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RESEARCH ARTICLE

Not all seed transfer zones are created equal: using fire history to identify seed needs in the Cold Deserts of the western United States

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Restoration planning requires a reliable seed supply, yet many projects occur in response to unplanned events. Identifying regions of greater disturbance risk could efficiently guide seed procurement. Using fire in U.S. Cold Deserts as an example, we demonstrate how historic disturbance can inform seed production choices. We compared differences in fire frequency, area burned, and percent of area burned among different management areas, identifying regions of particular need. We also present a case study focused on fire occurrence within important wildlife habitat, specifically looking at the greater sage-grouse priority areas for conservation (PACs) within the Northern Basin and Range ecoregion. We used geospatial seed transfer zones as our focal management areas. We broadly considered generalized provisional seed transfer zones, created using climate and stratified by ecoregion, but also present results for empirical seed transfer zones, based on species-specific research, as part of our case study. Historic fire occurrence was effective for prioritizing seed transfer zones: 23 of 132 provisional seed transfer zones burned every year, and, within each ecoregion, two provisional seed transfer zones comprised ≧50% of the total area burned across all years. Fire occurrence within PACs largely reflected the seed transfer zone priorities found for the ecoregion as a whole. Our results demonstrate that historic disturbance can be used to identify regions that encounter regular or large disturbance. This information can then be used to guide seed production, purchase, and storage, create more certainty for growers and managers, and ultimately increase restoration success.

Key words: fire, native plant, planning, restoration, seed needs, seed transfer zones

Implications for Practice

- Past disturbance can be used to forecast future seed needs, providing useful guidance for native seed planning, sourcing, and seed procurement decisions.
- Geospatial data on disturbances (here, historic fire occurrence, but also flood, drought, etc.) can be used to identify regions that are likely to be of greatest need for seed conservation and collection.
- Prioritizing the largest, most frequently disturbed regions for seed production is likely to be an effective strategy for seed producers, yet smaller, highly threatened or valuable regions also warrant special attention and seed development.

Introduction

Predicting seed needs for restoration is a worldwide challenge (Breed et al. 2018), and availability of desired seeds is a common limitation for restoration projects (Broadhurst et al. 2008; Harrison et al. 2020). Whether wild-collected or agriculturally produced, the complexity of plant life histories requires advanced planning to ensure that seeds are available when they are needed (Erickson & Halford 2020; Pedrini et al. 2020). When restoration projects occur in response to planned disturbances, proactive management can ensure that seeds are stored and available when needed, by conserving topsoil and associated seed banks (Golos et al. 2016) or collecting and producing seeds in anticipation of use (Erickson & Halford 2020).

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However, many restoration projects are conducted in response to disturbance events, such as hurricanes, floods, or fires (Michener 1997; BLM 2007). The uncertain timing, size, and location of this type of restoration make ensuring seed availability a challenge for such projects. While the decision to restore a particular area is affected by many societal and ecological factors (Gann et al. 2019), a broadscale view of geographic areas most likely to be disturbed could help reduce, if not eliminate, uncertainty. Specifically, by using historic information and prediction of future events to forecast needs, it may be possible to proactively ensure that required seed resources are available for the areas most likely to need them (Harrison et al. 2020).

Wildland fire is an unplanned disturbance that motivates restoration projects in many regions around the world. With climate change and other anthropogenic disturbances, even fire-adapted ecosystems may require active restoration to return to desirable states (Fulé 2008). For many plant communities, the question is not whether they will burn, but when (Pitman et al. 2007; Liu & Wimberly 2016), and what type of management may be needed to maintain desired successional trajectories (Ott et al. 2022). Sagebrush steppe shrubland, the predominant vegetation type in the western U.S. Cold Deserts, is made up of plant communities that are vulnerable and maladapted to increased wildfire (Winward 1985). Over 40% of the sagebrush steppe Cold Desert has significant cover of invasive annual grasses (Larson & Tuor 2021), such as cheatgrass (*Bromus tectorum*), which drive fire cycles and outcompete native vegetation under higher disturbance regimes (D'Antonio & Vitousek 1992; Pilliod et al. 2017*a*). Depending on site conditions, wildfire in invaded areas is between 2.5 and 22 times more frequent than it was prior to European settlement (Whisenant 1990; Balch et al. 2013). Once covering more than 600,000 km^2, 60–90% of the sagebrush steppe has been lost, fragmented, or degraded (Noss et al. 1995; Knick et al. 2003). Due to these disturbances, the sagebrush steppe ecosystem is facing a loss in native plant species and genetic diversity (McArthur & Fairbanks 2001; Mahood & Balch 2019), resulting in reduced ecosystem services such as water and soil retention and plant productivity (Kachergis et al. 2011; Nichols et al. 2021). These changes also threaten animal populations, including species of conservation concern, such as the greater sage-grouse (*Centrocercus urophasianus*) (Knick et al. 2003).

To counteract the effects of wildfire and exotic plant invasions, land management agencies, such as the U.S. Department of Interior, Bureau of Land Management (BLM), commonly seed a subset of land after fire in the sagebrush steppe. The BLM has seeded after fire since the 1940s, with significant increases in yearly seeding occurring in the 1980s and 2000s in response to increasing fire frequencies (Pilliod et al. 2017*b*). Between 2015 and 2020, the BLM spent $222 million on emergency stabilization and burned area rehabilitation, including $67 million on seed procurement of both native and non-native species, most of which was used in the sagebrush steppe (BLM 2015–2020). Nevertheless, short-term targets for soil stabilization and annual grass suppression have met with mixed success (Knutson et al. 2014), and attempts at establishing diverse native plant communities that support wildlife populations of conservation concern have generally been unsuccessful (Arkle et al. 2014). In addition to the challenges of restoring heavily invaded arid sites, these outcomes are influenced by the prominent use of non-native Eurasian bunchgrasses, which establish well and can outcompete annual grasses (Ott et al. 2019), but interfere with native species recovery (Nafus et al. 2015; Williams et al. 2017; Ott et al. 2022). However, even when native species are used, which is occurring with increasing frequency (Pilliod et al. 2017*b*), native seed sources may fail to establish and thrive due in part to a mismatch between the source environment, where the population has been subject to natural selection, and the environment at the restoration site (McKay et al. 2005). This may be especially true in sagebrush steppe ecosystems, where plant populations are often adapted to local environments (Baughman et al. 2019).

Several nations have policies and strategies that call for the use of seed transfer zones to guide the use of native plant seed sources for use in restoration (e.g. Prasse et al. 2010). The National Seed Strategy for Rehabilitation and Restoration (PCA 2015) provides this guidance in the United States, and state and regional frameworks have been developed for the sagebrush steppe ecosystem (e.g. NNSP 2020). Seed transfer zones are designed to limit the chances that seed sources are maladapted to restoration site conditions and can help identify populations important for genetic conservation (Kilkenny 2015; Massatti et al. 2018). Ideally, species-specific empirical seed transfer zones would be used for each species within a seed mix (Johnson et al. 2010). Empirical seed transfer zones are being developed for "workhorse" restoration species in the sagebrush steppe, such as bluebunch wheatgrass (*Pseudoroegneria spicata*) (St. Clair et al. 2013) and sagebrush (Richardson & Chaney 2018). However, given the number of species that are important to ecosystem resiliency in the sagebrush steppe and other ecosystems (Dumroese et al. 2015), developing empirical seed transfer zones for every species of interest is impractical. Generalized provisional seed transfer zones have been developed for use in restoration seed sourcing in the United States when empirical seed transfer zones are not available (Bower et al. 2014). These provisional seed transfer zones are based on two climate variables, winter minimum temperature and annual heat moisture index, that are adaptively important across plant taxa, and can be further stratified by ecoregions to further minimize instances of maladaptation (Omernik 1987; Bower et al. 2014).

The topographic and climatic complexity of the sagebrush steppe generates a relatively high number of provisional seed transfer zones within relatively small geographic areas. This creates a helpful framework to plan for seed needs, and can create opportunities to make the seed procurement process more efficient for land managers, seed collectors, and seed producers (Taylor et al. 2018). The sagebrush steppe has low productivity and, while wildland collection is possible for some species (e.g. widespread and abundant shrubs like *Artemisia tridentata*), for many species, wildland seed cannot be collected in sufficient quantities to fulfill restoration needs. Therefore, seed must be increased from initial collections using agricultural production methods (Pedrini et al. 2020). This process takes planning, funding, and logistic coordination over multiple years and reduces flexibility in matching genetically appropriate seed to unplanned disturbance events and restoration projects (Supplement S1). The majority of plant materials used in sagebrush steppe restoration were developed through rangeland improvement programs, some beginning in the 1930s, that maximized forage production (Vallentine 1989) over genetic appropriateness or ecological compatibility with local plant communities (Leger & Baughman 2015). Given the practical constraints of developing and producing genetically appropriate plant materials for post-fire restoration in the sagebrush steppe, we need to develop ways to prioritize seed production efforts.

Existing information regarding fire history and risk in the sagebrush steppe ecosystem can be used to prioritize seed needs. While fire forecasting models are improving (e.g. Krawchuk et al. 2009), we have now amassed sufficient fire history for this region to reveal patterns that can potentially be used as an indication of likely seed needs for the future (Fig. 1). This approach, where past disturbance is used to forecast future need, could be applied across management units, including seed transfer zones. Knowledge of likely seed needs would allow for the prioritization of seed collections for long-term genetic conservation and seed production for use in post-fire restoration. This could create reliable demand for seed growers, increase availability of desirable seed, and lead to improved post-fire restoration outcomes in the western United States.

Here, we consider fire history between 2000 and 2019 in the western U.S. Cold Deserts, presenting an example of how seed needs can be prioritized in an imperiled landscape. We use three components to assess the occurrence of fire in seed transfer zones within Cold Deserts and wildlife management areas: the frequency of fire (measured as the number of years an area has burned in our 20-year timeframe), the total area burned, and the percent of area burned (to identify potentially imperiled seed transfer zones). We first consider fire occurrence within provisional seed transfer zones, answering the following question:

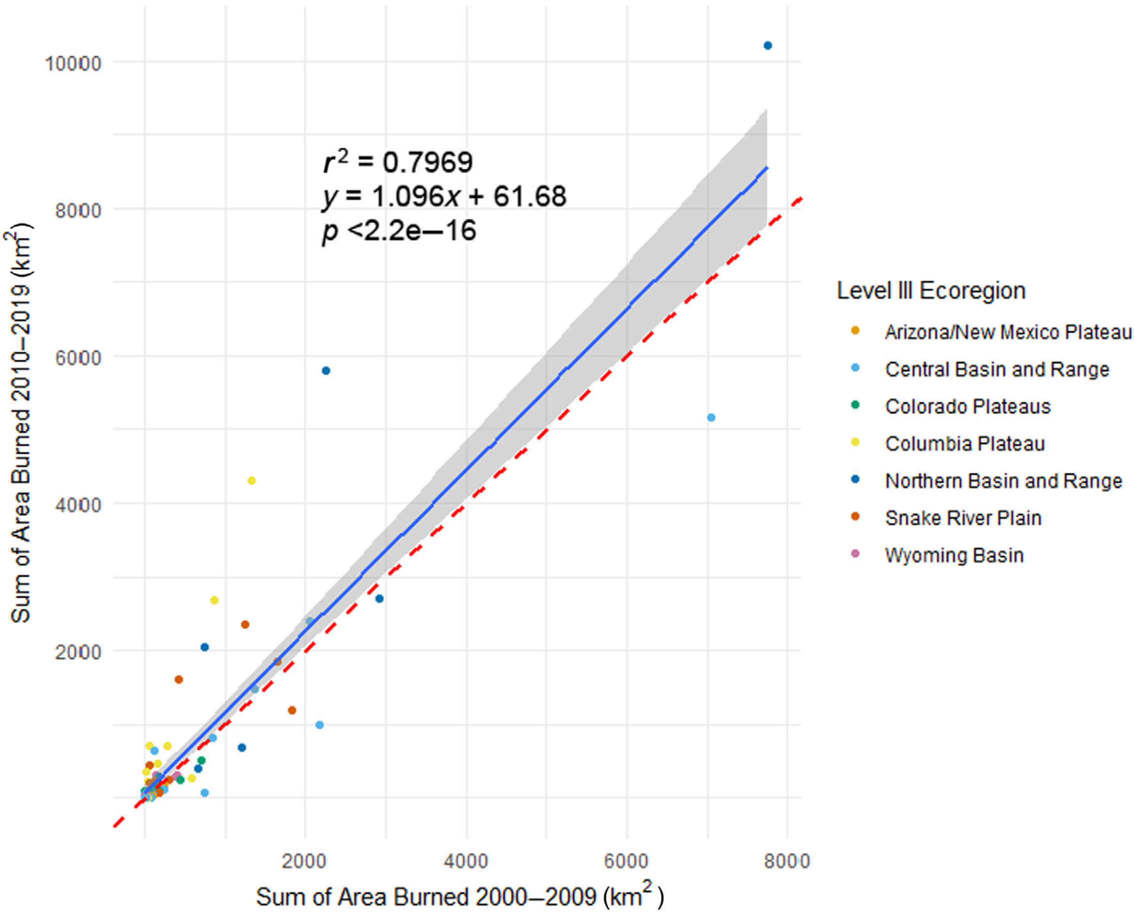

Figure 1. Results for each provisional seed transfer zone within each EPA level III ecoregion, comparing the of the sum of the area burned from 2000 to 2009 with the sum of the area burned from 2010 to 2019. The red dashed line represents the trendline if there were equal levels of burning within the two time periods, with points above the dashed line representing areas experiencing more burning than in the past. The actual trendline, in blue, represents the pattern of burning across all provisional seed transfer zones, with 95% CI in gray, showing that past levels of burning are generally predictive of future levels of burning. The p value reported above refers to the slope of the linear regression and the root mean square error for the model fit of the relationship between the area burned 2000–2009 (km^2) and the area burned 2010–2019 (km^2) is 608.

(1) What are the patterns of wildfire occurrence within Cold Desert ecoregions of the western United States, with a focus on provisional seed transfer zones?

Burned areas represent potential restoration opportunities, and while not every area that burns is seeded, identifying patterns of disturbance in specific management units, such as seed transfer zones, can provide information on the relative disturbance level, which can inform restoration planning.

Next, we present a case study demonstrating how this information could be used to prioritize seed development within wildlife habitat of particular value, which may be more likely to receive post-fire restoration. We focus on the greater sage-grouse priority areas for conservation (PACs), a designation of management units identified in the 2013 greater sage-grouse Conservation Objectives Team Report (USFWS 2013), within the Northern Basin and Range ecoregion, one of the most burned regions for this species of conservation concern. For this analysis, in addition to provisional seed transfer zones, we use empirical seed transfer zones that have been developed for two foundational species, bluebunch wheatgrass (*P. spicata* [Pursh] A. Löve) and Wyoming and basin big sagebrush (*A. tridentata* Nutt. ssp. *wyomingensis* Beetle & Young and *tridentata*). In this case study, we address the following question:

(2) What are the patterns of wildfire occurrence in a wildlife management area within an imperiled ecoregion?

We address this second question for greater sage-grouse PACs in the Northern Basin and Range ecoregion, considering both provisional seed transfer zones and empirical seed transfer zones for two key plant species, asking how much overlap there is between broad wildfire patterns and the needs of priority wildlife.

Based on our observations of wildfire occurrence in the Great Basin, we expected that fires would be concentrated in particular provisional seed transfer zones, rather than equally spread across Cold Deserts. Further, we expected that we would be able to identify priority seed transfer zones for seed needs for our focal species, which would help guide seed development. Finally, within the Northern Basin and Range ecoregion, we expected that there would be overlap between the priority seed transfer zones identified in question 1 and the occurrence of fire within a priority wildlife management area, which would indicate that information gleaned from broad fire patterns is also relevant for habitat needs. Through this work, we aim to illustrate how to identify seed collection locations that are likely to be needed for restoration, encompassing multiple species and habitat management goals.

Methods

Study Area

Environmental Protection Agency (EPA) defined ecoregions are areas that have similar biotic, abiotic, terrestrial, and aquatic ecosystem components and are designed to provide a meaningful spatial framework for assessing ecosystem management strategies (Omernik 1987). Our study focuses on the EPA level II ecoregion defined as Cold Desert, which is composed of seven EPA level III ecoregions (Table 1). These areas are generally defined as having hot, dry summers and cold or mild winters, with annual average precipitation that ranges from 4 mm in lower elevation basins to as much as 1,000 mm at higher elevations (Table 1). Vegetation is made up primarily of arid sagebrush steppe, grassland, or salt desert scrub plant communities.

Geospatial Data

All geospatial data processing was performed in ArcMap 10.5.1 (ESRI 2016). We used fire perimeters, representing the boundaries of the spatial area burned, from the Geospatial Multi-Agency Coordination Wildfire Application (GeoMac) to represent the areas burned within our analyses; GeoMac data are based on annual fire data and contain shapefiles with perimeters for individual fires recorded as separate features. Fire perimeters were downloaded for each fire year (2000–2019, accessed 9 Mar 2020), and the dissolve function (data management toolbox, generalization toolset) was used to aggregate all individual fire features into a single feature representing fires for a particular year. We used data from the Protected Areas Database of the United States to verify the proportion of burned area occurring on public lands, and thus likely to be a candidate for seeding (USGS 2022). Based on these data, we found that 95.9% of the area burned within our dataset occurred on land owned by federal, state, county, city, tribal, or non-governmental organizations; much of the remaining 4.1% of land existed within areas of checkerboard land ownership, where burned areas within private lands would likely be seeded along with adjacent public lands. We note here that our geospatial data for the ecoregion wide analyses did not exclude areas of impervious surfaces or unvegetated areas.

Geospatial data for provisional seed transfer zones for the United States and empirical seed transfer zones for *Artemisia tridentata* (ssp. *wyomingensis* and *tridentata*) and *Pseudoroegneria spicata* were obtained from the Western Wildland Environmental Threat Assessment Center (WWETAC) website (https://www.fs.fed.us/wwetac/threat-map/TRMSeedZoneData.php). Bower et al. (2014) delineated discrete provisional seed transfer zones for the continental United States using a combination of winter minimum temperature and aridity, measured as the annual heat:moisture index (AH:M), with larger numbers equating to higher aridity, and calculated as (MAT + 15)/MAP, where MAT is the mean annual temperature (°C) and MAP is the mean annual precipitation (m).

We further stratified the original 64 provisional seed transfer zones created by Bower, using EPA level III ecoregions, to create a total of 132 provisional seed transfer zones considered in our analyses. Richardson and Chaney (2018) created empirical seed transfer zones for *A. tridentata* using flowering phenology and survival from common gardens and climate from seed source locations to identify discrete seed transfer zones using a numeric naming convention. St. Clair et al. (2013) described empirical seed transfer zones for *P. spicata* using size, flowering phenology, and leaf width from common gardens and climate

Table 1. Descriptions of Omernik level III ecoregional characteristics within Cold Deserts as summarized from the U.S. Environmental Protection Agency level III ecoregion descriptions prepared by the Commission for Environmental Cooperation; MAT, mean annual temperature; MAP, mean annual precipitation.

Ecoregion	*Location/elevation*	*Dominant vegetation*	*Climate*
Columbia Plateau	Central and southeastern Washington, north-central Oregon, and a small part of northwestern Idaho; elevation 60–1,500 m	Sagebrush steppe and grassland	Hot, dry summers; cold winters; MAT 7–12°C, frost-free period 70–190 days; MAP 334 mm, range: 150–600 mm
Wyoming Basin	Central and western Wyoming with small extensions into Montana, Colorado, Utah, and Idaho; elevation 1,220–2,850 m	Arid grasslands and shrublands with some pinyon-juniper woodland	Warm-hot summers; cold winters; MAT 0–8°C, frost-free period 30–130 days; MAP 296 mm, range: 130–500 mm
Northern Basin and Range	Northern Great Basin, including: southeast Oregon, northern Nevada, southern Idaho, and small portion of northern Utah; elevation 800–3,000 m	Low elevations: sagebrush steppe and cool season grasses, high elevations: douglas fir and aspen	Hot summers; cold winters; MAT 5–9°C, frost-free period 30–140 d; MAP 351 mm, range: 150–1,000 mm
Snake River Plain	Southern Idaho; elevation 640–1,980 m	Sagebrush steppe	Warm summers; cold winters; MAT 6–10°C, frost-free period 50–170 d; MAP 316 mm, range: 110–650 mm
Central Basin and Range	Central Great Basin, including: Nevada, western Utah, and small extensions into California and southern Idaho; elevation 1,020–4,000 m	Sagebrush and saltbush-greasewood vegetation with some pinyon-juniper and douglas fir and aspen	Hot summers; mild winters; MAT 2–14°C, frost-free period 15–200 days; MAP 277 mm, range: 4–1,000 mm
Colorado Plateaus	Eastern and southern Utah, western Colorado, and small portions of northern Arizona and northwestern New Mexico; elevation 900–3,000 m	Blackbrush-saltbush, sagebrush, and pinyon-juniper	Hot, dry summers; cold, dry winters; MAT 5–15°C, frost-free period 50–220 days; MAP 298 mm, range: 130–800 mm
Arizona/New Mexico Plateau	Northern Arizona, northwestern New Mexico, and southern Colorado; elevation 1,370–3,000 m	Saltbush-greasewood vegetation, sagebrush, and pinyon-juniper	Hot, dry summers; cold, dry winters; MAT 5–16°C, frost-free period 50–250 days; MAP 293 mm, range: 125–380 mm

from seed source locations to delineate discrete seed transfer zones using an alpha-numeric naming convention.

Geospatial data for Greater Sage-Grouse PACs were obtained by request from the U.S. Fish and Wildlife Service and the U.S. Geological Survey. These data are described in the 2013 greater sage-grouse Conservation Objectives Team Report (USFWS 2013). The PACs represent areas identified by individual states as essential for the long-term conservation of greater sage-grouse. The Conservation Objectives Team has concluded that the PACs are key for range-wide species conservation.

Quantifying Fire Occurrence

We quantified fire occurrence in different provisional and empirical seed transfer zones within Cold Desert level III ecoregions and a priority greater sage-grouse conservation area using three components: burn frequency, the total area burned, and the percent of total area burned. We calculated burn frequency by overlaying all 20 years of fire data and merging them into a shapefile, indicating a count of the number of overlaps across all fire layers. We calculated the total area burned by dissolving fire layers for all 20 years into one layer that represented the area burned during that time period; this method represents the total area burned, but does not account for repeated burning of the same area across years. We calculated the percent of total area burned for each seed transfer zone by dividing the total seed transfer zone area burned by the total seed transfer zone area and multiplying by 100. We sorted the seed transfer zones for each ecoregion by total area burned and tabulated the number of seed transfer zones that comprised 50% or more of the total burned area within each ecoregion. All figures were created using the package ggplot2 (Wickham 2016) within Program R (R Development Core Team 2018). All area calculations and maps were created using ArcMap 10.5 (ESRI 2016). We note here that our geospatial fire layers provide a general representation of fire occurrence and do not contain any additional details regarding fire characteristics that may be considered during restoration planning (e.g. severity, timing, and intensity).

We tested whether past fire was predictive of future fire by running a linear regression in Program R (R Development Core Team 2018). First, we summed the total area burned for each provisional seed transfer zone within each Cold Desert level III ecoregion across two different time periods, 2000–2009 and 2010–2019. Then, we performed linear regression using the command line lm function to determine the relationship between the total area burned for the two time periods, and the associated r^2 and p value.

Results

Overall, the seven ecoregions that contribute to Cold Deserts within the United States varied in total size and their relative

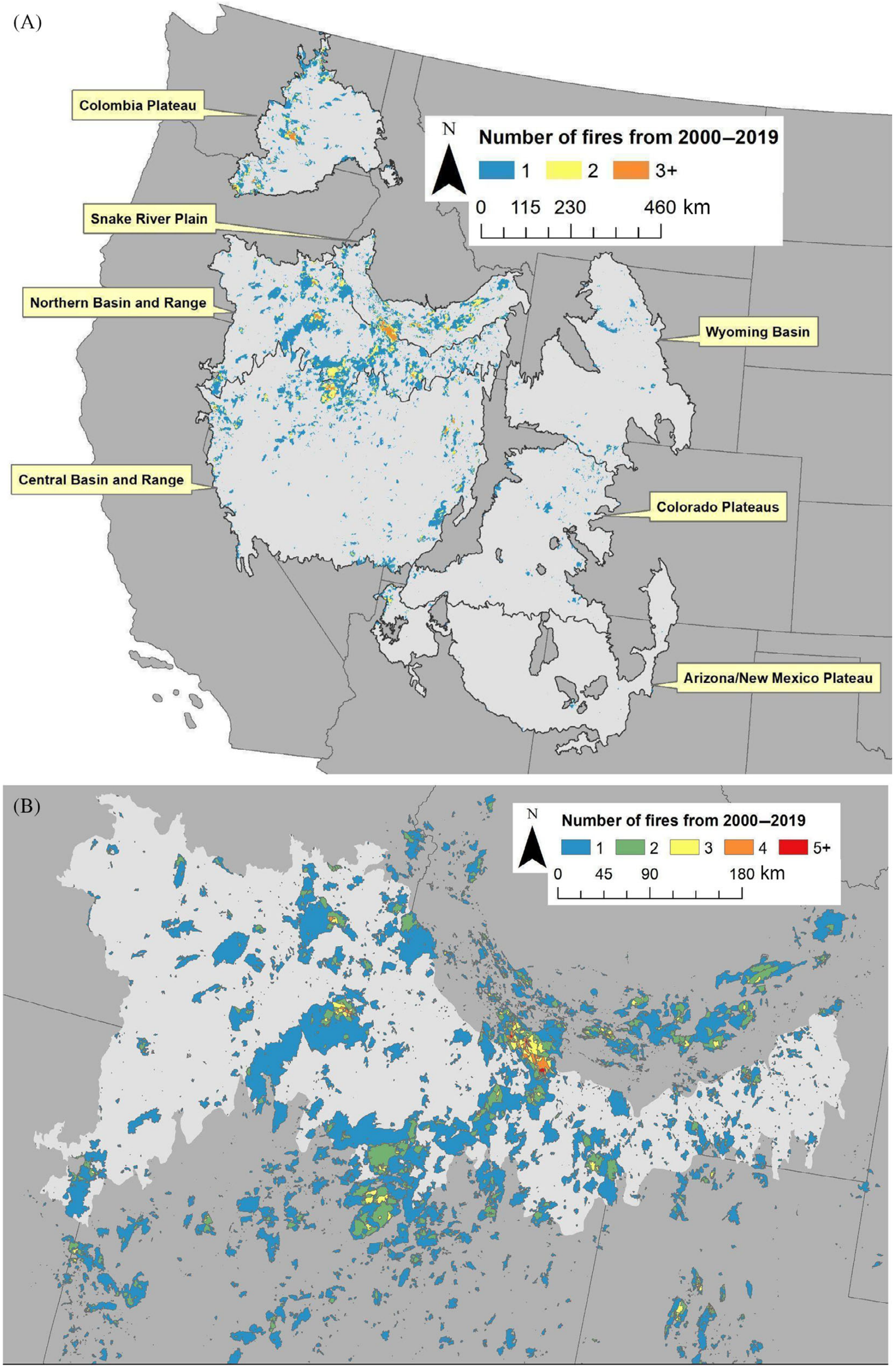

Figure 2. Maps showing burn frequencies of different areas within (A) areas of Cold Desert showing the different Omernik level III ecoregions and (B) a close-up of the Northern Basin and Range ecoregion, the ecoregion containing the most area burned, with cooler colors representing less frequent burning and hotter colors representing more frequent burning.

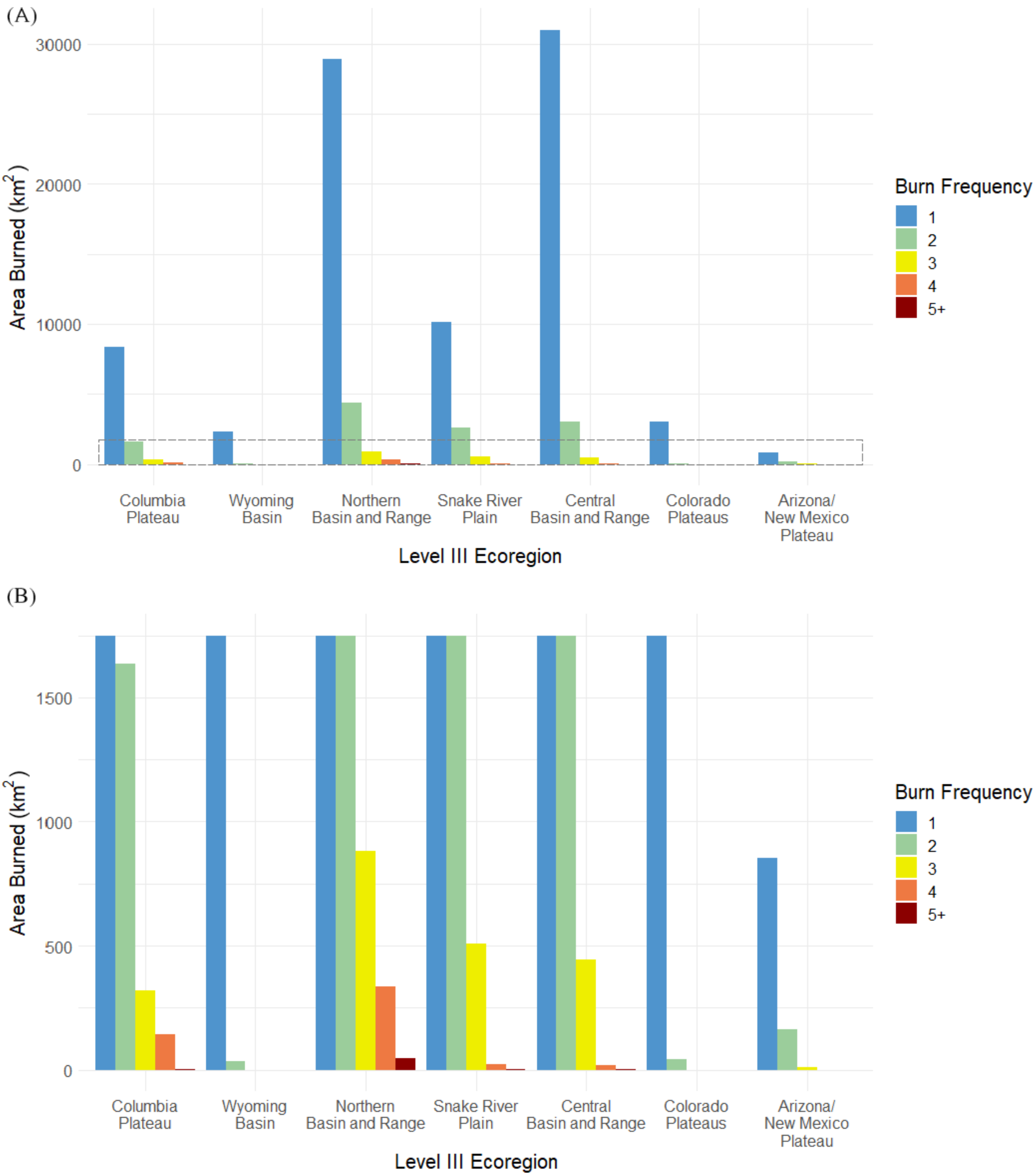

Figure 3. Summary of burn frequencies for level III ecoregions from 2000 to 2019 showing (A) the total area burned for each burn frequency within each ecoregion and (B) a zoomed-in view of the area within the dashed box in panel (A), showing a *y*-axis cut-off at 1,750 km^2, to accentuate areas experiencing higher burn frequencies. Note that the total area of each ecoregion differs, see Results section.

contribution to the total area of fire occurrence across all ecoregions from 2000 to 2019: (Area—% contribution to total burned area) Columbia Plateau (83,131 km^2—13%), Wyoming Basin (132,682 km^2—3%), Northern Basin and Range (140,198 km^2—38%), Snake River Plain (53,626 km^2—3%), Central Basin and Range (308,791 km^2—28%), Colorado Plateaus (136,576 km^2—4%), and Arizona/New Mexico Plateau (146,859 km^2—1%). Below, we present results for the provisional seed transfer zones created by Bower et al. (2014) stratified by ecoregion.

While there was some deviation over time, as would be expected, the correspondence between total area burned in later years (2010–2019) and total area burned in earlier years (2000–

Table 2. Provisional seed transfer zones (Bower et al. 2014) with the greatest total area burned for each ecoregion. For each ecoregion, two provisional seed transfer zones encompass at least 50% of the total area burned. The percent of total area burned within each ecoregion for each listed provisional seed transfer zone and the number of years (out of a possible 20) the ecoregion burned is in parentheses. Bower et al. (2014) delineated discrete provisional seed transfer zones for the continental United States using a combination of winter minimum temperature and aridity (see Methods section for more information).

Ecoregion	*Provisional seed transfer zones most burned*		*Total % area burned, summed for the two most burned provisional seed transfer zones*
Columbia Plateau	20–25F/6–12 (43%—19 years)	25–30F/6–12 (26%—20 years)	69%
Wyoming Basin	10–15F/3–6 (30%—20 years)	10–15F/6–12 (29%—20 years)	59%
Northern Basin and Range	15–20F/6–12 (45%—20 years)	20–25F/6–12 (19%—20 years)	64%
Snake River Plain	20–25F/6–12 (26%—20 years)	15–20F/6–12 (24%—20 years)	50%
Central Basin and Range	15–20F/6–12 (43%—20 years)	20–25F/6–12 (17%—20 years)	60%
Colorado Plateaus	10–15F/3–6 (38%—20 years)	15–20F/3–6 (23%—20 years)	61%
Arizona/New Mexico Plateau	25–30F/6–12 (31%—19 years)	30–35F/6–12 (23%—16 years)	54%

2009) was generally high ($r^2 = 0.7969, \beta = 1.096, p < 0.0001$). For example, the 20–25F/6–12 Northern Basin and Range seed transfer zone burned more in the later time frame (5,790 km^2) than the earlier time frame (2,248 km^2), representing a 157% increase in burned area.

Question 1—Wildfire Occurrence Within Cold Desert Ecoregions of the United States

Frequency of Fire. Most areas that burned within Cold Deserts during our focal 20-year timeframe only burned one time, accounting for 83.5% of total area burned (Fig. 2A). Areas that burned twice during that time frame accounted for 13.5% of total area burned, followed by burning three times (2.3%), four times (0.6%), and five or more times (0.06%). The Northern Basin and Range experienced the most area burned, with 28,898 km^2 burning one time, 4,350 km^2 burning two times, 880 km^2 burning three times, and 383 km^2 burning four or more times from 2000 to 2019 (Fig. 3). This was followed closely by the Central Basin and Range, where more area burned a single time (31,007 km^2), but there was less area experiencing repeated burning (Fig. 3). Only small areas within four ecoregions experienced fire five or more times within the focal time frame: Northern Basin and Range (47 km^2), Central Basin and Range (17 km^2), Columbia Plateau (2 km^2), and Snake River Plain (1 km^2). The three ecoregions where fire was less frequent experienced less repeated burning overall, relative to total area burned: Arizona/New Mexico Plateau (17%), Colorado Plateaus (2%), and Wyoming Basin (2%).

Total Area Burned Within Provisional Seed Transfer Zones. Ecoregions varied in which provisional seed transfer zones were burning the most, as measured by total area burned (Tables 2 and S1; Fig. 4). Though there are 132 provisional seed transfer zones across all ecoregions within the Cold Deserts as a whole, a majority of the burned area in each ecoregion occurred within two provisional seed transfer zones, ranging from 50.1% in the Snake River Plain to 69.1% in the Columbia Plateau (Table 2). In addition, greater than 82% of the burned area within each ecoregion occurred within five provisional seed transfer zones (ranging from 82.5% in the Arizona/New Mexico Plateau to 95.8% in the Wyoming Basin [Table S1; Figs. 4 and S1]).

Sometimes the total area burned was proportional to the size of the ecoregion. For example, in the Northern Basin and Range and the Snake River Plain, the total area burned within different provisional seed transfer zones was proportionate to their total area (Fig. 4A & 4B). However, in other ecoregions, like the Central Basin and Range and Colorado Plateaus, there was less of a consistent relationship between total provisional seed transfer zone area and the total area burned (Fig. 4C & 4D).

Percent of Total Provisional Seed Transfer Zone Area Burned. Ecoregions varied in which provisional seed transfer zones burned at a high proportion, as measured by total area burned across all years (Table S2; Fig. 4). There was only one provisional seed transfer zone where 100% of the area burned in a single fire, Northern Basin and Range 25–30F/6–12. There were five other provisional seed transfer zones where greater than 50% of the area burned over the 20-year observation period. For two of these provisional seed transfer zones, Columbia Plateau 25–30F/2–3 (68%) and Colorado Plateaus 10–15F/<2 (62%), the fires took place in 1 or 2 years, whereas in the others, Central Basin and Range 25–30F/3–6 (56%), Colorado Plateaus 10–15F/2–3 (53%), and Central Basin and Range 30–35F/6–12 (51%), the cumulative burning took place in fires that occurred in 5–7 different years.

Across all 132 provisional seed transfer zones, 21 provisional seed transfer zones had no fires within our focal 20-year timeframe. For provisional seed transfer zones which did experience fire, 29 experienced burning in less than 1% of their area, 36 experienced burning in 1–10% of their area, and 40 experienced burning in 10–50% of their area.

Additional results for an ecoregional case study examining fire occurrence across provisional seed transfer zones and empirical seed transfer zones for *Pseudoroegneria spicata* and *Artemisia tridentata* within the Northern Basin and Range ecoregion can be found in Supplement S2.

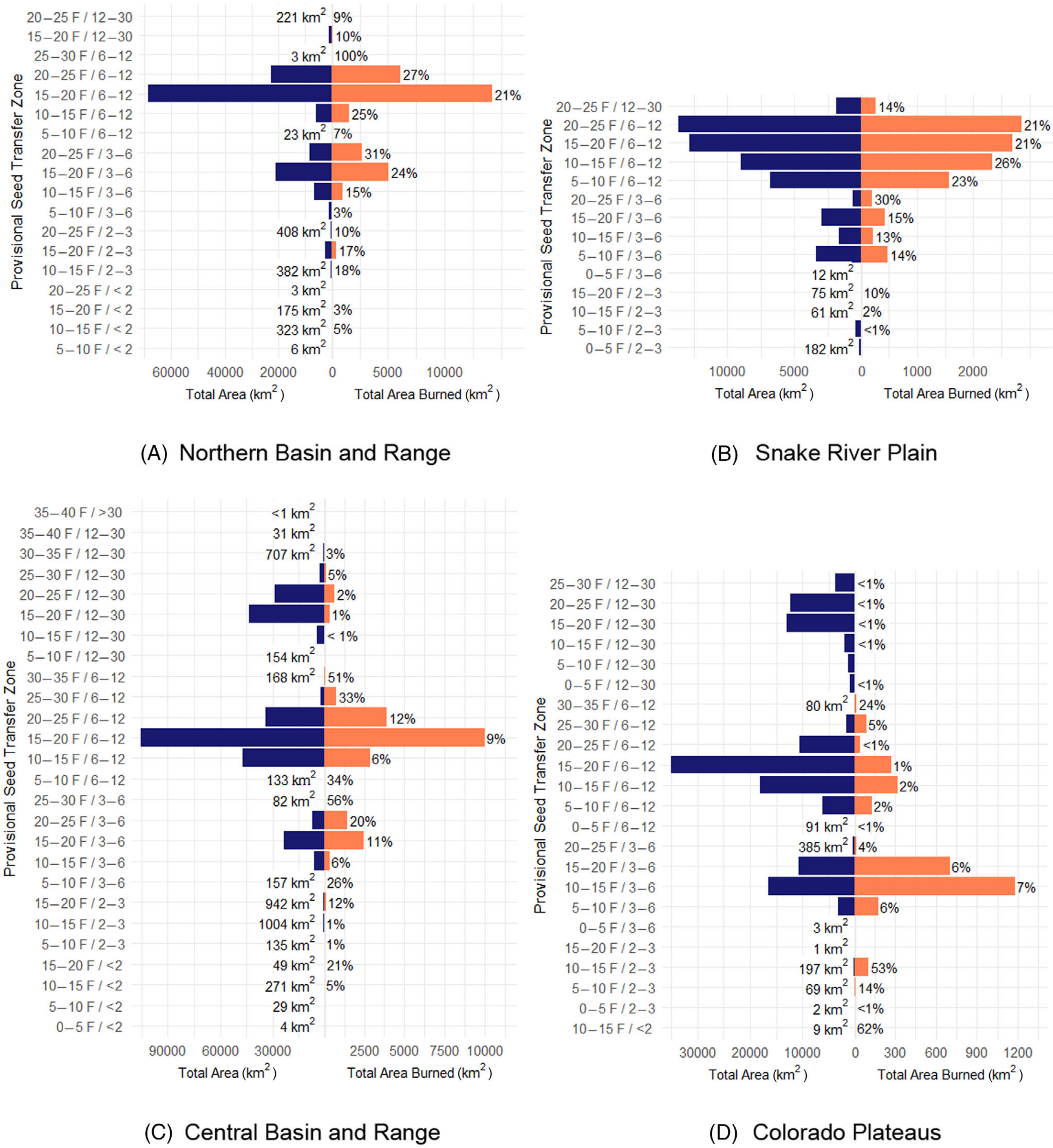

Figure 4. Total area (blue, left) and area burned (orange, right) for each provisional seed transfer zone within the (A) Northern Basin and Range, (B) Snake River Plain, (C) Central Basin and Range, and (D) Colorado Plateaus ecoregions of the U.S. Cold Desert. Notice different *x*-axis scales for total area, on the left, and total area burned, on the right. The total area of a provisional seed transfer zone is presented numerically on the left when the value was too small to be visible as a blue bar. Percentages shown to the right of the orange bars indicate the percent of the total provisional seed transfer zone area burned; when a percentage is missing, that indicates that the area did not burn. The *y*-axis shows seed transfer zones as delineated by Bower et al. (2014) for the continental United States using a combination of winter minimum temperature and aridity (see Methods section for more information).

Question 2—Case Study—Occurrence of Wildfire in Greater Sage-Grouse Priority Areas for Conservation (PACs) Within the Northern Basin and Range

Overlaying the boundaries of the priority greater sage-grouse habitat areas (Fig. S3A) within the Northern Basin and Range ecoregion (Fig. S3B) allowed us to ask whether particular seed transfer zones could be prioritized for restoration in these areas of overlap, and whether results were appreciably different for PACs than for the ecoregion as a whole. We found that fire frequencies and total area burned for both provisional and empirical seed transfer zones were very similar in prime habitat and the entire ecoregion, as were calculations of the percent of each seed transfer zone burned (Fig. S4A & S4B). There were some small differences in the proportion of empirical seed transfer zones burned for *A. tridentata* when considering the PACs or entire ecoregion. For example, 32% of empirical seed transfer zone 28 burned in the PACs versus 16% in the ecoregion as a whole (Figs. S2A & S4C). Similarly, for *P. spicata*, the larger empirical seed transfer zones experienced fire more frequently (19–20 years) and in comparable proportion to the entire ecoregion, with the exception of empirical seed transfer zone 5; 32% of this zone burned in the PACs area, relative to 22% in the entire ecoregion (Figs. S2B & S4D). Further information regarding the occurrence of fire within greater sage-grouse PACs can be found in Supplement S3.

Discussion

Meeting seed needs for ecological restoration can be a daunting task, but a regional focus and clearly designated management areas can lead to more clearly defined seed procurement priorities and efficient seed use (NASEM 2023). In particular, seed transfer zones can make restoration more effective, as they indicate areas where seeding is likely to be successful (Kilkenny 2015). However, seed transfer zones present practical challenges as well, by introducing complexity into the collection, agricultural production, and purchase of native seeds (Nevill et al. 2016). Here, we sought to simplify this process, asking whether we could identify priority seed transfer zones using geospatial information from historical fire records to identify likely seed needs.

Our hope was that historical data could be used to anticipate restoration and procurement needs so that seed is available within the tight timelines imposed by practical and ecological constraints (Erickson & Halford 2020). Indeed, past burning (2000–2009) was broadly, if not perfectly, predictive of later burning (2010–2019), and while there were multiple seed transfer zones represented in each ecoregion, we found that only two provisional seed transfer zones made up a majority of the total area burned within each ecoregion. Additionally, some of these provisional seed transfer zones burned every year (23 provisional seed transfer zone-ecoregion combinations out of a total of 132 examined here). In some cases, larger seed transfer zones experienced more burning, but not always; sometimes area burned was higher than expected based on the total seed transfer zone extent. However, it is important to note that the positive relationship between past burning and future burning is partially contingent on the size of the seed transfer zones relative to each other; thus, caution should be made in comparing the relative increase in burning of seed zones that differ in size. Though many factors influence the decision to restore particular land areas (including land ownership, proximity to roads, fire size and severity, and restoration potential, among many other considerations), our results indicate that historic fire data and information on the most widely and frequently burned seed transfer zones may help forecast future seed needs if conditions remain similar, and that ecoregionally specific seed transfer zones experiencing high fire occurrence can be used as targets for seed needs planning for restoration (Robichaud et al. 2009; Morgan et al. 2015; Erickson & Halford 2020). We also found that considering high-priority conservation goals (in our case, preservation of greater sage-grouse core habitat) provided only slightly different recommendations for seed procurement than considering the ecoregion as a whole. Together, our findings provide a framework for prioritizing restoration activities within Cold Desert ecoregions, including seed collection for gene conservation and seed production, procurement, storage, and planning for post-fire seeding and wildlife habitat improvement projects. Additionally, the methods presented here can be adapted for use in other systems around the world, especially in regions where geospatial layers for climate and ecological disturbance are available (e.g. Tareq et al. 2018).

Disturbance size and frequency is changing in response to human activity around the globe (Turner 2010). Historic observations of fire frequency in Cold Deserts of the western United States have clear patterns of shorter fire return intervals driven by annual grass invasions and other land use impacts (D'Antonio & Vitousek 1992; Pilliod et al. 2017*a*). As we saw here, the Northern Basin and Range experienced three or more fires in 1,263 km^2 across the 20-year timeframe, making up 3.7% of the total area burned within the ecoregion. These small areas of repeated fire may be driving the perception that fire return intervals are less than 5 years across Cold Deserts (e.g. Whisenant 1990). However, other estimates of fire return intervals are more modest (e.g. Balch et al. 2013), consistent with what we observed in our study: 83.5% of the area burned across all Cold Desert ecoregions burned a single time during our focal 20-year timeframe. This might seem contradictory to our result demonstrating that the same seed transfer zones burned consistently; however, it is important to recognize that different areas within these seed transfer zones were burning each time. This was true both across the Cold Desert as a whole and for the area included in our case study. Because of the greater likelihood of retaining native species after a single burn event (Winward 1985), some sites with longer fire return intervals and less overall disturbance may be good targets for restoration activities (Chambers et al. 2014; Svejcar et al. 2017), as they could be least likely to be redisturbed and reinvaded. Conversely, we also identified relatively small areas experiencing repeated burning, which may be more vulnerable to invasion (Bradley et al. 2018). Areas with more frequent fire can be challenging to restore and generally require additional considerations when planning and implementing restoration activities, such as the need for triage approaches that may include herbicide use or other targeted site preparation methods (Miller et al. 2013; Creutzburg et al. 2022). Our approach of identifying areas that burn frequently or to great extent could be followed with an assessment of plant community composition and fire behavior in these regions, creating guidance for seed needs that also considers potential barriers to restoration, such as fire intensity and degree of invasion.

We were also interested in identifying seed transfer zones that experienced burning across all or most of their extent to prioritize potentially imperiled ecological communities that could be a target for conservation, which is a crucial step for guiding seed procurement and other actions (Castillo-Mandujano & Smith-Ramírez 2022). In our study, seed transfer zones varied in the proportion of wildfire occurrence, with some being much more affected by fire than others. The persistence of these imperiled native plant communities may depend on the availability of appropriate seed, and restoration could benefit from identifying areas for seed banking and gene conservation (Povilitis 2001). In particular, our case study of *Artemisia tridentata* empirical seed transfer zones illustrated that there was a major increase in the proportion burned within the greater sage-grouse priority habitat area (32% of empirical seed transfer zone 28 burned within the Northern Basin and Range PACs, relative to 16% in the entire ecoregion), which is important information for wildlife habitat restoration. In other regions, identifying seed transfer zones with a high proportion of disturbance from development, floods, or mining may also be helpful when considering imperilment as a criterion for prioritizing seed production (e.g. Silcock & Fensham 2018). This consideration of historic disturbance conducted here could also identify regions that have not experienced disturbance, which could serve as valuable reservoirs for seed collection for important species. We note, however, that over-interpretations of measures, like the fraction burned, should be avoided for some of the very small seed transfer zones represented in this study. Use of specified boundaries (such as when we reduced our study area to Cold Deserts within the western United States or reduced it further to priority habitat for greater sage-grouse) will necessarily generate small sections of seed transfer zones that primarily exist outside of the boundaries of interest. These sections will represent only a portion of the area of the associated seed transfer zone and are thus potentially subject to sample area bias and edge effects. However, in some cases this may be worth considering, despite the potential for bias.

Our case study focusing on greater sage-grouse habitat (PACs) demonstrates how geospatial data can be used to identify seed needs for specific habitat conservation actions. Native plants are the foundation of intact sagebrush steppe plant communities and provide essential habitat that greater sage-grouse depend on for breeding, nesting, and foraging (Pennington et al. 2016), and thus these areas may be prioritized for post-fire restoration. We found that fire occurrence in greater sage-grouse PACs within the Northern Basin and Range ecoregion reflected a similar pattern to fire occurrence within the ecoregion as a whole, with a few exceptions showing slight shifts in seed transfer zone priority or for imperiled seed transfer zones. This indicates that restoration planning based on ecoregional data will largely satisfy the specific needs for post-fire restoration in greater sage-grouse PACs within this ecoregion, and is consistent with the habitat mitigation strategies being adopted by regional land management agencies (Creutzburg et al. 2022). Sagebrush steppe plant communities are a focus area for the Bipartisan Infrastructure Law (BIL 2021) and Federal directives encourage that native plant materials be used in seeding (e.g. BLM 2008); our findings provide a way to prioritize restoration to ensure that the right seed is available. Specifically, in Cold Deserts, focusing seed production efforts on (1) seed transfer zones with the greatest incident of fire and (2) seed transfer zones within the most imperiled ecoregions (experiencing fire in a large proportion of habitat) would be an excellent way to prioritize seed sourcing. In other ecosystems, investigating the alignment of overlapping restoration needs (e.g. regional vs. wildlife habitat) may identify ways to balance the efficient acquisition of appropriate seed with limited resource availability.

While many ecological disturbances are unplanned and somewhat unpredictable, data on past disturbance patterns are available for many regions of the world (Pandey et al. 2019) and could become more widely available with increased access to global environmental monitoring systems (e.g. Sundareshwar et al. 2007). Though data quality matters greatly when using the past as a guide for the future, the methods presented here may help generate prioritization strategies for seed collection and production, which are likely to be useful for restoration in response to unplanned disturbance. In our focus on patterns of fire over a 20-year timeframe in Cold Deserts of the western United States, we demonstrated that fire occurrence, while widespread, tends to be concentrated in a small number of seed transfer zones, suggesting that prioritization of the use of the genetic resources represented by those seed transfer zones could lower the cost and increase the efficiency and success of restoration projects in this region. A follow-up study seeking to corroborate our assumption that areas with the greatest fire occurrence also experience the most restoration would be helpful, but in the meantime, focusing on procurement and storage of seeds from the most burned seed transfer zones appears to be a realistic and feasible effort, as a small number of seed transfer zones likely represent large areas of need. Additionally, seed collection for gene conservation from potentially imperiled seed zones, due to high fire frequency or burning across a majority of their extent, is needed to preserve genes and phenotypic traits that will be useful in future restoration (Leger 2008), especially with the mounting effects and interacting drivers of global change (Finch et al. 2021). Further work could also focus on specifically identifying imperiled or highly valuable areas in need of additional seed development to support restoration efforts and approaches for overcoming species-specific challenges to acquiring seed transfer zone appropriate seed resources. This is a win–win for seed producers, seed collectors, and seed users, and we have created information that has the potential to better match supply to demand. We note, however, that this approach is only effective if past disturbance is predictive of future disturbance, and as the pace of global change increases, further prioritization methods that incorporate complexity and uncertainty may be needed to manage this challenge.

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Supporting Information

The following information may be found in the online version of this article:

Figure S1. Total area (blue, left) and area burned (orange, right) for each provisional seed transfer zone within the (A) Columbia Plateau, (B) Wyoming Basin, and (C) Arizona/New Mexico Plateau ecoregions of the U.S. Cold Desert.

Figure S2. Total area (blue, left) and area burned (orange, right) within the Northern Basin and Range ecoregion for (A) empirical seed transfer zones for sagebrush (*Artemisia tridentata* ssp. *wyomingensis* and *tridentata*) and (B) empirical seed transfer zones for bluebunch wheatgrass (*Pseudoroegneria spicata*).

Figure S3. Maps showing (A) the priority areas of conservation (PACs) for greater sage-grouse within the western United States and (B) the frequency of fire within the Northern Basin and Range PACs.

Figure S4. Total area (blue, left) and area burned (orange, right) for priority areas of conservation (PACs) for greater sage-grouse within the Northern Basin and Range.

Supplement S1. Seed procurement implications.

Supplement S2. Ecoregional case study—occurrence of wildfire in the Northern Basin and Range.

Supplement S3. Greater sage-grouse case study—occurrence of wildfire in priority areas for conservation (PACs) within the Northern Basin and Range.

Table S1. Total area (km^2) and area burned (km^2) for all provisional seed transfer zones within the U.S. Cold Desert level III ecoregions from 2000 to 2019.

Table S2. Number of years burned and total percent burned for all provisional seed transfer zones within the U.S. Cold Desert level III ecoregions from 2000 to 2019.

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