebrush sites compared to native sagebrush sites, but only for soils at 0–10 cm.

However, these increases in C storage are likely reversed after fire, once cheatgrass becomes the dominant vegetation. One study showed that conversion from sagebrush to cheatgrass reduced AGB C by as much as 90% (Bradley et al., 2006). Similarly, Austreng (2012) showed that conversion to cheatgrass led to a 50% loss of soil and below-ground biomass (BGB) C. Some studies have shown that cheatgrass-dominated landscapes store significantly less SOC, but this also depends on soil depth sampled and whether the site has burned recently (Germino et al., 2016; Norton et al., 2004a; Rau et al., 2011). For example, Rau et al. (2011) found reduced SOC below 60-cm depth in sites with the highest cheatgrass cover.

Due to the extensive cheatgrass coverage across the Great Basin, it is likely that the impacts on C are similarly widespread. But data from disparate studies have not yet been analysed to assess C pools across a range of cheatgrass invasion. This study synthesizes existing studies to estimate mean C storage in three vegetation types (native sagebrush, sagebrush invaded by cheatgrass and cheatgrass-dominated grassland) in five carbon pools (AGB C, BGB C, litter C, SOC and total soil C). We hypothesized higher biomass C in invaded sagebrush compared to native sagebrush, but lower biomass C in cheatgrass-dominated compared to native sagebrush due to the loss of shrub biomass. We expected higher litter C in invaded sagebrush and cheatgrass-dominated compared to native sagebrush sites due to an increase in litter from the productive grass. We predicted that SOC would increase in invaded sagebrush and cheatgrass-dominated systems compared to native sagebrush, but total soil C would decrease in cheatgrass-dominated compared to native and invaded sagebrush, particularly below the rooting zone of cheatgrass. Overall, we expected conversion from sagebrush to cheatgrass to lead to a substantial net loss in C storage across pools.

2 | MATERIALS AND METHODS

We conducted searches using Web of Science in July 2019 for cheatgrass, sagebrush and salt desert scrub. Detailed search criteria can be found in Appendix S1. We examined the articles to identify those that reported biomass dry weight, C content or C concentration for one or more of the target pools (AGB, BGB, litter, SOC, total soil C) in one or more of the target vegetation types. We also included any additional articles that were referenced within the returned articles if they included data for any of the C pool-vegetation combinations of interest (e.g. SOC in native sagebrush). Only articles that contained a description of vegetation composition or percent cover were included. Although a search was conducted for salt desert scrub, it did not yield enough information to include in further data analysis; however summary data are presented in Table S1.

If an article described a site as 'sagebrush' or 'native sagebrush' or 'sagebrush-dominated' with no mention of cheatgrass, we labelled the site as 'native sagebrush'. We designated sites that were described in the article as 'cheatgrass present' in sagebrush or where sagebrush sites contained >2% cover cheatgrass (after Blank & Norton, 2006) as 'invaded sagebrush'. We defined 'cheatgrass' sites as cheatgrass-dominated or a near-monoculture of cheatgrass vegetation.

In order to estimate average C stored in a given pool-vegetation combination, we needed raw data such that these data could be recombined into a regional mean estimate. We contacted the authors of recent studies (2010 or later) to request raw data. For the studies that we did not have raw data, we included the mean value as an individual data point in our dataset ($n = 26$ articles).

2.1 | Above-ground and below-ground biomass and litter carbon calculations

Some articles reported only above-ground, below-ground or litter biomass (dry mass/area), but not C content. For these studies ($n = 14$ for AGB, $n = 3$ for BGB, $n = 1$ for litter), a mean cheatgrass or sagebrush %C was applied from studies that reported %C to calculate AGB, BGB or litter C content (C mass/area; Table S2). While the biomass and litter mass dry weight can vary greatly by site or across vegetation types, the %C within these pools (e.g. AGB %C for cheatgrass) varies little.

2.2 | Soil carbon content calculations

Soil carbon stocks were calculated as:

$$C_{stock} = C_{conce} \times BD \times d \times 10,000,$$

where C_{stock} is the C content (g C/m^2) within a sampled depth interval, C_{conce} is the C concentration (g C/g), BD is the soil bulk density (g/cm^3), d is the depth of the sample (cm) and the conversion factor of 10,000 cm^2/m^2. Several studies did not report soil bulk density (BD). When BD was not reported for a particular soil horizon/depth, the mean BD was applied from: the horizon/depth above and/or below at the same site, another site nearby, or a mean from other studies at the same horizon/depth.

Soil C content is reported here for commonly sampled shallow–mid depths: 0–10, 10–20 cm. For deeper soils (>20 cm), soil C content was calculated on a per cm basis (dividing C content by the thickness (cm) of the soil layer sampled) to standardize across depths/horizons in different datasets.

2.3 | Site burn information

We expected that the burn history of each site could impact C storage as the system equilibrates following fire. Immediate declines in AGB and litter from volatilization should be apparent following fire (Miller et al., 2013) and gradual losses in deep soil C following cheatgrass replacement of sagebrush after fire can also be expected (Rau et al., 2011). Therefore, we included years since fire in our analyses. If the date of the most recent fire was reported in the article, we used that value; otherwise, we used the date (prior to field sampling) detected by either the Monitoring Trends in Burn Severity (Eidenshink et al., 2007) or the Burned Area Essential Climate Variable (Hawbaker et al., 2017) products.

2.4 | Statistical analysis

All statistical analyses were conducted in R 3.6.1 (R Core Team, 2019). To estimate C storage for each pool-vegetation combination, we calculated mean and variance estimates using all available data. First, we tested the assumptions of linear regression and ANOVA including normally distributed residuals. When the data were nonnormally distributed, log and square root transformations were attempted. When this did not improve normality, we used nonparametric Kruskal–Wallis one-way analysis of variance with Dunn's multiple comparisons test for pairwise comparisons of pool-vegetation combinations.

We constructed linear mixed models to determine significant predictors (vegetation type, time since last burn (years), fire category (recent: <5 years, mid: 5–20 years and old: >20 years) and soil depth (cm) and depth category (shallow: bottom depth sampled <10 cm, mid: ≤20 cm and deep: >20 cm) of C storage using the 'LME4' (Bates et al., 2015) and 'LMERTEST' (Kuznetsova et al., 2017) R packages. We used backwards selection to build these models, following Zuur et al. (2009). We used the Article ID (article) as a random intercept. We included vegetation type, time since most recent fire (continuous number or categorized (recent, mid, old)), and soil depth (continuous number or categorized (shallow, mid, deep)) as fixed effects. For AGB C, BGB C and SOC, we log-transformed the dependent variables to meet normality assumptions. Random and fixed effects structures

were explored by building models with restricted maximum likelihood and selecting the model with the lowest AIC.

In order to isolate the effect of the vegetation conversion through cheatgrass invasion and dominance, we used paired observations in a meta-analysis. The majority of the studies (24/41) were not paired (i.e. only one vegetation type) and thus could not be used because they lacked a baseline for comparison. Additionally, studies where the *n* or *SE* was not reported were not included. Meta-analysis was only possible for SOC (all three vegetation types), total soil C (invaded sagebrush versus. cheatgrass) and AGB (invaded sagebrush versus. cheatgrass). The sample sizes for total soil C and AGB C were $n = 4$ and $n = 3$ respectively.

We conducted a meta-analysis using the METAFOR (Viechtbauer, 2010) and MCMCGLMM (Hadfield, 2010) packages in R. To measure the effect size, we calculated Hedges *g* for each pair of vegetation types per study with the least invaded vegetation type as the baseline. To test whether C storage changed with cheatgrass invasion, we assessed whether or not the 95% credible interval overlapped zero based on 300,000 samples (100,000 iterations after burn-in × 3 chains, thinning interval = 1) after checking visually for convergence. We used uninformative priors and included Article ID as a random effect in the model to account for site differences between studies. Soil depth and time since fire can be important determinants of C pools, but our sample sizes were sufficiently small that we omitted these as fixed model effects.

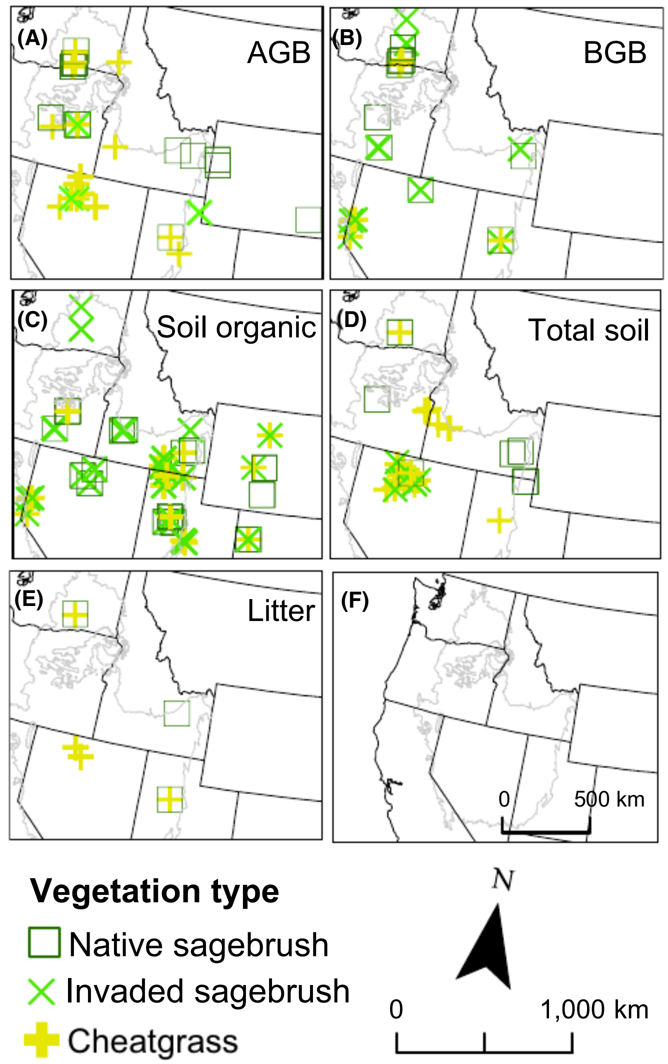

FIGURE 1 Map of study locations by carbon (C) pool: (A) above-ground biomass (AGB) C, (B) below-ground biomass, (C) soil organic C (SOC), (D) total soil C, and (E) litter C. Panel (F) shows the Great Basin ecoregion of the western United States, outlined in grey

3 | RESULTS

To compare C storage in native sagebrush, invaded sagebrush and cheatgrass, we used the data from 41 individual articles (Table S3). Study locations from these 41 articles across the Great Basin are shown in Figure 1. The distribution of all C data by pool is shown in Figure S1.

3.1 | Carbon pools: Regional mean estimates

The regional mean estimates of ABG C, BGB C and litter C across all vegetation types (native sagebrush, invaded sagebrush and cheatgrass together) were 68 ± 10, 154 ± 21, 137 ± 11 g C/m^2 respectively. Despite the 55% reduction in AGB C with cheatgrass dominance, AGB C was not significantly different across vegetation types according to the Kruskal–Wallis analysis (Table 1; Figure 2A). BGB carbon was significantly lower ($p = 0.02$) in cheatgrass than native sagebrush (Table 1; Figure 2A). Litter C was significantly higher ($p < 0.0001$) in cheatgrass compared to native sagebrush (Table 1; Figure 2A).

The regional mean estimate of SOC across all vegetation types was 1,680 ± 30 g C/m^2 from 0 to 10 cm and 1,010 ± 60 g C/m^2 from 10 to 20 cm. Among vegetation types, organic C in surface soils (0–10 cm) was significantly higher in cheatgrass than invaded sagebrush ($p < 0.0001$) and native sagebrush ($p < 0.0001$; Table 1; Figure 2B). Additionally at 10–20 cm, SOC was significantly higher in cheatgrass than in invaded sagebrush ($p = 0.02$; Table 1; Figure 2B). In deeper soils where the bottom depth sampled was >20 cm, SOC content (on a per cm basis) was not significantly different among vegetation types (Figure 2C).

The regional mean estimate of total soil C from 0 to 10 cm across all vegetation types was 1,390 ± 70 g C/m^2. Total soil C in surface soils (0–10 cm) was not significantly different in cheatgrass and invaded sagebrush (Table 1; Figure 2D).

3.2 | Vegetation type, fire and soil depth as predictor variables of C storage

The linear mixed models indicated that vegetation type was a significant predictor of AGB C, and there was a significant interaction between vegetation type and fire as a categorical variable (Table 2a; Figure 3A). The time since the most recent fire (years)

TABLE 1 Mean and standard error (*SE*) of carbon content (g C/m^2) by pool and vegetation type. AGB, above-ground biomass; BGB, below-ground biomass; SOC, soil organic carbon

Pool	Vegetation type	Mean (g C/m^2)	*SE* (g C/m^2)	*n*
AGB C	Native sagebrush	89.4	27.5	96
AGB C	Invaded sagebrush	138.1	39.0	110
AGB C	Cheatgrass	39.8	3.8	338
BGB C	Native sagebrush	238.4	60.1	18
BGB C	Invaded sagebrush	146.0	25.8	29
BGB C	Cheatgrass	90.4	17.5	20
Litter C	Native sagebrush	32.2	12.4	10
Litter C	Invaded sagebrush	NA	NA	NA
Litter C	Cheatgrass	154.0	11.8	65
SOC: 0–10 cm	Native sagebrush	1,552	39.5	176
SOC: 0–10 cm	Invaded sagebrush	1,605	90.4	73
SOC: 0–10 cm	Cheatgrass	1,864	37.9	162
SOC: 10–20 cm	Native sagebrush	1,126	128.6	39
SOC: 10–20 cm	Invaded sagebrush	898.4	68.7	54
SOC: 10–20 cm	Cheatgrass	1,266	140.7	5
Total Soil C: 0–10 cm	Native sagebrush	NA	NA	NA
Total Soil C: 0–10 cm	Invaded sagebrush	1,447	109.3	69
Total Soil C: 0–10 cm	Cheatgrass	1,346	81.1	98

was a significant predictor of BGB C (–) and litter C (–) (Table 2a; Figure 3B,C). As a categorical variable, the time since the most recent fire was a significant predictor of SOC, as was the interaction of soil depth and vegetation type (Table 2b; Figure 3D). Results suggested a three-way interaction of vegetation type, time since fire and soil depth on total soil C (Table 2c; Figure 3E).

3.3 | Effect size of vegetation type on soil C: Meta-analysis

Only a subset of the 386 studies were paired and a smaller subset of these were able to be used in the meta-analysis. Table S4 shows the mean, sample size and variance of all paired studies (i.e. C storage for multiple vegetation types). Results suggest the effect sizes for SOC for any paired vegetation combination were not significantly different than zero (Table 3). For total soil C and AGB C, sample sizes were very small ($n < 5$) and the effect sizes for invaded sagebrush versus cheatgrass were not significantly different than zero (Table S5).

4 | DISCUSSION

The Great Basin is an extensively managed region with land treatments frequently centred on vegetation restoration after wildfire, control of cheatgrass and other invasive plant species, and sagebrush

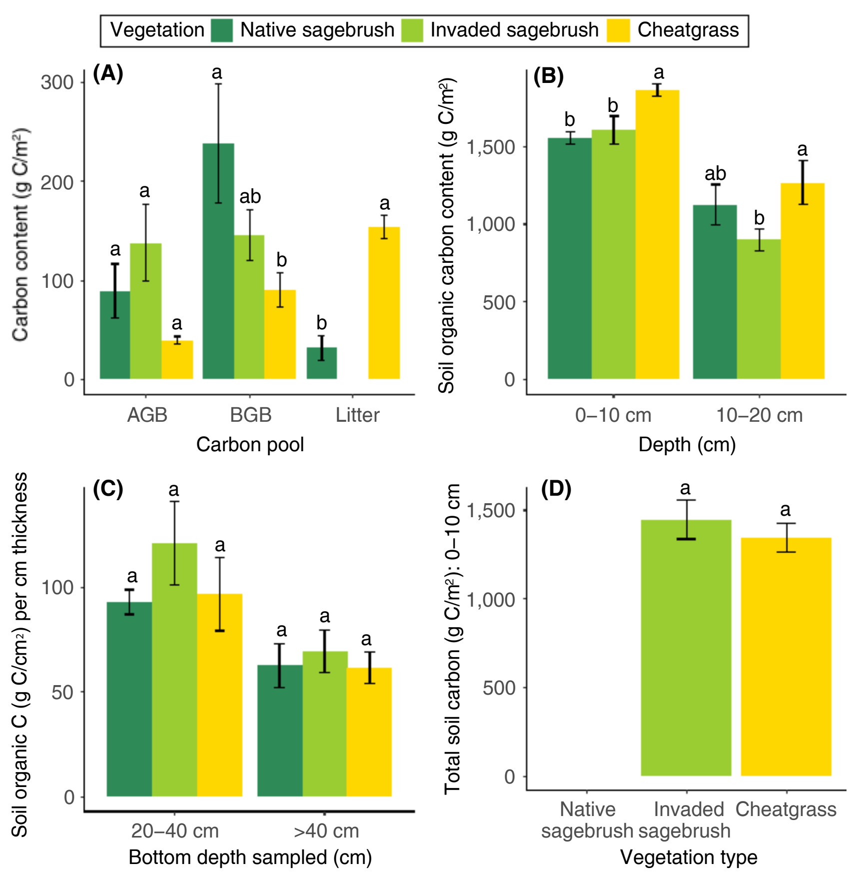

FIGURE 2 Mean and standard error (*SE*) carbon content (g C/m^2) by vegetation type for (A) above-ground biomass (AGB), below-ground biomass (BGB) and litter, (B) organic soil by soil depth (0–10 and 10–20 cm), (C) organic soil C by soil depth in deeper soils (on a per cm basis) and (D) total soil from 0 to 10 cm

TABLE 2 Results from linear mixed models of carbon content (g C/m^2) for (a) above-ground biomass (AGB) C, below-ground biomass (BGB) C and litter C, (b) soil organic carbon (SOC) and (c) total soil C. Shown here are the best models for each pool including the model coefficient and standard error in parenthesis. Vegetation (veg) types are native sagebrush, invaded sagebrush (INV) and cheatgrass (CG). Fire categories are: most recent fire <5 years prior to sampling (recent), 5–20 years prior to sampling (fire(mid)) and >20 years prior to sampling (fire(old)). 'Time since fire' is a continuous variable in years. Soil depth categories are: shallow (bottom depth sampled ≤10 cm), mid (bottom depth sampled ≤20 cm: soil(mid)) and deep (bottom depth sampled >20 cm: soil(deep)). 'Bottom depth' of the soil interval sampled is a continuous variable in cm. Significance levels are indicated with asterisks: *$p < 0.1$, **$p < 0.05$, ***$p < 0.01$. AIC, Akaike information criterion; BIC, Bayesian information criterion

(a)	Dependent variable		
	log(AGBC + 1)	log(BGBC + 1)	Litter C
veg(INV)	−0.146 (0.151)		
veg(CG)	0.353** (0.151)		
fire(mid)	2.755*** (0.878)		
fire(old)	1.477** (0.741)		
veg(INV):fire(mid)	−0.819 (0.691)		
veg(CG):fire(mid)	−2.304*** (0.654)		
veg(INV):fire(old)	0.504 (0.720)		
veg(CG):fire(old)	−1.122*** (0.410)		
time since fire		−0.057** (0.022)	−1.142*** (0.360)
Constant	2.951*** (0.649)	6.453*** (0.805)	121.50*** (31.26)
Observations	544	67	75
Log Likelihood	−743.24	−78.67	−427.55
AIC	1,508.47	169.34	863.10
BIC	1,555.76	182.57	872.37

(b)	Dependent variable
	log(SOC)
fire(mid)	−0.586*** (0.184)
fire(old)	−0.806*** (0.161)
veg(INV)	0.084 (0.143)
veg(CG)	−0.390 (0.526)
soil(mid)	−0.201 (0.150)
soil(deep)	0.075 (0.177)
fire(mid):veg(INV)	−0.166 (0.241)
fire(old):veg(INV)	0.173 (0.182)
fire(mid):veg(CG)	0.626 (0.611)
fire(old):veg(CG)	0.511 (0.529)
fire(mid):soil(mid)	−0.301 (0.260)
fire(old):soil(mid)	−0.182 (0.227)
fire(mid):soil(deep)	1.060* (0.622)
veg(INV):soil(mid)	−0.397** (0.202)
veg(CG):soil(mid)	0.272 (0.222)
veg(INV):soil(deep)	0.031 (0.201)
veg(CG):soil(deep)	−0.447** (0.179)
fire(mid):veg(INV):soil(mid)	0.404 (0.341)
fire(old):veg(INV):soil(mid)	0.577** (0.295)

(Continues)

TABLE 2 (Continued)

(b)	Dependent variable
	log(SOC)
fire(mid):veg(INV):soil(deep)	−0.438 (0.693)
fire(mid):veg(CG):soil(deep)	−0.157 (0.740)
Constant	7.877*** (0.177)
Observations	702
Log Likelihood	−502.05
AIC	1,052.10
BIC	1,161.39

(c)	Dependent variable
	log(Total Soil C)
time since fire	0.011 (0.014)
veg(INV)	0.685 (0.439)
veg(CG)	−0.412 (0.763)
bottom depth	−0.027 (0.039)
time since fire:veg(INV)	−0.021* (0.011)
time since fire:veg(CG)	−0.030* (0.016)
time since fire:bottom depth	0.0003 (0.001)
veg(CG):bottom depth	0.065 (0.054)
time since fire:veg(CG):bottom depth	0.003** (0.001)
Constant	7.016*** (0.661)
Observations	243
Log Likelihood	−216.60
AIC	457.20
BIC	499.12

restoration (Pilliod et al., 2017). Cheatgrass invasion of sagebrush ecosystems in the Great Basin has well documented effects on C (Germino et al., 2016; Zouhar, 2003), and a holistic, large-scale understanding of impacts, such as those on C storage is necessary to identify, prioritize and adapt management decisions (Chambers & Wisdom, 2009). Many studies have examined one or more C pools in one or more vegetation types (Figure 1), yet these studies have not been synthesized to date. We expected that cheatgrass invasion and fire would reduce C storage through changes in production and decomposition. We observed widespread loss of biomass C and gains in litter C while the changes in soil C are more nuanced and are related to soil depth and time since fire.

Despite using data from varying ecoregions/habitats, our results show consistent loss of biomass C: cheatgrass-dominated sites averaged 55% lower AGB C and 62% lower BGB C compared to native sagebrush sites (Figure 2A; Tables 1 and 2a). This loss of biomass C is supported by previous studies with paired sites, although our losses of AGB C are lower and our estimated losses of BGB C are higher. For example, Hooker et al. (2008) reported a 68% reduction in AGB C and a 17% reduction in BGB C from native sagebrush to cheatgrass. The reduction in AGB C in cheatgrass systems is due to the replacement of shrub woody biomass with a non-woody, shorter grass. Similarly, the shallow, fine roots of cheatgrass replace deeper sagebrush roots and reduce BGB C (Austreng, 2012). Our estimated loss of biomass C (198 g C/m^2; or net change in biomass + litter: 76 g C/m^2) reflects the vegetation type conversion from native sagebrush to cheatgrass-dominated and associated changes in fire frequency: the greatest reduction in AGB C was observed >5 years after a fire, corresponding to the persistent state change in vegetation (Figure 3A). Invaded sagebrush systems are likely vulnerable to fire, after which, AGB C and BGB C storage will be reduced (Table 1; Figure 2A).

Our regional mean estimate suggests significantly higher organic C in surface soils in cheatgrass (Figure 2B; Table 1), which could be facilitated by higher litter inputs in cheatgrass sites. Indeed, our study found greater litter accumulation in cheatgrass-dominated systems (Table 2a), consistent with other studies (Hooker et al., 2008; Norton et al., 2004a). The increase in SOC in surface soils was related

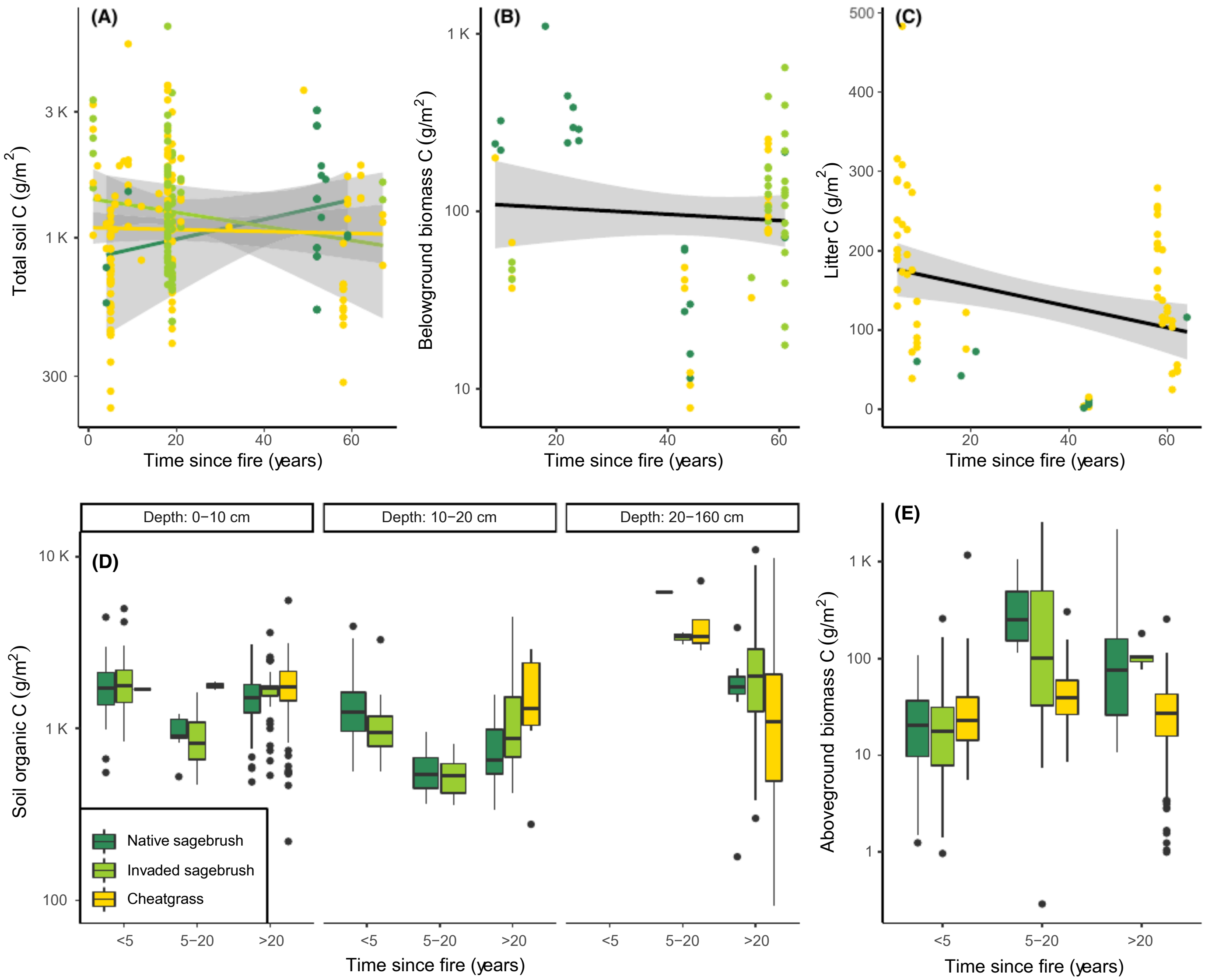

FIGURE 3 Carbon content (g C/m^2) by pool as a function of the time since most recent burn (years) for (A) total soil (B) below-ground biomass, (C) litter, (D) soil organic carbon (SOC) and (E) above-ground biomass. SOC is faceted by depth categories (≤10, ≤20, >20 cm), based on the bottom depth (cm) of the sampling interval. For the boxplots (D, E), the middle line in the boxes is the median and the top and bottom lines of the box are the 25th and 75th percentiles. The whiskers are 1.5 × IQR, where IQR is the interquartile range

TABLE 3 Comparison of carbon storage in different pool-vegetation combinations using meta-analysis with Hedge's *g*. Posterior median value and the upper and lower limits of the 95% credible interval. SOC, soil organic carbon

Pool	Vegetation comparison	Explanatory variables	Effect size	Posterior median (50%)	Lower limit (2.5%)	Upper limit (97.5%)
SOC	Native sagebrush versus invaded sagebrush ($n = 16$)	Random = article	Not significant	0.28	−60,200	61,100
SOC	Invaded sagebrush versus cheatgrass ($n = 15$)	Random = article	Not significant	−0.18	−4.31	4.03
SOC	Native sagebrush versus cheatgrass ($n = 8$)	Random = article	Not significant	−0.31	−29.5	29.5

to the time since fire with gains seen only after 5 years post fire (Figure 3D), as litter and inputs to SOC are immediately removed in combustion. Other soil changes that were not tested in this study, including greater labile organic C (Norton et al., 2004b) and lower lignin:nitrogen (N) ratios (Hooker et al., 2008) in cheatgrass soils that may lead to faster decomposition and greater CO_2 losses, reducing slow and passive soil organic matter (SOM) pools over time (Stark & Norton, 2015), warrant study across these vegetation types.

In contrast to surface soils, we expected to find losses of C in deeper soils following cheatgrass invasion. We observed a

significant interaction of vegetation and fire on SOC at deeper depths (>20 cm), with losses seen after as little as 5 years (Figure 3D), but no effect of vegetation type alone on SOC > 20 cm deep (Figure 2C). Previous studies attribute SOC losses in deeper soils to reduced organic inputs when cheatgrass replaces sagebrush (Germino et al., 2016; Rau et al., 2011) and we suggest that fire likely contributes to the losses as well. Additional information about the time since cheatgrass invasion and degree of sagebrush exclusion could elucidate deeper SOC dynamics, particularly below the cheatgrass rooting zone.

Total soil C in surface soils was not significantly different between invaded sagebrush and cheatgrass and we were unable to compare these vegetation types to native sagebrush (Figure 2D; Table 1). In our regional mean estimates, total soil C (organic + inorganic) was sometimes less than SOC because the measurements were made in different study locations (Figure 2B,D); very few studies measured both total soil C and SOC. Our meta-analysis in invaded sagebrush versus cheatgrass also suggested that the effect of cheatgrass dominance/sagebrush exclusion did not lead to a significant change in total soil C in invaded sites (Table S5).

We hypothesized that fire would be a strong predictor of C stocks and we found that all C pools were related to the time since the most recent fire. Thus, cheatgrass removal (and/or sagebrush restoration) and wildfire may need to be managed in concert to preserve C storage. To improve the explanatory power of burn history on C stocks (Figure 3; Table 2), further information including burn frequency, temperature and severity could be included (Allen et al., 2011; Jones et al., 2015). Additionally, gradients and interannual variability of climatic variables across the study region (e.g. temperature, precipitation), as well as disturbance, may lead to different responses of vegetation following fire (Pilliod et al., 2017; Taylor et al., 2014).

We acknowledge that by comparing data from studies across the Great Basin that were not conducted in a paired framework, other factors undoubtedly varied between sites (e.g. soil properties, climate variables) and may confound these results, particularly in the regional mean estimates. The significant differences observed in our regional mean estimates could be instead or in addition due to the geography of the data collection rather than differences caused by cheatgrass invasion/dominance. However, the broad coverage across the region for all pools (Figure 1) suggests that the patterns we are seeing are likely due to differences in vegetation cover.

This study presents the most comprehensive review to date of cheatgrass invasion effects on sagebrush ecosystem C storage. Future studies could fill remaining gaps including (a) litter quantification in invaded sagebrush, (b) total soil C measurements in native sagebrush and in deeper soils and (c) paired comparisons of C pools across vegetation types. It would also be useful to study decomposition and litter quality (e.g. leaf litter and root C:N, lignin:N) to better understand inputs to and turnover of soil C including C fractions (i.e. active, slow, passive) in the three vegetation types. This work is the foundation of a critical understanding of C storage in dryland systems that are experiencing simultaneous changes in climate, vegetation and fire regimes.

Land cover conversion to cheatgrass is extensive in the Great Basin (Germino et al., 2016; Mack, 1981) and land managers in the region identify cheatgrass management as one of their greatest challenges (NC CASC, 2019). In the absence of restoration efforts, this transition is likely permanent across much of the southern Great Basin and lower elevation areas (Chambers et al., 2014) as cheatgrass promotes a self-perpetuating grass-fire cycle (Fusco et al., 2019). However, practices including targeted grazing, cheatgrass biomass and litter removal, restoration of sagebrush and other native species, and planting native fuel breaks, may increase resilience of native vegetation to future disturbances, reduce the likelihood of severe fires, store more C (Porensky et al., 2018) and reduce costs to the economy and human health. The United States spends $8 billion/year managing terrestrial invasive plant species (Pimentel et al., 2005) and $2–3 billion/year on fire suppression (Gorte, 2013; NIFC, 2019). Programs such as C markets that provide incentives for limiting the spread of invasive species like cheatgrass, restoring shrublands and increasing C storage could offset costs of cheatgrass removal and fire suppression (Meyer, 2012). Restoration of native vegetation remains one of the most promising options for C sequestration and climate change mitigation (Bastin et al., 2019).

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AUTHORS' CONTRIBUTIONS

R.C.N., E.J.F., J.K.B. and B.A.B. designed research; R.C.N., E.J.F. and B.A.B. performed research; R.C.N., E.J.F., A.M., J.T.F., J.M.A. and B.A.B. analysed data; and R.C.N., E.J.F., A.M., J.T.F., J.M.A., J.K.B. and B.A.B. wrote the paper.

DATA AVAILABILITY STATEMENT

Data available via the Dryad Digital Repository https://doi.org/10.5061/dryad.4mw6m9082 (Nagy et al., 2020b). Code is available on Zenodo https://doi.org/10.5281/zenodo.4037178 (Nagy et al., 2020a).

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SUPPORTING INFORMATION

Additional supporting information may be found online in the Supporting Information section.

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