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## Estimates of fine fuel litter biomass in the northern Great Basin reveal increases during short fire-free intervals associated with invasive annual grasses



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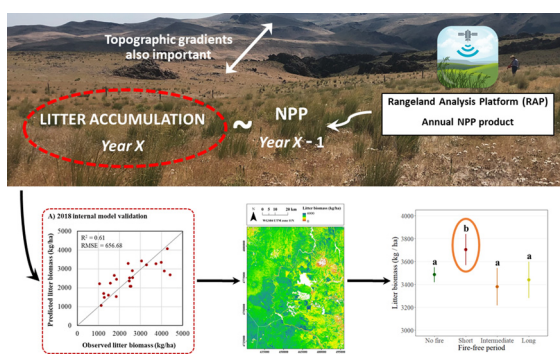
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## HIGHLIGHTS

- Exotic annual grasses promoted a grass-fire cycle in the northern Great Basin.
- NPP by plant traits was highly associated to litter biomass in sagebrush rangelands.
- The extrapolation of litter biomass model over time featured a reasonable accuracy.
- Short times since last wildfire promoted litter accumulation feedbacks.

## GRAPHICAL ABSTRACT



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## ABSTRACT

Exotic annual grasses invasion across northern Great Basin rangelands has promoted a grass-fire cycle that threatens the sagebrush (*Artemisia* spp.) steppe ecosystem. In this sense, high accumulation rates and persistence of litter from annual species largely increase the amount and continuity of fine fuels. Here, we highlight the potential use and transferability of remote sensing-derived products to estimate litter biomass on sagebrush rangelands in southeastern Oregon, and link fire regime attributes (fire-free period) with litter biomass spatial patterns at the landscape scale. Every June, from 2018 to 2021, we measured litter biomass in 24 field plots (60 m × 60 m). Two remote sensing-derived datasets were used to predict litter biomass measured in the field plots. The first dataset used was the 30-m annual net primary production (NPP) product partitioned into plant functional traits (annual grass, perennial grass, shrub,

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and tree) from the Rangeland Analysis Platform (RAP). The second dataset included topographic variables (heat load index -HLI- and site exposure index -SEI-) computed from the USGS 30-m National Elevation Dataset. Through a frequentist model averaging approach (FMA), we determined that the NPP of annual and perennial grasses, as well as HLI and SEI, were important predictors of field-measured litter biomass in 2018, with the model featuring a high overall fit ( $R^2 = 0.61$ ). Model transferability based on extrapolating the FMA predictive relationships from 2018 to the following years provided similar overall fits ( $R^2 \approx 0.5$ ). The fire-free period had a significant effect on the litter biomass accumulation on rangelands within the study site, with greater litter biomass in areas where the fire-free period was <10 years. Our findings suggest that the proposed remote sensing-derived products could be a key instrument to equip rangeland managers with additional information towards fuel management, fire management, and restoration efforts.

## 1. Introduction

Global rangelands represent approximately half of the terrestrial land surface, including grasslands, savannas, and shrub steppe ecosystems (Gilmanov et al., 2004; Wilmer et al., 2020). Besides their support as a food resource for wildlife and livestock (Selemani, 2020), these ecosystems provide key services like carbon sequestration (Henderson et al., 2015), accounting for 30 % of the global carbon pool (Briske et al., 2020), supply of fuelwood (Scheiter et al., 2019), soil conservation (Mousavi et al., 2020), and biodiversity support (Boone et al., 2018).

Among the rangelands of the Great Basin in the western United States (U.S.), the sagebrush (*Artemisia* spp.) steppe is one of the most widely distributed vegetation alliances (Davies et al., 2006; Davies and Bates, 2010). Yet, the sagebrush ecosystem in this region is threatened with surface area losses of approximately 45 % with respect to the historical distribution (Miller et al., 2011). In areas where the soil is warmer and precipitation is scarce, typically associated with lower elevations, wildfire is considered a primary threat to the sagebrush steppe and is associated with the invasion and dominance of exotic annual grasses (Whisenant, 1990; D'Antonio and Vitousek, 1992; Chambers et al., 2014). Under historical fire disturbance regimes, wildfires were relatively infrequent in these landscapes, with fire return intervals ranging from decades to centuries (Mensing et al., 2006; Bukowski and Baker, 2013). In this sense, the non-invaded sagebrush steppe was fuel-limited compared to current plant communities, which may be attributed to less fuel load, reduced fuel continuity, and higher moisture in non-invaded shrub-bunchgrass plant communities (Davies and Nafus, 2013; Reisner et al., 2013).

Today, exotic annual grasses -such as cheatgrass (*Bromus tectorum* Huds.) and medusahead (*Taeniatherum caput-medusae* [L.] Nevski)- promote a grass-fire cycle that perpetuates exotic annual grass encroachment and dominance (Brooks et al., 2004). Consequently, the resilience of native sagebrush and perennial herbaceous species to altered fire disturbance regimes is low, as is its resistance to invasion (Chambers et al., 2014), primarily due to advantageous life history traits of exotic annual grasses. These traits include early germination and seedling emergence from fall to spring (Reynolds et al., 2001), improved growth rates in nutrient-poor soils (James et al., 2011), and a high production rate of viable seeds (Pilliod et al., 2017). The rapid establishment, growth and reproductive capacity of annual grass species enable them to vigorously compete with native perennial species in the early growing season, competitively displacing them (Nasri and Doescher, 1995; Rafferty and Young, 2002; Humphrey and Schupp, 2004).

The summer post-fire environments across the Great Basin, usually with low precipitation, create even more favorable conditions for the recovery of annual grasses as compared to native perennial herbs and shrubs (Smith et al., 2022a). Furthermore, these environments foster the steady degradation of sagebrush ecosystems, particularly after repeated wildfires in the context of global change (Abatzoglou and Kolden, 2011; Brummer et al., 2016). Ultimately, this land cover transition may involve shifts in ecosystem functions and services, such as nutrient cycling and water regulation (Wilcox et al., 2012; Chambers et al., 2014). As annual grass litter accumulates, the microenvironment for the establishment of these species is further improved (Evans and Young, 1970; Facelli and Pickett, 1991; Newingham

et al., 2007; Wolkovich et al., 2009), favoring feedback within the annual grass-fire cycle. The low decomposition rate of litter from annual species favors its accumulation throughout the landscape over several years (Davies and Svejcar, 2008), further increasing the amount, continuity, and flammability of fine fuels (Pilliod et al., 2017). Despite evidence that litter biomass distribution in annual grass-invaded communities can mitigate wildfire risk and inform adaptive management strategies (Stephenson et al., 2022; Smith et al., 2022b), there remains a paucity of spatially-explicit methods. In general, litter biomass is viewed as an understudied component of the fuel complex in the northern Great Basin (Pilliod et al., 2017).

The extensive sagebrush steppe ecosystem is monitored in relatively few local locations with field sampling usually associated with restoration or research purposes. While litter biomass can be accurately estimated in the field at plot scales, it is not feasible for land managers to either capture rangeland spatial heterogeneity (Applestein and Germino, 2022; Kearney et al., 2022) or provide spatially-explicit estimates (Fernández-Guisuraga et al., 2022a) on these vast landscapes. In this context, new remote sensing-derived products at a moderate spatial resolution (~30 m), like the net primary production (NPP) product (Jones et al., 2021) from the Rangeland Analysis Platform (RAP), offer a reliable way to accomplish these goals. The NPP is a direct proxy for litter biomass (Clark et al., 2001a) and RAP provides annual NPP estimates partitioned into plant functional types (PFT). It combines a fractional cover dataset (Allred et al., 2021) with a Landsat-derived NPP model (Robinson et al., 2018) to account for within-pixel mixed land cover in heterogeneous rangelands (Robinson et al., 2019). While RAP provides a litter cover product derived from Landsat surface reflectance and field data (Allred et al., 2021), estimating litter as ground percentage cover may not capture changes in the litter layer thickness and load. That prediction remains unexplored to date and is an important driver of wildfire behavior (Davies et al., 2021a). In addition, topographic/environmental indices, as well as abiotic indices, both computed from geospatial layers -such as the USGS 30 m National Elevation Dataset (Gesch et al., 2002)- have strong potential for mapping species composition and productivity (Iverson et al., 1997; Davies et al., 2007; Davies et al., 2010a), and thus for litter biomass estimation.

The potential of these remote sensing-derived products for mapping litter biomass has not been considered in the rangeland literature, particularly in sagebrush ecosystems of the northern Great Basin threatened by changing fire regimes promoted by invasive grass-fire cycles. In this paper, we (i) evaluate the potential of remote sensing-derived products (NPP partitioned in rangeland plant functional types and topographic indices) to estimate litter biomass in a sagebrush steppe ecosystem in southeastern Oregon (northern Great Basin); (ii) assess the transferability of the predictive relationships between different time periods because of the importance of attaining transferable ecological models (Fernández-Guisuraga et al., 2019); and (iii) link fire regime attributes with the spatial patterns of predicted litter biomass at a landscape scale by extrapolating the model to about 800,000 ha of rangeland ecosystems in southeastern Oregon. We hypothesized that increased litter biomass accumulation driven by annual invasive species would promote the fine-fuel complex and the feedbacks associated with short fire-free periods in rangeland ecosystems (Davies and Svejcar, 2008; Pilliod et al., 2017).

2. Materials and methods

2.1. Study site and field experimental design

The study site was in southeastern Oregon (Malheur County) within the Owyhee watershed (7670 km<sup>2</sup>; Fig. 1). Site elevation ranged from 787 m to 1986 m above sea level, with slopes between 0 % and 150 %. The climate is cold semi-arid (Köppen-Geiger climate classification BSk; Kottek et al., 2006), with mean annual temperature and precipitation, for a 30-year period (1991–2020), of 8.9 °C and 315 mm, respectively (PRISM, 2022). Soils are classified by the harmonized World Soil Database as Haplic Xerosols (Xh) and Luvic Kastanozems (Kl) (Nachtergaele et al., 2010). The study site is dominated by Wyoming big sagebrush (*Artemisia tridentata* Nutt. subsp. *wyomingensis* Beetle & Young) steppe communities invaded by two exotic annual grasses—cheatgrass (*Bromus tectorum* Huds) and

medusahead (*Taeniatherum caput-medusae* [L.] Nevski). Other native shrubs included rubber rabbitbrush (*Ericameria nauseosa* [Pall. ex Pursh] G.L. Nesom & Baird) and antelope bitterbrush (*Purshia tridentata* [Pursh] DC.). The most abundant perennial grasses include Thurber's needlegrass (*Achnatherum thurberianum* [Piper] Barkworth), bluebunch wheatgrass (*Pseudoroegneria spicata* [Pursh] A. Löve), prairie Junegrass (*Koeleria macrantha* [Ledeb.] J.A. Schultes), bottlebrush squirreltail (*Elymus elymoides* [Raf.] Swezey), and Sandberg bluegrass (*Poa secunda* J. Presl).

Thirty-five percent of the study site (around 2700 km<sup>2</sup>) has been affected by one or more wildfires in the last 38-years. Of these burned areas, 68 % feature a fire-free period or time since the last wildfire (TSLF) ≤ 20 years, and 40 % exhibit a TSLF ≤ 10 years. Most of the surface of the study site burned in the last 38 years has been affected by a single wildfire (67 %), while 9.36 % of these areas have been affected by 3 or more wildfires.

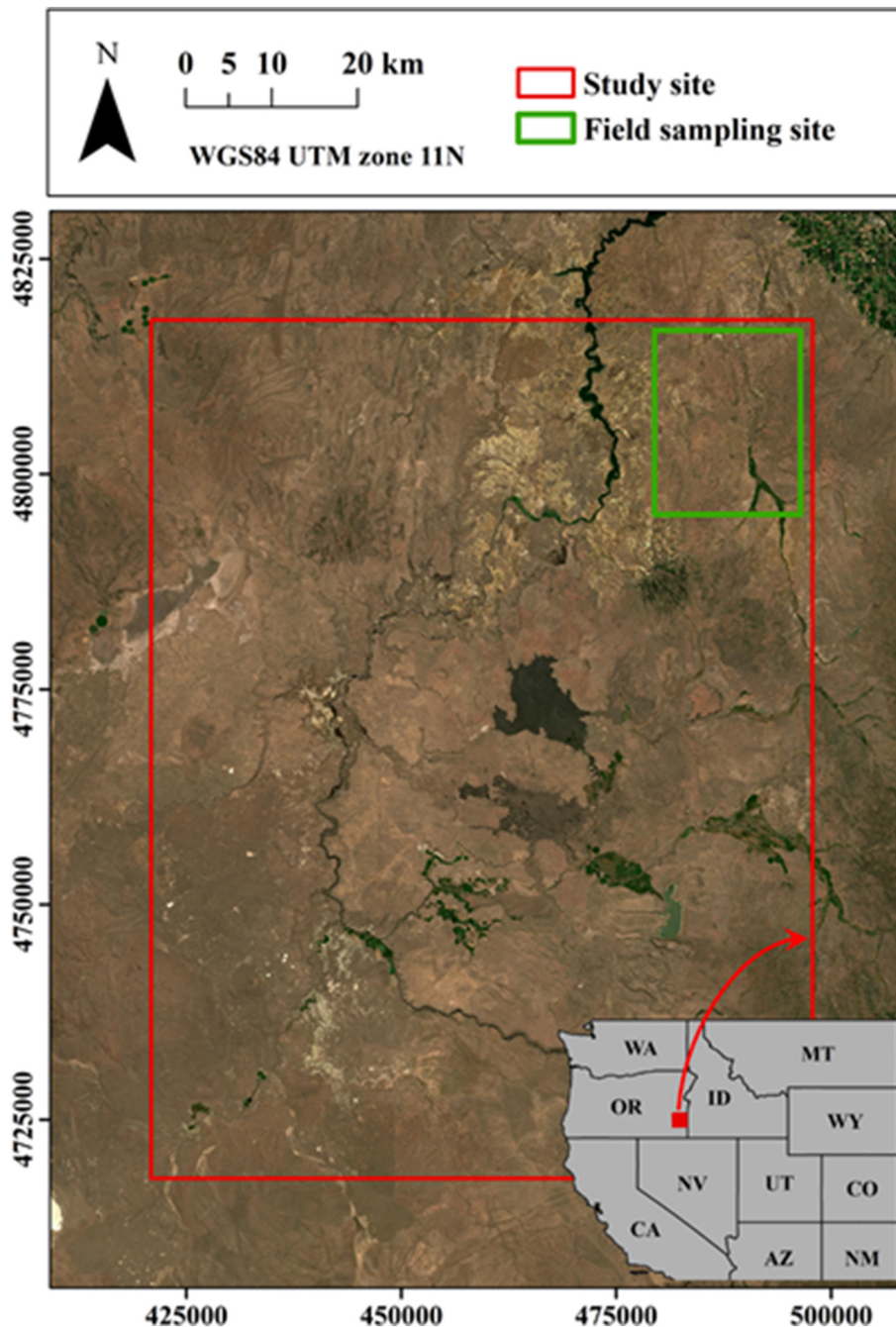


Fig. 1. Location of the study site in southeastern Oregon (OR) within the Owyhee watershed, and area where experimental field plots have been established.



In June 2018, 24 plots of 60 m × 60 m were established in the field within the northeast section of the study site (Fig. 1). The location of the field plots was determined using a sub-centimeter accuracy real-time kinematic (RTK) GPS receiver.

The field plots were surveyed in June 2018, 2019, 2020, and 2021 to collect aboveground litter biomass of shrub and grass species. Within each plot, we established 15 quadrats of 0.5 m × 0.4 m placed at 10-m intervals along three parallel 50 m transects spaced 25 m apart. The detached plant litter accumulated on the soil surface was collected within each quadrat and transferred to the laboratory for analysis. The litter samples were cleaned of remaining soil particles from field collection and then oven dried at 60 °C for 48 h. Dry litter biomass was then weighed and averaged over each 60 m × 60 m plot.

## 2.2. Vegetation, topographic variables, and fire datasets

Two geospatial datasets were used to predict litter biomass measured in the field plots: (i) 30 m annual NPP product from the RAP database; and (ii) topographic variables computed from the USGS 30 m National Elevation Dataset. The 30 m annual NPP product partitioned into PFT (annual grass, perennial grass, shrub, and tree) (Jones et al., 2021), spans the western U.S. since 1986. It was acquired from the RAP database (<https://rangelands.app/>) for each preceding year of field sampling dates (i.e., 2018–2021) because litter usually represents the accumulation of dead plant matter from the previous year (Scurlock et al., 2002; Pilliod et al., 2017). This product is developed from two core datasets: the 16-day Landsat normalized difference vegetation index (NDVI) composites computed from TM, ETM+ and OLI surface reflectance for the continental U.S. (Robinson et al., 2017), and the RAP Cover 3.0 product (Allred et al., 2021). The RAP product uses data from nearly 75,000 vegetation monitoring field plots of U.S. government agencies, together with Landsat Collection 2 TM, ETM+ and OLI surface reflectance, for training a temporal convolutional network and predicting rangeland fractional cover by PFTs. Using both core datasets, NDVI is disaggregated at pixel level to the constituent PFT fractions by linear unmixing models and weighted by the phenology of each PFT in the ecoregions of the conterminous U.S. (Omernik and Griffith, 2014). Finally, a Landsat-adapted MOD17 NPP model (Robinson et al., 2018) and daily GRIDMET data (Abatzoglou, 2013) are used to calculate daily NPP per PFT, which is then aggregated to annual values ( $\text{g C m}^{-2} \text{ yr}^{-1}$ ). We used the coterminous U.S. rangelands product (Reeves and Mitchell, 2011) at 30 m of spatial resolution to mask undesired areas from the annual NPP product (i.e., non-rangeland pixels). This product is based on a geospatial decision framework integrating spatially-explicit data from the Landscape Fire and Resource Management Planning Tools (LANDFIRE) project to delineate rangeland extension on the basis of Natural Resources Inventory (NRI) rangeland definition. The geospatial model resulted in area estimates of 268 Mha.

Two environmental indices were computed from the USGS 30 m (one arc-second) National Elevation Dataset over the continental U.S. and acquired from the Cornell University Geospatial Information Repository (CUGIR; <https://cugir.library.cornell.edu/>). The heat load index (HLI; McCune and Keon, 2002) is computed from the geographic latitude, aspect and slope data layers, and includes values ranging from 0 (warmest southwest facing slopes) to 1 (coolest northeast facing slopes). The site exposure index (SEI; Balice et al., 2000) rescales aspect to a north/south axis and considers the steepness of the slope and represents relative solar exposure ranging from -100 to 100 (coolest to warmest).

Predictor variables were extracted for each field plot of 60 m × 60 m by averaging the predictor values in a regular grid of points (spacing of 6 m) systematically sampled within each plot due to the inclusion of several pixels on the plot (Picotte and Robertson, 2011).

Wildfire perimeters within the study site with an extent  $\geq 405$  ha were acquired from the Monitoring Trends in Burn Severity (MTBS) project (Eidenshink et al., 2007). It provides the extent of U.S. wildfires since 1984, generated by on-screen interpretation and delineation at a scale between 1:24000 and 1:50000 of post-fire Landsat surface reflectance imagery.

It also includes differenced Normalized Burn Ratio (dNBR) and relative differenced Normalized Burn Ratio (RdNBR) images computed from pre- and post-fire Landsat imagery. We characterized the fire regime of the study site from 1984 to 2021 according to the fire-free period, i.e., time since last wildfire in years, by classifying the study area into short (years  $\leq 10$ ), intermediate ( $10 < \text{years} \leq 20$ ) and long (years  $> 20$ ) periods.

## 2.3. Data analyses

Litter biomass measured in the field plots in summer 2018 was modeled on the basis of 30-m annual NPP product by PFTs and topographic variables computed from the USGS 30-m National Elevation Dataset (Table 1), using a frequentist model averaging approach (FMA; Burnham and Anderson, 2002). This modeling approach supports weighted parameter estimates from the candidate models in a full model set resulting from all the possible predictor combinations, instead of using single model estimates (Nakagawa and Freckleton, 2011). In this sense, FMA can robustly handle model parametrization uncertainty, exhibiting better predictive ability than single candidate models through reduced bias (Burnham and Anderson, 2002; Dormann et al., 2018).

We checked for possible multicollinearity issues among the predictors even though FMA is less sensitive than single candidate models to multicollinearity (Freckleton, 2010). For that purpose, we computed bivariate Pearson correlations. All pairs of predictors had low correlation coefficients ( $r_{\text{Pearson}} < |0.7|$ ), and thus multicollinearity issues can be dismissed (Fernández-Guisuraga et al., 2022b). Candidate litter biomass models were fitted using multivariate linear models. We retained in the full model set those models with an  $\Delta$ -value  $< 2$  of the Akaike Information Criterion adjusted to small sample sizes, following the recommendation of Burnham and Anderson (2002), obtaining a top model set to average. The performance of FMA calibrated for 2018 litter field data (internal model validation with observed data) was evaluated from the coefficient of determination ( $R^2$ ) and the root-mean-squared error (RMSE). We checked FMA transferability performance using the above statistics by extrapolating the model to predict 2019, 2020 and 2021 litter field data (external model validation with unobserved data). Finally, the 2018 model object was applied to generate a spatially-explicit litter prediction map for 2021 across the study site using contemporary NPP by PFTs and topographic variables.

We performed a random sampling of 1000 points within the rangelands of the study site, ensuring a minimum distance of 100 m between points, for extracting litter biomass and the corresponding fire-free period, using the 2021 litter biomass map and the MTBS derived map. A one-way ANOVA and subsequent Tukey's HSD test were performed to evaluate litter biomass differences between fire-free period scenarios. Statistical significance was determined at the 0.05 level. Normality and homoscedasticity assumptions were evaluated using Shapiro-Wilk and Levene tests, respectively. All statistical analyses were implemented in R (R Core Team, 2021) using the "MuMIn" (Barton, 2020), "caret" (Kuhn, 2020), "raster" (Hijmans, 2021) and "rgdal" (Bivand et al., 2021) packages.

## 3. Results

The NPP of annual and perennial grasses, as well as the NPP of shrub species, extracted from the 30-m annual NPP product of the RAP database,

**Table 1**  
Litter biomass predictors considered in the frequentist model averaging approach (FMA).

Product	Predictor	Reference
30-m annual NPP product	Annual herbs NPP <sup>a</sup>	Jones et al., 2021
	Perennial herbs NPP <sup>a</sup>	
	Shrub NPP <sup>a</sup>	
	Tree NPP <sup>a</sup>	
Topographic variables	Heat load index (HLI)	McCune and Keon, 2002
	Site exposure index (SEI)	Balice et al., 2000

<sup>a</sup> Predictor variables with a one-year time lag.

**Table 2**

Average litter biomass model output for 2018 data computed from the frequentist model averaging (FMA) approach. HLI = heat load index; SEI = site exposure index.

Response variable	Parameter	Estimate	Standard error	z value	p-value
Litter biomass	(Intercept)	9.576E+03	9.491E+03	1.001	0.317
	HLI	-3.466E+04	8.513E+03	3.799	<0.001
	SEI	-1.777E+02	4.862E+01	3.405	<0.001
	Annual herbs NPP	2.822E+00	7.434E-01	3.542	<0.001
	Perennial herbs NPP	-4.422E+00	1.025E+00	4.061	<0.001
	Shrub NPP	-4.826E+01	3.146E+01	1.425	0.154

were selected as important variables in the litter biomass averaged model calibrated for 2018 data in the rangelands through the FMA approach. Specifically, both grass NPP variables featured a high significance in the model (*p-values* < 0.001). Conversely, the NPP of tree species was not selected in the averaged model. The topographic variables computed from the USGS 30-m National Elevation Dataset, HLI and SEI, also featured a high significance (*p-values* < 0.001). All the predictors exhibited an inverse relationship with litter biomass in the rangelands, except for the NPP of annual grass species, which featured a direct relationship (Table 2).

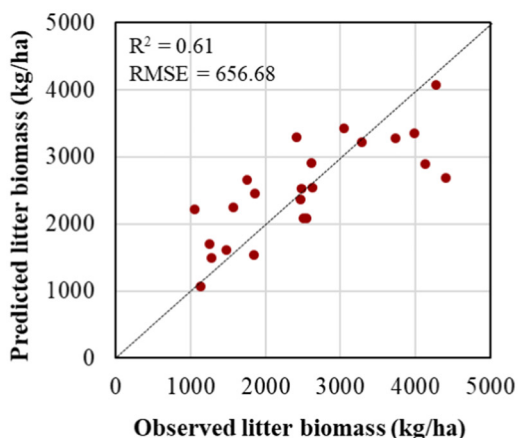
The litter biomass model for 2018 data, corresponding to an internal model validation scenario with observed data, featured a significant, high

overall fit ( $R^2 = 0.61$ ) and predictive capacity ( $RMSE = 657 \text{ kg ha}^{-1}$ ). Model predictions were closely tailored to the 1:1 line (Fig. 2). Model transferability based on the extrapolation of the FMA predictive relationships from 2018 to the following years (2019–2021; external model validation scenario with unobserved data) provided encouraging results. The coefficient of determination in all cases ranged around 0.5, which implies only a slight reduction in the overall fit with respect to the internal model validation ( $R^2 = -0.1$ ).

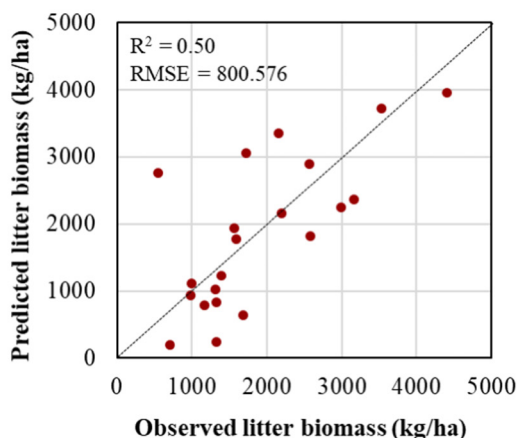
A spatially-explicit prediction map of litter biomass for 2021 was computed from FMA predictions applied to NPP by PFTs and topographic variables (Fig. 3). The spatial distribution pattern of litter biomass largely corresponded to that of annual grass species NPP for the previous year (Figure SM1 of the Supplementary Material), which featured a direct relationship with litter biomass in the FMA approach.

The fire-free period had a significant effect on the litter biomass (*F-value* = 3.82; *p-value* < 0.01), being significantly higher in areas with TSLF lower than 10-years (short fire-free period) (Fig. 4; *p-values* < 0.05). In fact, annual grass species exhibited a greater cover in short fire-free period areas, as evidenced by a query to the RAP cover product (Figure SM2 of the Supplementary Material), matching the behavior of litter spatial variability in the site (Fig. 3) and FMA outputs. Remarkably, none of the PFT cover variables of RAP product differed significantly between fire-free periods (Figure SM2 of the Supplementary Material), in contrast to litter biomass.

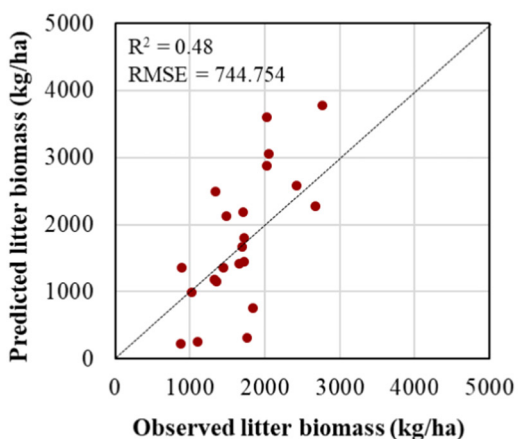
**A) 2018 internal model validation**



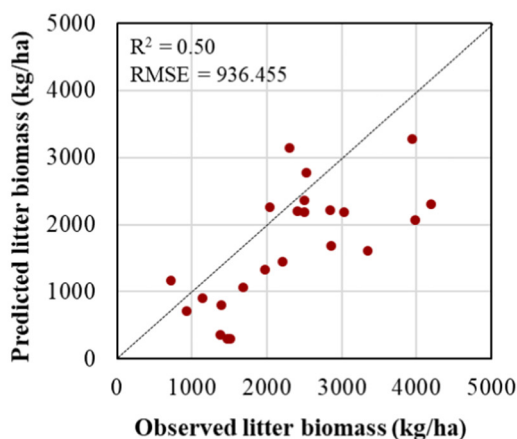
**B) 2019 model extrapolation**



**C) 2020 model extrapolation**



**D) 2021 model extrapolation**



**Fig. 2.** Relationship between observed and predicted litter biomass for 2018 data (internal model validation) and for the following years (model extrapolation) through the frequentist model averaging (FMA) approach. All the relationships were significant (*p-values* < 0.001). The dotted black line represents the 1:1 line.

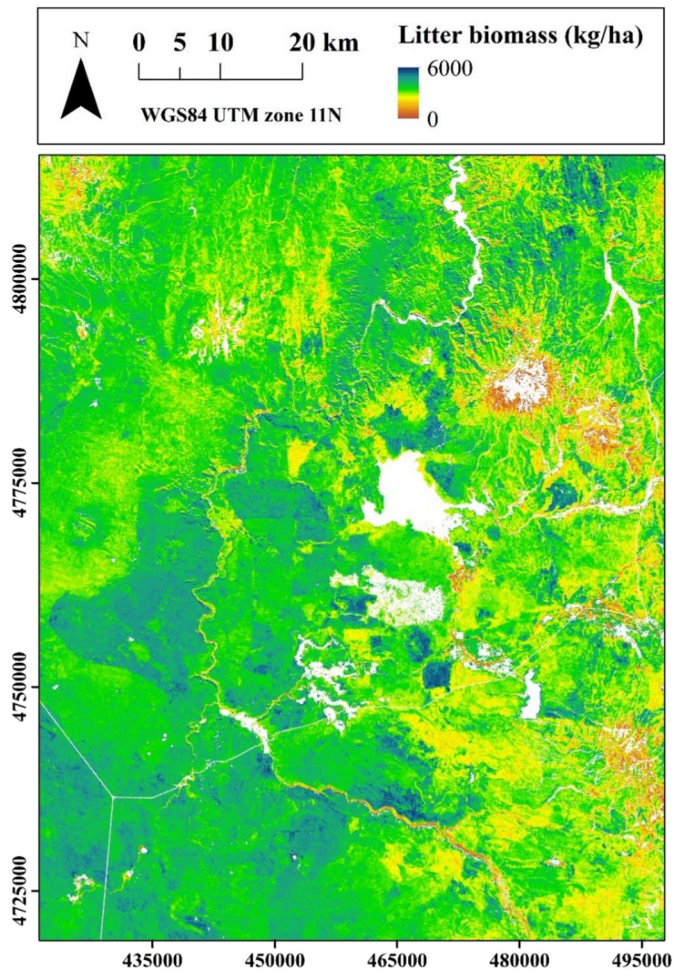


Fig. 3. Spatially-explicit prediction map of litter biomass by the frequentist model averaging (FMA) approach for 2021. Blank regions within the study site correspond to non-rangeland areas.

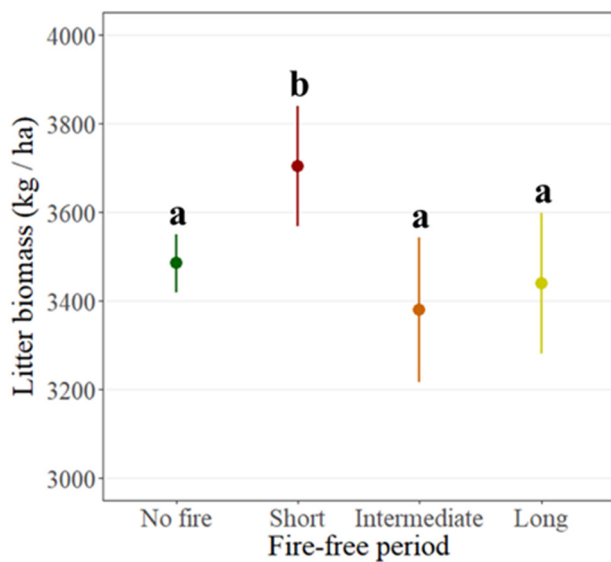


Fig. 4. Predicted effect (mean  $\pm$  95 % confidence intervals) of fire-free period on litter biomass of the rangelands in the study site. Lowercase letters denote significant differences at the 0.05 level.

#### 4. Discussion

Assuming an ecosystem steady state, annual net carbon photosynthetic uptake by plants is balanced by carbon return to the atmosphere through decomposition of soil organic matter and litter (i.e., soil respiration) (Verlinden et al., 2013). Additionally, litter production must be approximately equal to aboveground and belowground NPP at the end of the growing season if soil respiration is dominated by litter decomposition (Matthews, 1997; Chou et al., 2008). Thus, NPP is a direct proxy of litter production, which explains the significant relationship between the spatial variability of litter biomass in sagebrush steppe rangelands and annual NPP partitioned into PFTs from RAP. In fact, litter biomass usually corresponds to the largest fraction of operational estimates of actual NPP in the field (Clark et al., 2001b), particularly in rangeland ecosystems (Luo et al., 2002).

Remote sensing-based NPP products have a stronger physical basis than the simple use of spectral vegetation indices in empirical models (Running et al., 2004), traditionally used for monitoring rangeland ecosystems (Washington-Allen et al., 2006). Contrary to spectral indices, NPP products are not based on site-specific empirical relationships between remote sensing parameters and grassland production traits, but on well-established and transferable models involving light-use efficiency theory (Reinermann et al., 2020). In addition, the annual NPP product from RAP accounts for the spatial heterogeneity of rangeland productivity at sub-pixel scales (Robinson et al., 2019), which may include several PFT with different functional and spectral responses. Annual and perennial grass species feature a completely distinct NPP pattern throughout the seasons in the northern Great Basin because of differences in their life history traits (Alba et al., 2015). In this context, NPP products based on categorical land cover maps would lead to the simplification of heterogeneous land surfaces, limiting the ability of predictive models to understand ecological processes and inform land management (Jones et al., 2018). For example, our results revealed that the relationship of annual and perennial grasses NPP with litter biomass accumulation followed an opposite pattern, which agrees with previous field-based research in the northern Great Basin (e.g., Goergen et al., 2011; Parkinson et al., 2013), and illustrates that accumulation of litter biomass is promoted by the life history traits of annual invasive grasses. Spatially-explicit products generated from NPP models that do not account for sub-pixel dynamics of specific PFTs would therefore be unrealistic.

Topographic-related variables computed from the USGS 30-m National Elevation Dataset (i.e., HLI and SEI indices) represent a gradient of site temperature, available moisture, and potential evapotranspiration over the landscape (Johnson and Miller, 2006). Thus, the influence of direct incident solar radiation on plant productivity through controls on vegetation moisture stress and plant growing conditions in the rangelands (Reeves et al., 2018) could explain the correlation between the spatial variability of litter biomass and topographic indices related to landscape configuration of the rangelands. Previous research in Wyoming big sagebrush steppe communities of southeastern Oregon and northern Nevada also reported the importance of topographic-related variables in driving vegetation cover and productivity of several PFTs (Passey et al., 1982; Davies et al., 2007; Mahood and Balch, 2019).

The modeling performance in our study is not comparable to previous research since (i) to date, mapping of litter biomass has not been considered in rangeland ecosystems, and (ii) the application of remote sensing-based techniques with a physical basis for estimating biomass production remains underrepresented in the rangeland literature (Reinermann et al., 2020). In addition, previous research regarding biomass production in rangelands often lacks temporal replication for validation purposes with unobserved data (Kearney et al., 2022). In our study, model transferability based on temporal extrapolation of the predictive relationships exhibited similar performance to that of the internal model validation with observed data. This may be related to the (i) reduced bias and increased predictive performance of the FMA modeling approach (Tsalyuk et al., 2017; Dormann et al., 2018), and (ii) the physical nature of the annual NPP product from RAP, which improves model performance (Reinermann et al., 2020).



Despite litter biomass being a relatively unexplored component of the fuel complex in the northern Great Basin (Pilliod et al., 2017), the present study provided spatially-explicit evidence to support previous assumptions (Davies and Nafus, 2013; Davies et al., 2021a) that high biomass per unit area and early senescence of annual species in grass-invaded communities leads to massive horizontal fuel amount and continuity because of litter biomass accumulation. In fact, our models revealed that litter biomass, favored by the presence of annual invasive grasses, was significantly higher in rangelands featuring short fire-free periods (TSLF lower than 10-years). Bradley et al. (2018) found that about 75 % of the wildfires in cheatgrass-dominated landscapes of the Great Basin were human-caused, and these landscapes are strongly associated with anthropic infrastructures that act as a vector for the spread of invasive species. Also, litter accumulation from grasses promotes the establishment of invasive grass species (Wolkovich et al., 2009), and sustains the fine fuel complex (Davies and Nafus, 2013). These factors could explain the feedbacks within the invasive annual grass-fire cycle and the evidenced shorter fire-free periods. In line with our results, Smith et al. (2022b) demonstrated that time-lagged, grass fuel biomass accumulation was a strong predictor of wildfire probability in the Great Basin from 1988 to 2019. However, previous research found no association between the number of fires from 1980 to 2014 in the whole Great Basin ecoregion and litter cover (Pilliod et al., 2017). This may be due to a mismatch between the extent of the study sites, or by litter cover estimates that may not capture the variability in the actual fine fuel depth and load and wildfire behavior (Davies et al., 2021a). In addition, our results demonstrated that none of the PFT cover variables of RAP product differed significantly between fire-free period scenarios, in line with the results of Pilliod et al. (2017). Again, vegetation cover by PFT may not be an adequate proxy for wildfire behavior.

The findings of our study may have broad implications for the management of sagebrush steppe communities invaded by exotic annual grasses in the northern Great Basin to minimize the prevailing grass-fire cycle. Within this region, repeated livestock grazing during the growing season can promote invasive annual grass proliferation (Mack and Thompson, 1982; Chambers et al., 2007; Chambers et al., 2014). Yet, moderate grazing in the region has little impact on sagebrush steppe plant communities when alternated between the growing season and the dormant season in the fall and winter when perennial bunchgrasses are less susceptible to grazing. A long-term grazing exclusion study, spanning >50 years, highlighted the effectiveness of moderate grazing to reduce invasive annual grass proliferation and promote perennial bunchgrasses after fire (Davies et al., 2010b). While these results were obtained with a limited sample size ( $n = 3$ ), recent work highlighted that moderate livestock grazing in the dormant season before fire can promote perennial bunchgrasses and reduce invasive annual grass biomass post-fire (Davies et al., 2021b). Based on our results, land managers may consider fall-winter grazing treatments -where deemed appropriate- aimed at reducing the litter production by annual grass species in the previous year's growing season, instead of attempting to reduce the cover of these species (Perryman et al., 2018).

The proposed remote sensing-derived products may be a key instrument to meet this objective and prioritize areas for the maintenance of fuel breaks, seeding of perennial grass species and fall-winter grazing, which could be appropriate actions for reducing the risk of frequent wildfires in sagebrush steppe communities with a high fine fuel load (Redmond et al., 2013; Pilliod et al., 2017; Davies et al., 2021a).

## 5. Conclusions

Our results demonstrated that the annual NPP product from the RAP database was able to account for productivity by PFTs and litter accumulation at sub-pixel scales. Also, topographic variables, computed from the National Elevation Dataset, provided additional information related to the spatial variability of litter biomass across rangelands, including connection with temperature, available moisture, and potential evapotranspiration over the landscape. The generalization ability of NPP models, related to their high physical basis, enabled an accurate time extrapolation of litter

biomass predictive relationships and thus offer high potential for evaluating wildfire risk and informing adaptive management strategies. According to our expectations, litter biomass accumulation, favored by the presence of annual invasive and perennial grasses, explained feedbacks within the grass-fire cycle that promote short fire-free periods in sagebrush steppe rangeland communities. Annual invasive grasses are currently increasing across Great Basin rangelands, which makes their management important.

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## CRedit authorship contribution statement

**José Manuel Fernández-Guisuraga:** Conceptualization, Methodology, Formal analysis, Investigation, Writing – original draft. **Leonor Calvo:** Conceptualization, Methodology, Writing – review & editing, Supervision. **Paulo M. Fernandes:** Conceptualization, Formal analysis, Writing – review & editing, Supervision. **April Hulet:** Methodology, Investigation, Writing – review & editing. **Barry Perryman:** Methodology, Investigation, Writing – review & editing. **Brad Schultz:** Methodology, Investigation, Writing – review & editing. **K. Scott Jensen:** Methodology, Investigation, Writing – review & editing. **Josh Enterkine:** Methodology, Investigation, Writing – review & editing. **Chad S. Boyd:** Methodology, Investigation, Formal analysis, Writing – review & editing. **Kirk W. Davies:** Methodology, Investigation, Writing – review & editing. **Dustin D. Johnson:** Methodology, Investigation, Writing – review & editing. **Katherine Willstein:** Methodology, Investigation, Writing – review & editing. **William J. Price:** Methodology, Investigation, Formal analysis, Writing – review & editing. **Sergio A. Arispe:** Conceptualization, Investigation, Writing – review & editing, Supervision, Project administration, Funding acquisition.

## Data availability

Data will be made available on request.

## Declaration of competing interest

The authors declare that they have no known competing financial interests or personal relationships that could have appeared to influence the work reported in this paper.

## Appendix A. Supplementary data

Supplementary data to this article can be found online at <https://doi.org/10.1016/j.scitotenv.2022.160634>.

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