Rewilding the American West

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After taking office, President Biden signed an executive order announcing his America the Beautiful plan to conserve 30% of US land and water by 2030. He challenged Americans to collaboratively "conserve, connect, and restore the lands, waters, and wildlife upon which we all depend" at a national scale (US Departments 2021, p. 9). Here, we take a major step in advancing President Biden's plan by envisioning a bold and science-based rewilding of publicly owned federal lands (hereafter, *federal lands*) in the American West. Beyond concerns for human survival and flourishing, a principled commitment to the natural world and a sense of moral urgency underpins the motivation for our proposal.

In general, rewilding aims to reestablish vital ecological processes that can involve removing troublesome nonnative species and restoring key native species. Our rewilding call is grounded in ecological science and is necessary regardless of changing political winds. Our objective is to follow up on President Biden's vision to conserve, connect, and restore by identifying a large reserve network in the American West suitable for rewilding two keystone species, the gray wolf (*Canis lupus*) and the North American beaver (*Castor canadensis*).

We focus first on the gray wolf, a wide-ranging species requiring extensive areas of habitat. Gray wolves were largely eradicated from the American West following Euro-American colonization and manifest conquest of the West. Through measures afforded by the US Endangered Species Act, in the mid- to late 1990s, gray wolves were reintroduced to portions of the northern Rocky Mountains and Mexican gray wolves (*Canis lupus baileyi*) to portions of New Mexico and Arizona. Nevertheless, the wolf's current range in the 11 Western states is approximately 14% of its historical range (figure 1a). Once likely numbering in the tens of thousands, there may be as few as approximately 3500 wolves in the American West today (supplemental table S1). As an apex predator, wolves can trigger strong ecological effects on prey and plants across a variety of landscapes of western North America (Beschta and Ripple 2009).

Beaver restoration forms a second key feature of our rewilding proposal. Beaver populations had once been robust across the American West but were decimated by an estimated 90% to 98% in the wake of settler colonialism and are now extirpated from many streams (Butler and Malanson 2005). By felling trees and shrubs and building dams, beavers enrich fish habitat, increase water and sediment retention, maintain water flows during drought, provide wet fire breaks, improve water quality, initiate recovery of incised channels, increase carbon sequestration, and generally enhance habitat for many riparian plant and animal species (Castro et al. 2015). Beaver restoration is a cost-effective means of repairing degraded riparian areas. Although riparian areas occupy less than 2% of the landscape, they provide habitat for up to 70% of wildlife species (Poff et al. 2012).

The Western Rewilding Network

To identify prospective habitat for rewilding, we considered potential gray wolf core habitat on federal lands in 11 Western states (see the supplemental material). We began with wolves, because their recovery and persistence require large areas. We then identified areas of contiguous federally managed lands within core wolf habitat that were at least 5000 square kilometers [km^2].

That analysis revealed a potential network of 11 large reserves spanning the American West, which we term the Western Rewilding Network (figure 1b, supplemental figure S1, supplemental table S2). We mapped the spatial links between certain pairs of these 11 reserves using connectivity modeling (figures 1c, supplemental figures S2, S3, and S4).

Finally, we cataloged the threatened and endangered plant and animal species, including subspecies and distinct population segments, that had at least 10% of their ranges within the Western Rewilding Network. For each of these species, we determined threats, at least in part, associated with resource extraction industries, including livestock grazing, logging, mining, and oil and gas drilling (see the supplemental material).

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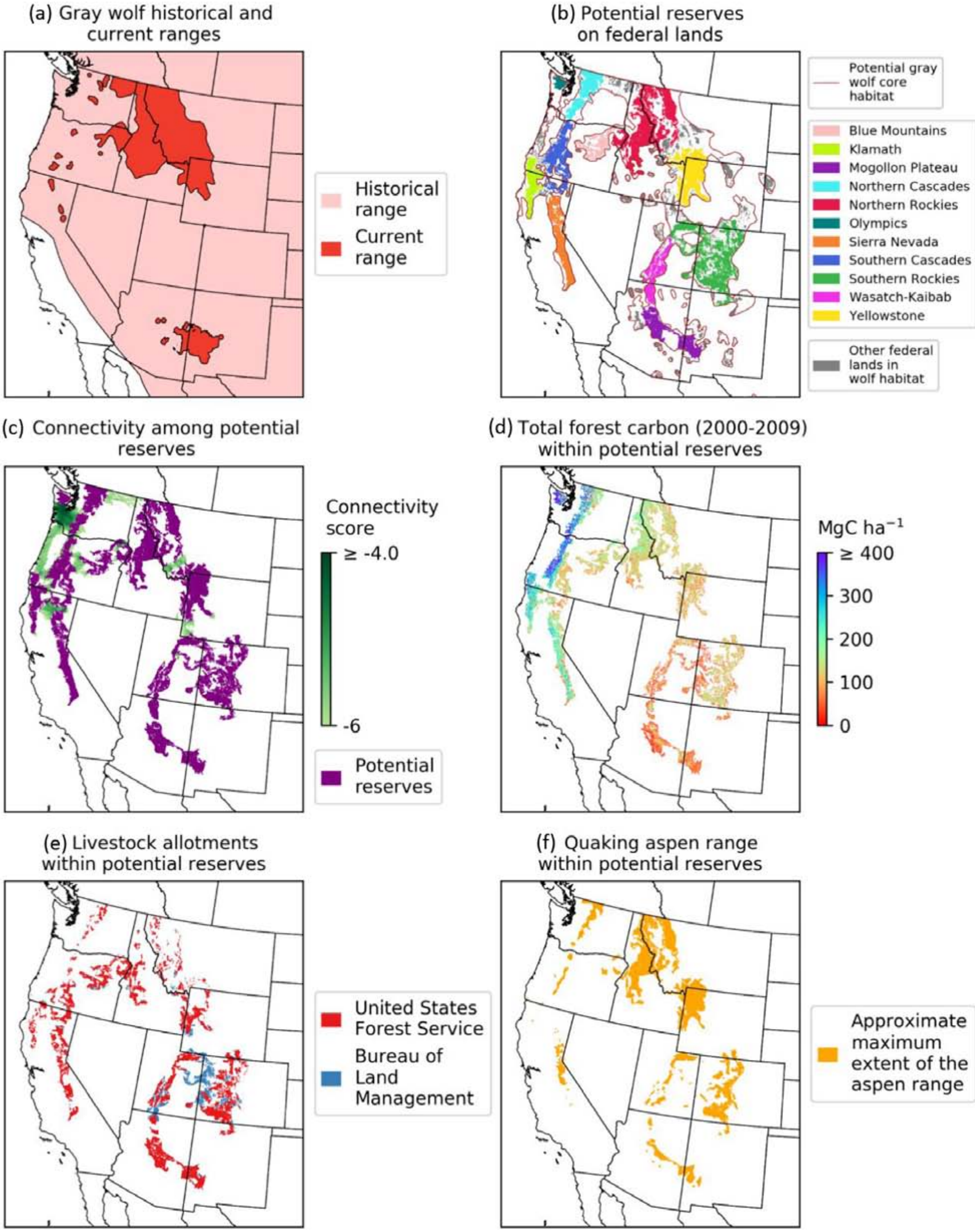

Figure 1. Proposed reserve network for the American West. The gray wolf range (a) could be expanded significantly through the establishment of large reserves corresponding to patches of potential core habitat on federally managed lands that cover at least 5000 square kilometers (b). Most reserves are closely connected to nearby reserves as shown in green (c). The proposed reserves harbor large amounts of forest carbon (d) and successful rewilding will depend on retirement of grazing allotments within potential reserves (e), thus offering great benefits for biodiversity, including aspen (f) and other species. See the supplemental material for data sources.

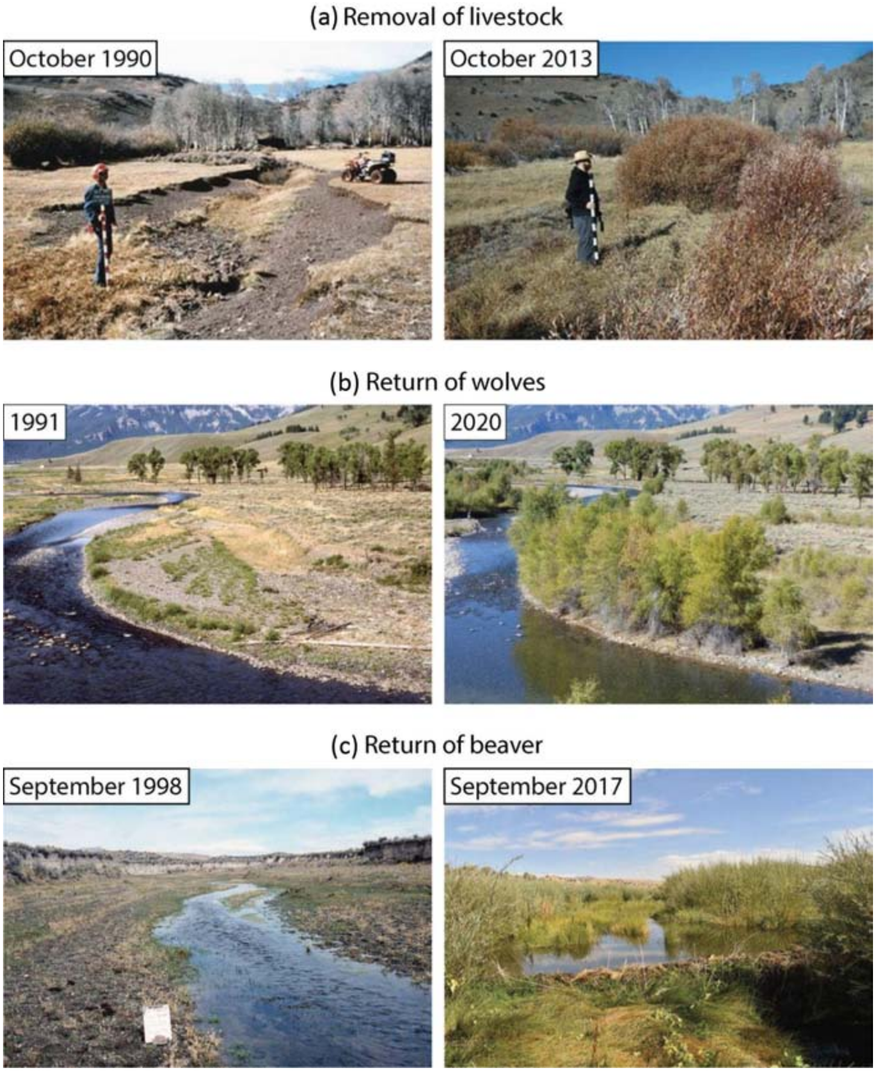

Figure 2. Paired photo examples of recovering riparian or aquatic habitats. The removal of livestock in 1991, Hart Mountain National Antelope Refuge, south-central Oregon (a). The reintroduction of wolves in 1995–1996, northern range of Yellowstone National Park, north-western Wyoming (b). Altered livestock grazing management that allowed sufficient riparian plant community recovery for beavers to return, north-central Nevada (c). Photographs: (a) Removal of Livestock, left photo from US Fish and Wildlife Service, right from photo Jonathan Batchelor; (b) Return of Wolves, left photo from National Park Service, right photo from Robert L. Beschta; (c) Return of Beaver, left and right photos from US Bureau of Land Management.

The Western Rewilding Network currently includes 92 threatened and endangered species across nine taxonomic groups: five amphibians, five birds, two crustaceans, 22 fishes, 39 flowering plants, five insects, 11 mammals, one reptile, and two snail species (supplemental table S3). The reserves with the greatest numbers of threatened and endangered species were the Mogollon Plateau (n = 24) and the Southern Rockies (n = 23). Overall, livestock grazing poses by far the most common threat (48% of species; n = 44), followed by mining (22%; n = 20), logging (18%; n = 17) and oil and gas drilling (11%; n = 10; supplemental figure S5). In 7 of the 11 potential reserves, at least half of the listed species are threatened by livestock grazing (supplemental figure S6). In all of the 11 potential reserves, average stream densities (stream orders 2–7) exceed 50 meters per km^2, suggesting significant opportunities for high density beaver restoration (supplemental figure S7).

Livestock grazing is ubiquitous on federal lands in the American West (figure 1e, supplemental figure S8) and, astoundingly, even occurs within some protected areas, such as wilderness areas, wildlife refuges, and national monuments (supplemental figure S9, table S2). Federal lands with managed livestock allotments often have various ecological impacts because of the multiple direct and indirect effects of these introduced large herbivores. For example, in many areas, livestock grazing causes stream and wetland degradation, affects fire regimes, and inhibits the regeneration of woody species, especially willow (*Salix* sp.; Beschta et al. 2013, Kauffman et al. 2022).

Although the effects of livestock grazing management on riparian areas are well known, there are also possible multitrophic effects on a host of wild animals such as herbivores, pollinators, and predators (Filazzola et al. 2020), as evidenced by the 23 animal species within the proposed reserves at risk from livestock grazing (table S3). Ruminant livestock are also a significant source of greenhouse gas emissions, especially methane, and their ecosystem impacts can exacerbate warmer and drier conditions, potentially shifting landscapes from carbon sinks to carbon sources (Kauffman et al. 2022). Moreover, limiting grazing and logging within strategic areas of federal lands can play an important role in mitigating climate change by protecting existing carbon stocks (figure 1d, supplemental figure S10; Law et al. 2021).

Based on our analysis, we suggest a rewilding plan for the proposed reserve network that includes: (1) retiring livestock grazing allotments on federal land within the proposed reserve network; (2) protecting, reestablishing, or recovering gray wolves, especially within the network; and (3) reintroducing beaver in suitable habitat within the network. These three rewilding steps could greatly improve ecosystem structure and function, especially in riparian areas (figure 2). It is important to consider the order of the rewilding steps. For example, it generally makes sense to reintroduce beaver after livestock grazing on federal lands has been halted, allowing for a period of initial restoration of riparian woody vegetation on which beaver depend (Small et al. 2016).

Rewilding benefits

The ecological benefits of our rewilding plan would accrue over time, becoming greatest when wolves and beaver are allowed to reach ecologically effective densities (Soulé et al. 2003). In addition to eliminating the adverse effects of livestock grazing within the identified reserve network, it would be important to limit resource extraction industries and off-road vehicles. Because our plan prioritizes potential core areas of wolf habitat that occur mostly in forested areas, it spatially complements the proposed Sagebrush Sea Reserve Network, which is focused on protecting the greater sage grouse (*Centrocercus urophasianus*) and a host of other species in the sagebrush steppe (supplemental figure S11).

Considering our plan suggests reducing grazing allotments on federal lands by 29% (285,000 km^2 out of a total of 985,000 km^2 in the 11 western states), an economically and socially just federal compensation program for those who relinquish their government grazing permits would be appropriate provided these allotments are permanently retired. However, the net economic benefits would be substantial given the social carbon cost of livestock grazing on federal lands (Kauffman et al. 2022). For all allotments, receipts from grazing fees were $125 million less than federal appropriations in 2014 (Glaser et al. 2015). There would also need to be an action plan for managing potential conflict associated with wolves and beavers in cases where they move out of the reserve network.

Our proposed network across the West offers substantial connectivity between pairs of identified reserves, supporting gene flow, climate-related range shifts, and population viability of wide-ranging native species (figure 1c). The Western Rewilding Network would help protect and restore the 44 threatened and endangered species at risk because of livestock grazing (supplemental figure S12). And, over time, it would restore riparian systems, streams, and biodiversity; ameliorate altered fire regimes; and provide climate change mitigation through increased carbon storage. Restoration efforts could also be focused on the high connectivity areas between reserve pairs with land acquisitions or easements, which would form important wildlife corridors benefitting a variety of species (figures 1c and S3, supplemental table S4). In general, rewilding will be most effective when participation concerns for all stakeholders are considered, including livestock ranchers, local communities, hunters and fishers, recreationists, state and local governments, nonprofit organizations, and other private landowners (Fleischner 2010). Indigenous people and their governments would become the key partners.

Retiring allotments on some federal lands would also decrease livestock-related conflicts between humans and large predators. Moreover, adding and preserving wolves could assist in the natural control of overabundant native ungulates. This would allow for native vegetation regrowth of important species such as aspen (*Populus tremuloides*; figure 1f), which supports highly diverse plant and animal assemblages and is in major decline in the West, often because of browsing by livestock and wild ungulates in the absence of wolves (Seager et al. 2013). Restoring another keystone species, the beaver, to streams within the network would bolster and widen the ecological benefits to riparian areas. Currently, wolf management by some of the western state governments is geared toward reducing their numbers, and it is essential that these policies be reversed and federal protected status be fully restored (see the supplement for an overview of the policies).

Although our proposal may at first blush appear controversial or even quixotic, we believe that ultra ambitious action is required (Fleischner 2010). We are in an unprecedented period of converging crises in the American West, including extended drought and water scarcity, extreme heat waves, massive fires triggered at least partly by climate change (Ripple et al. 2021), and biodiversity loss with many threatened and endangered species (table S3). Furthermore, we note that the lands in the proposed network are already owned by the public and meat produced from all federal lands forage accounts for only approximately 2% of national meat production (Leshy and McUsic 2008).

President Biden's America the Beautiful plan needs a bold, scientifically grounded organizing principle like that provided by the Western Rewilding Network and the three steps proposed for rewilding these federal lands. If implemented alongside fine-scale conservation planning, it would restore critical ecological processes with minimal human interference, protect many endangered and at-risk species, increase resilience to climate change, and sustain an array of ecosystem services. Therefore, our plan represents a historic opportunity to rewild significant portions of the American West that could serve as an inspiring model for other regions and would ensure our natural heritage remains intact for future generations.

Acknowledgments

This Viewpoint is dedicated to the lifetime work of our friend and colleague Michael Soulé (28 May 1936–17 June 2020). We thank Matthew G. Betts, Christopher Ketcham, Josh Osher, Jodi Hilty, Gary Tabor, and Roger Worthington for reviewing an early draft of the manuscript or providing information and support for the project. WJR received funding from the Environmental Research Fund, Oregon State University Agricultural Research Foundation. RLB received funding from the Ecosystem Restoration Research Fund, Oregon State University Foundation. DAD received funding from the Wilburforce Foundation.

Supplemental material

Supplemental data are available at *BIOSCI* online

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Supplemental Materials for

Rewilding the American West

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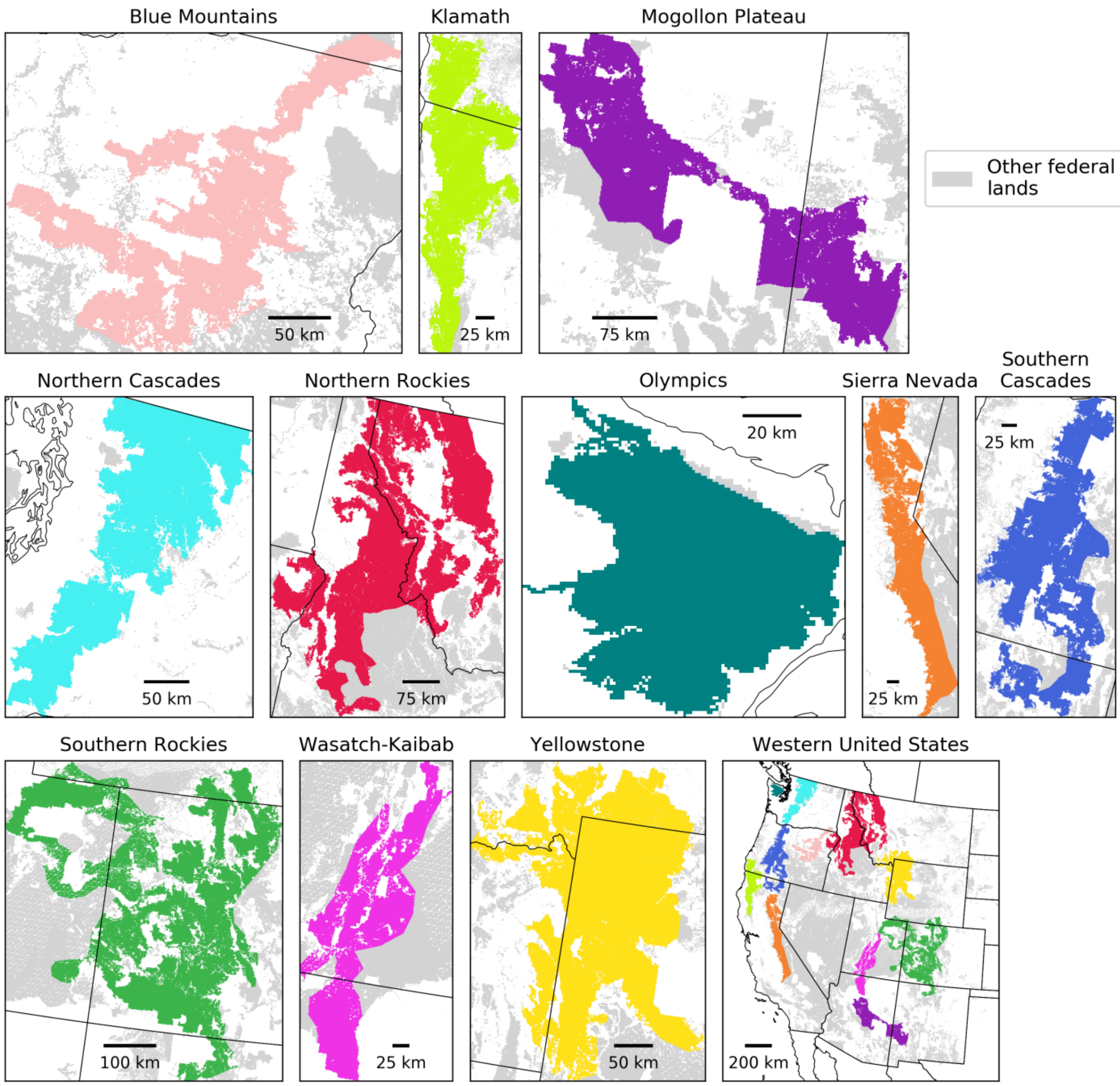

Figure S1. Maps of potential reserves. Each of the 11 potential reserves is shown using a different color. The bottom right map shows all the reserves for context (see also Figure 1b). The potential reserves are entirely within federal lands and potential core gray wolf habitat. Other federal (National Park Service, Bureau of Land Management, Forest Service, and Fish & Wildlife Service) lands are shown in gray for context.

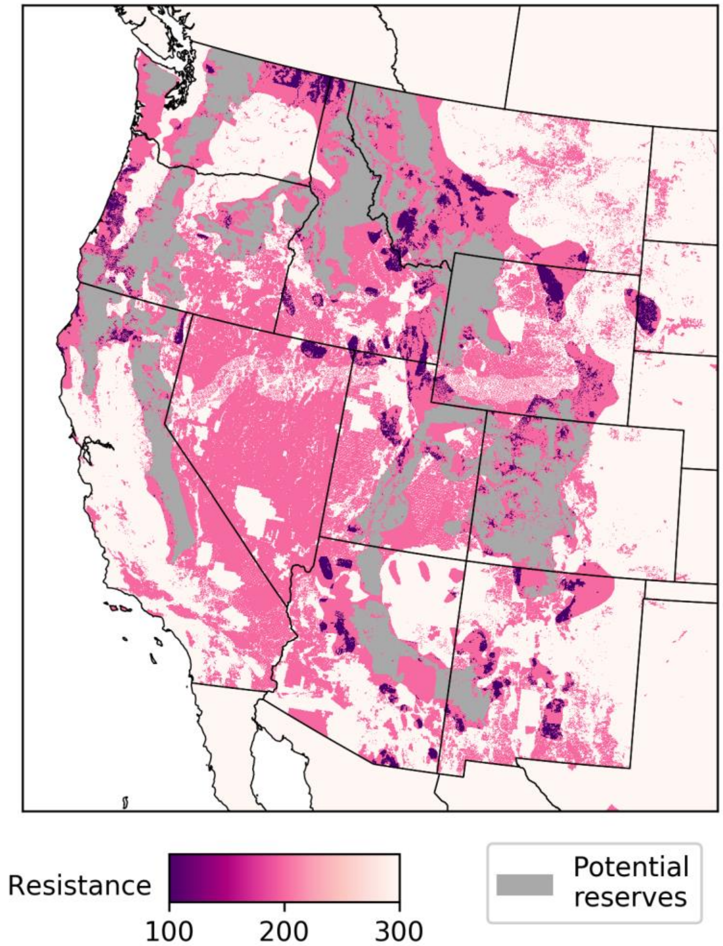

Figure S2. Landscape resistance map. Resistance, i.e., the relative difficulty of movement by wolves, based on the occurrence of core wolf habitat and National Park Service, Bureau of Land Management, Forest Service, and Fish & Wildlife Service federal lands. Potential reserves are shown in gray. Resistance was estimated using maps of federal lands and potential gray wolf core habitat (Carroll et al. 2021; Esri et al. 2021). See Supplemental Methods for details.

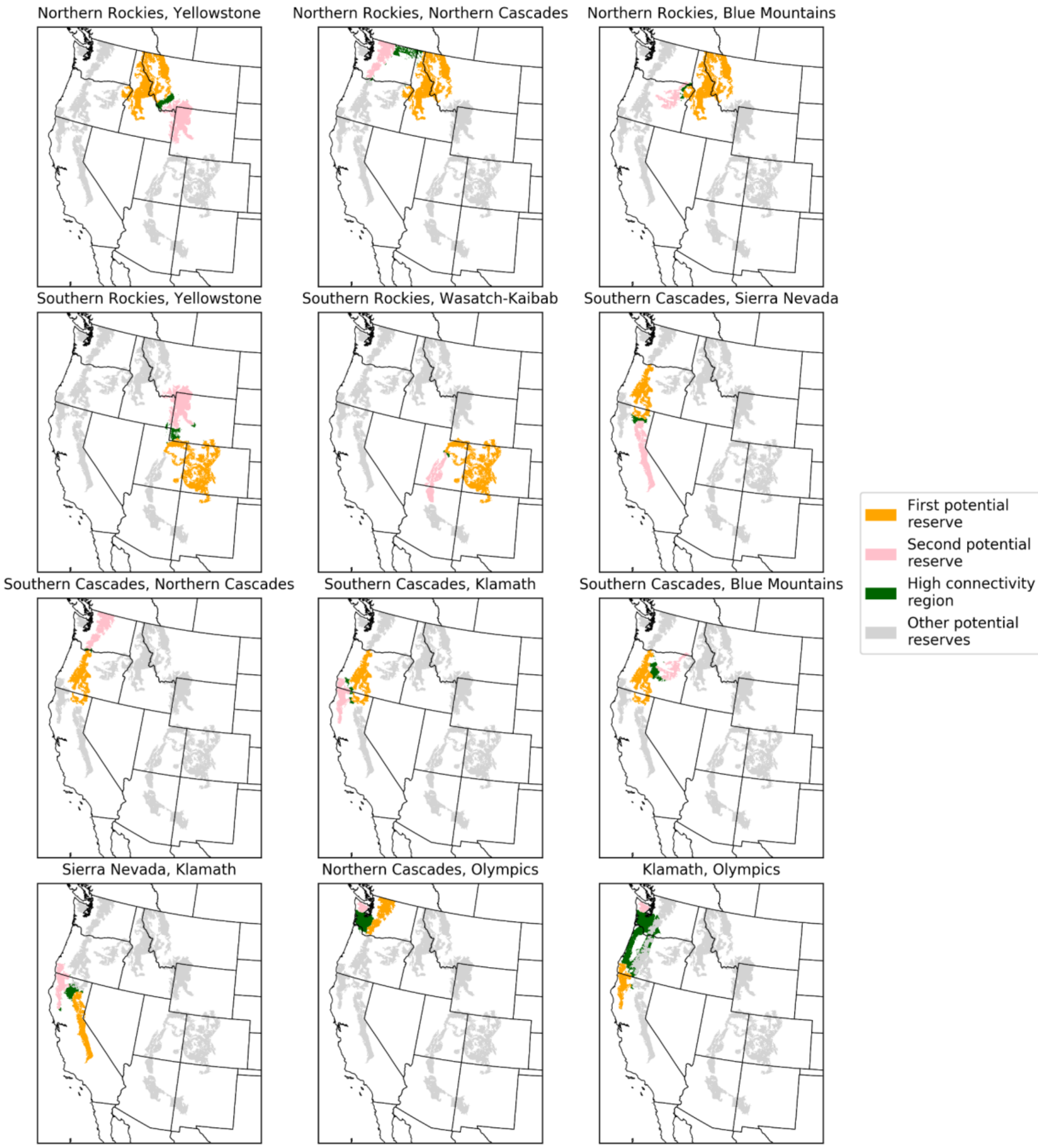

Figure S3. Pairwise connectivity among potential reserves. Each map shows high connectivity regions associated with the pair of reserves (i.e., first and second) listed in its title. Connectivity was modeled using the Circuitscape software with a resistance raster derived from maps of federal lands and potential gray wolf core habitat (Anantharaman et al. 2020; Carroll et al. 2021; Esri et al. 2021; Figure S2). The overall connectivity potential map was derived by taking the maximum over the pairwise component maps (Figure 1c). See Figure S4 for zoomed-in versions.

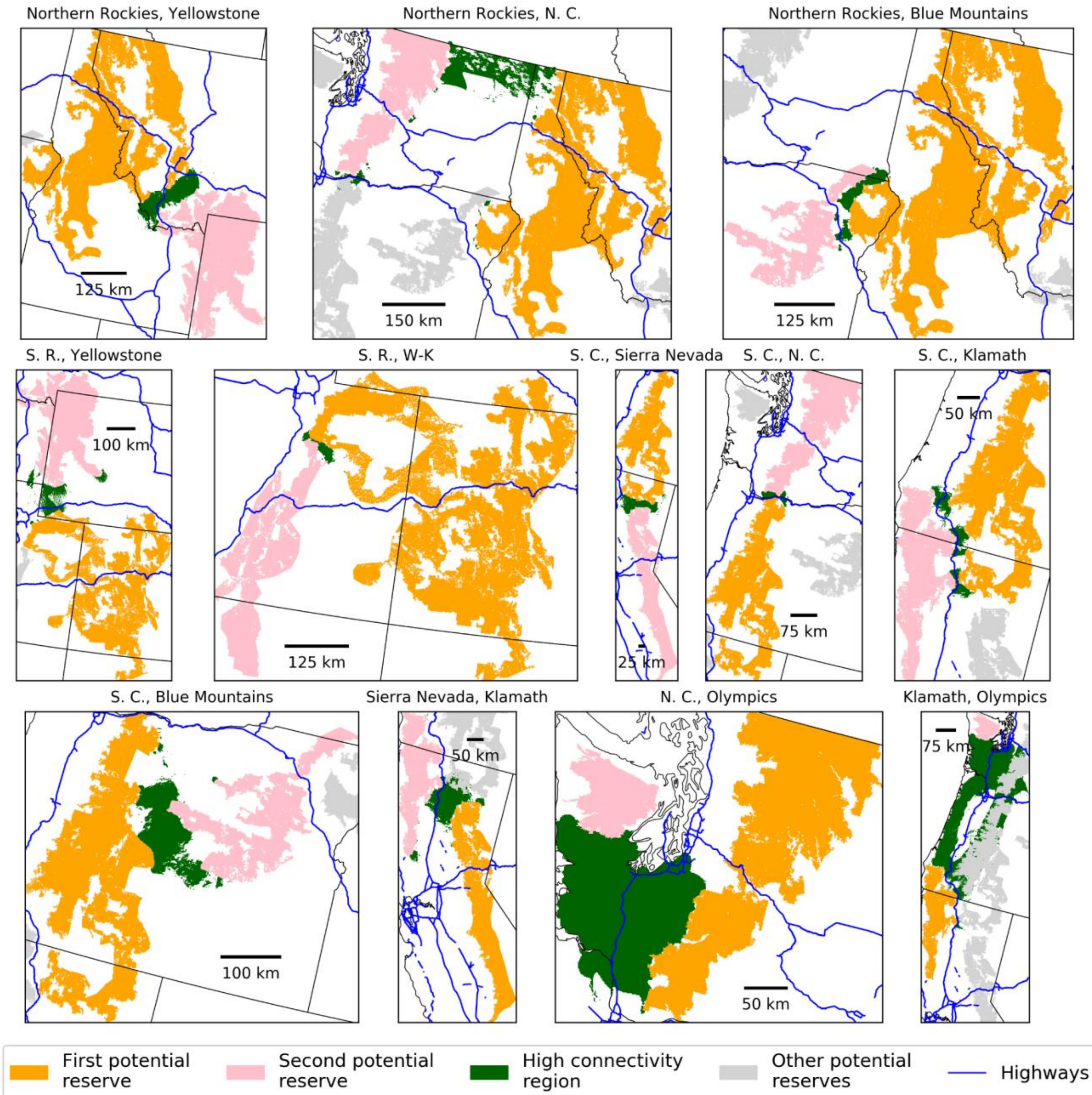

Figure S4. Pairwise connectivity among potential reserves (zoomed-in version). Connectivity was modeled using the Circuitscape software with a resistance raster derived from maps of federal lands and potential gray wolf core habitat (Anantharaman et al. 2020; Carroll et al. 2021; Esri et al. 2021; Figure S2). Each map shows high connectivity regions associated with the pair of reserves (i.e., first and second) listed in its title (see supplemental methods for details). The overall connectivity potential map was derived by taking the maximum over the pairwise component maps (Figure 1c). Highway data are from the GRIP global roads database (Meijer et al. 2018). See Figure S3 for similar maps at a broader scale. Abbreviations: "S. R" - Southern Rockies, "S. C." - Southern Cascades, "N. C." - Northern Cascades, "W-K" - Wasatch-Kaibab.

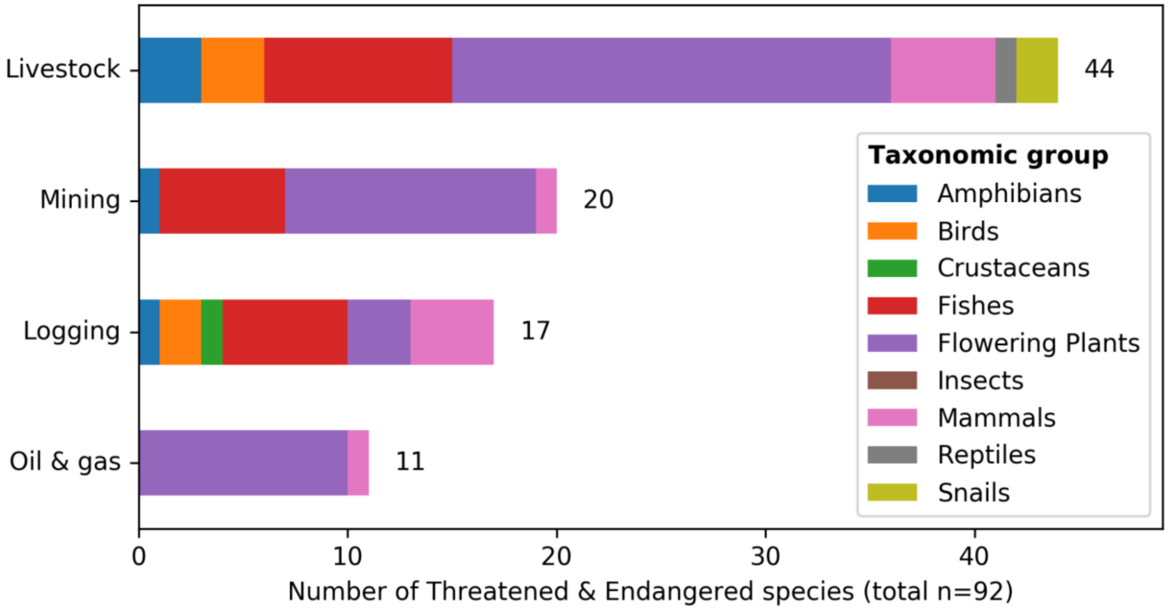

Figure S5. Extractive threats to Threatened and Endangered species in potential reserves. We manually identified extractive threats to each species using NatureServe Explorer's "Threat Comments" (NatureServe 2022). Numbers of species facing each threat are shown after the associated bar. Colors indicate taxonomic groups.

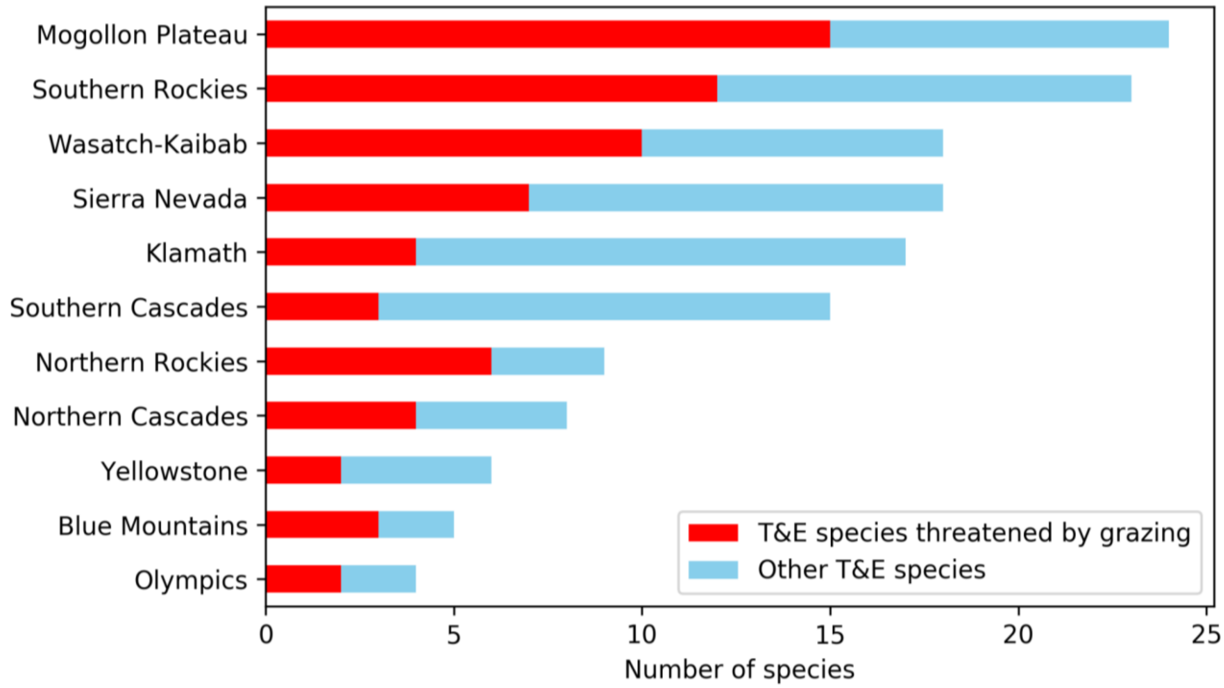

Figure S6. Threatened and Endangered (T&E) species in potential reserves. For each potential reserve, the number of Threatened and Endangered species with ranges overlapping the reserve is shown. Species are grouped according to whether we identified livestock grazing as a threat (red bars) or not (blue bars). Species threatened by grazing were identified using NatureServe Explorer's "Threat Comments" sections (NatureServe 2022).

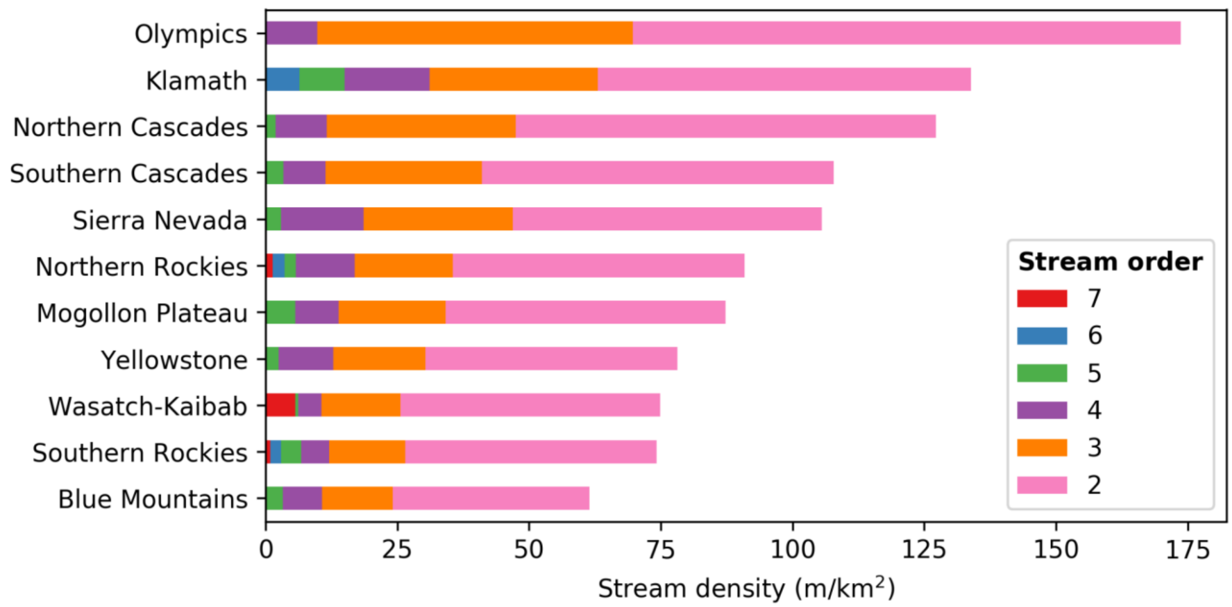

Figure S7. Stream densities in potential reserves. Stream densities by Strahler stream orders 2 through 7, with order 2 the smallest and order 7 stream the largest. First order streams were omitted since they may be unsuitable for beavers (Strahler 1957). Stream data are from the World Wildlife Fund (WWF) HydroRIVERS database (Lehner & Grill 2013).

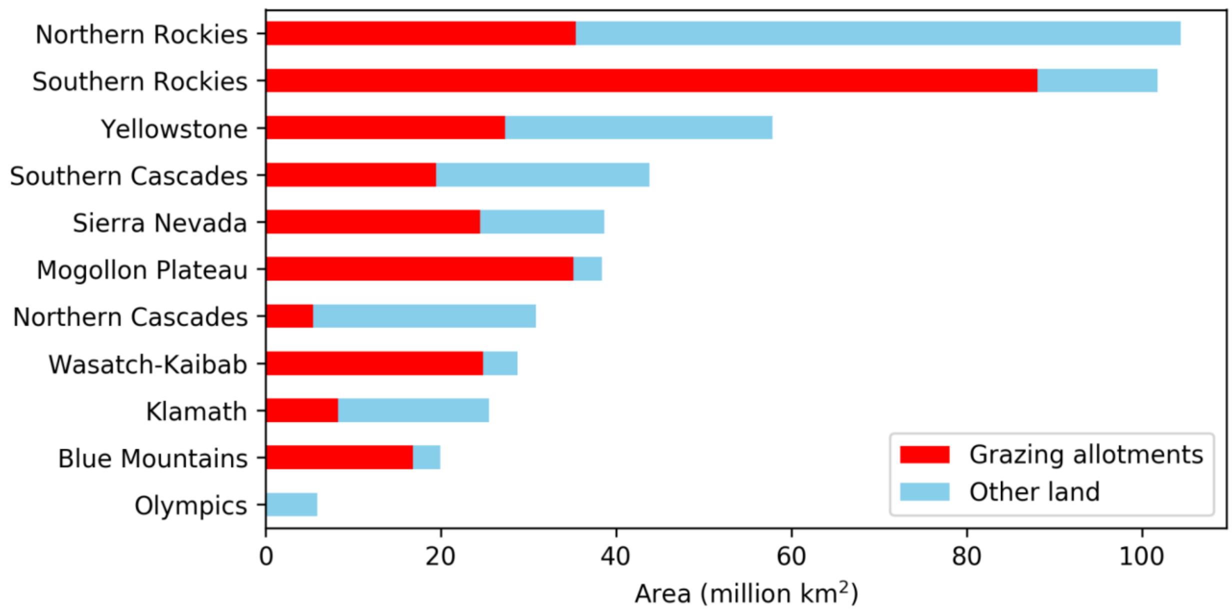

Figure S8. Summary of potential reserve areas. Reserves include grazing allotments (shown in red) and other National Park Service, Bureau of Land Management, Forest Service, and Fish & Wildlife Service lands (shown in blue). See Table S2 for details.

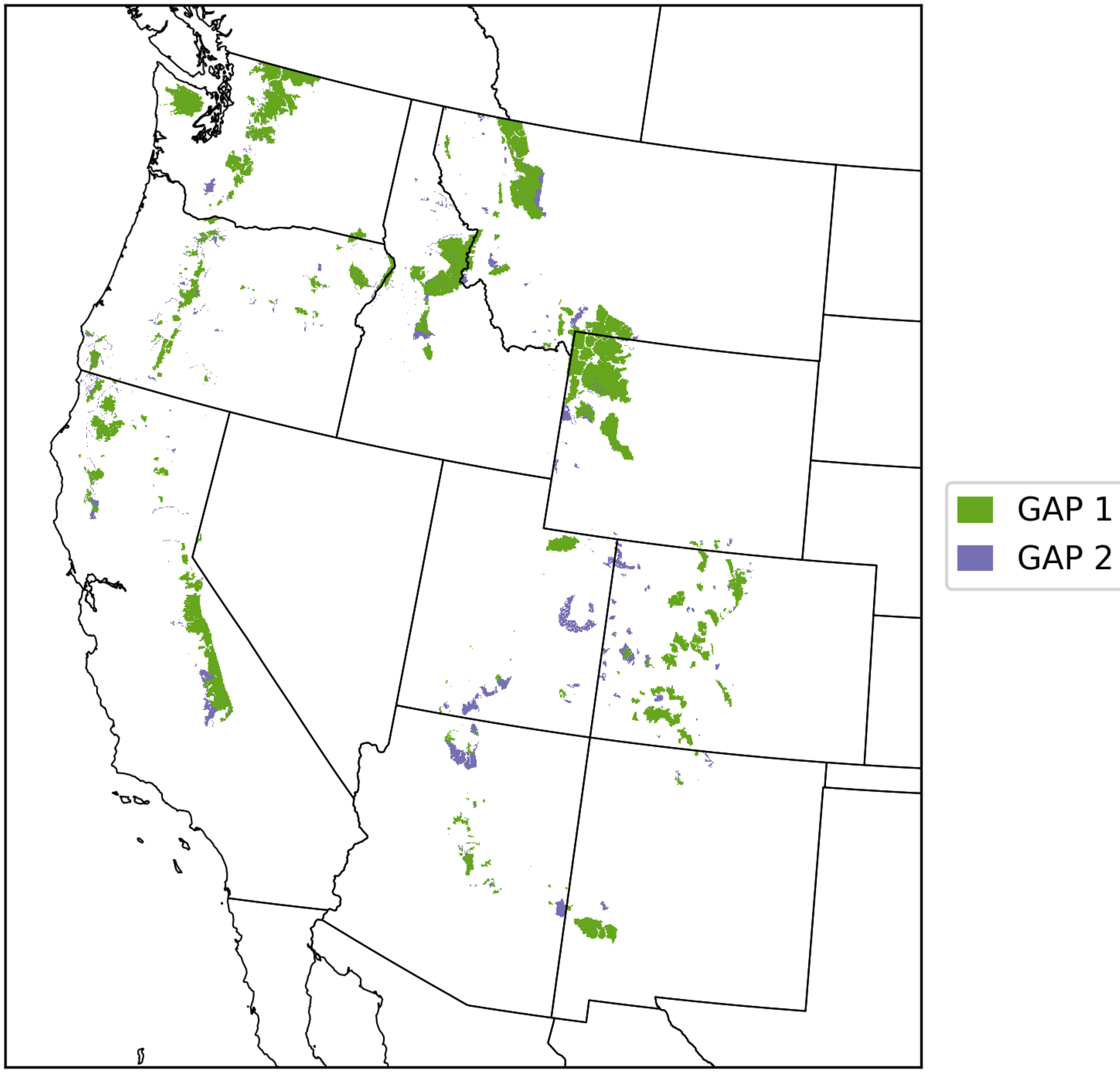

Figure S9. Protected areas within potential reserves. Colors indicate Gap Analysis Project (GAP) status (PAD-US 2020). Both GAP 1 and GAP 2 protected areas are managed for biodiversity. In GAP 1 protected areas, disturbance events proceed normally, whereas they are suppressed in GAP 2 protected areas. In total, GAP 1 and GAP 2 protected areas cover 6.8% and 4.1% of the Western US, respectively. They cover 22.7% and 4.9% of the proposed Western Reserve Network, respectively. Data are from the Protected Areas Database of the United States (PAD-US 2020). Note that livestock grazing is allowed within some of these protected areas.

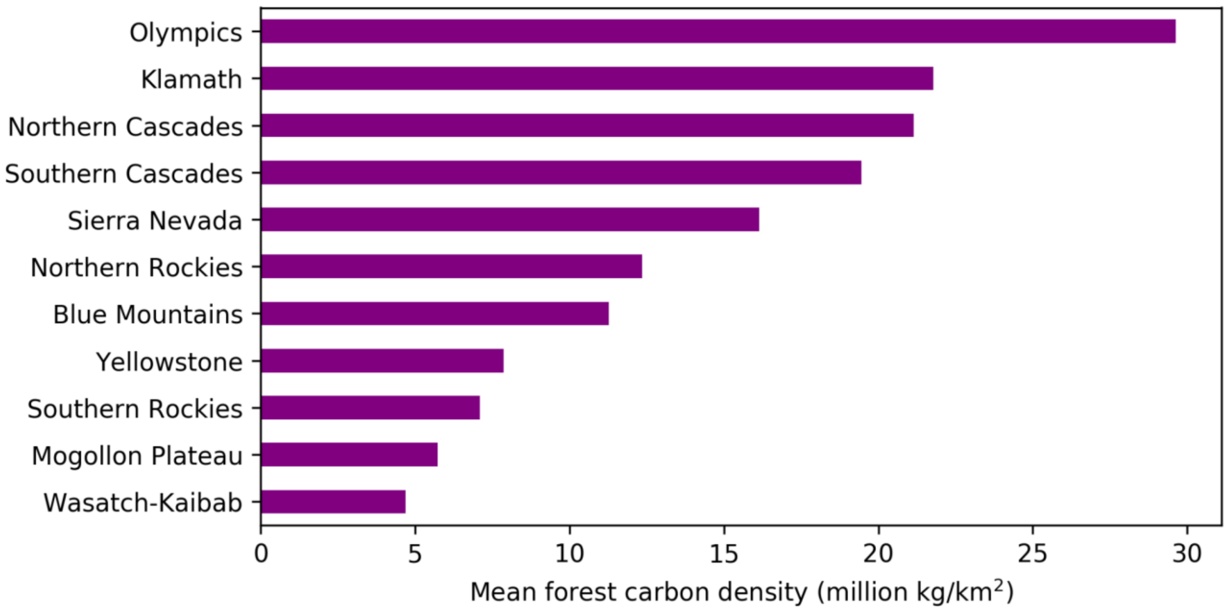

Figure S10. Summary of forest carbon density in potential reserves. Average forest carbon density varies greatly, with potential reserves in the Pacific Northwest having particularly high carbon density. See Table 1 for details. Forest carbon data are from Wilson et al. (2013).

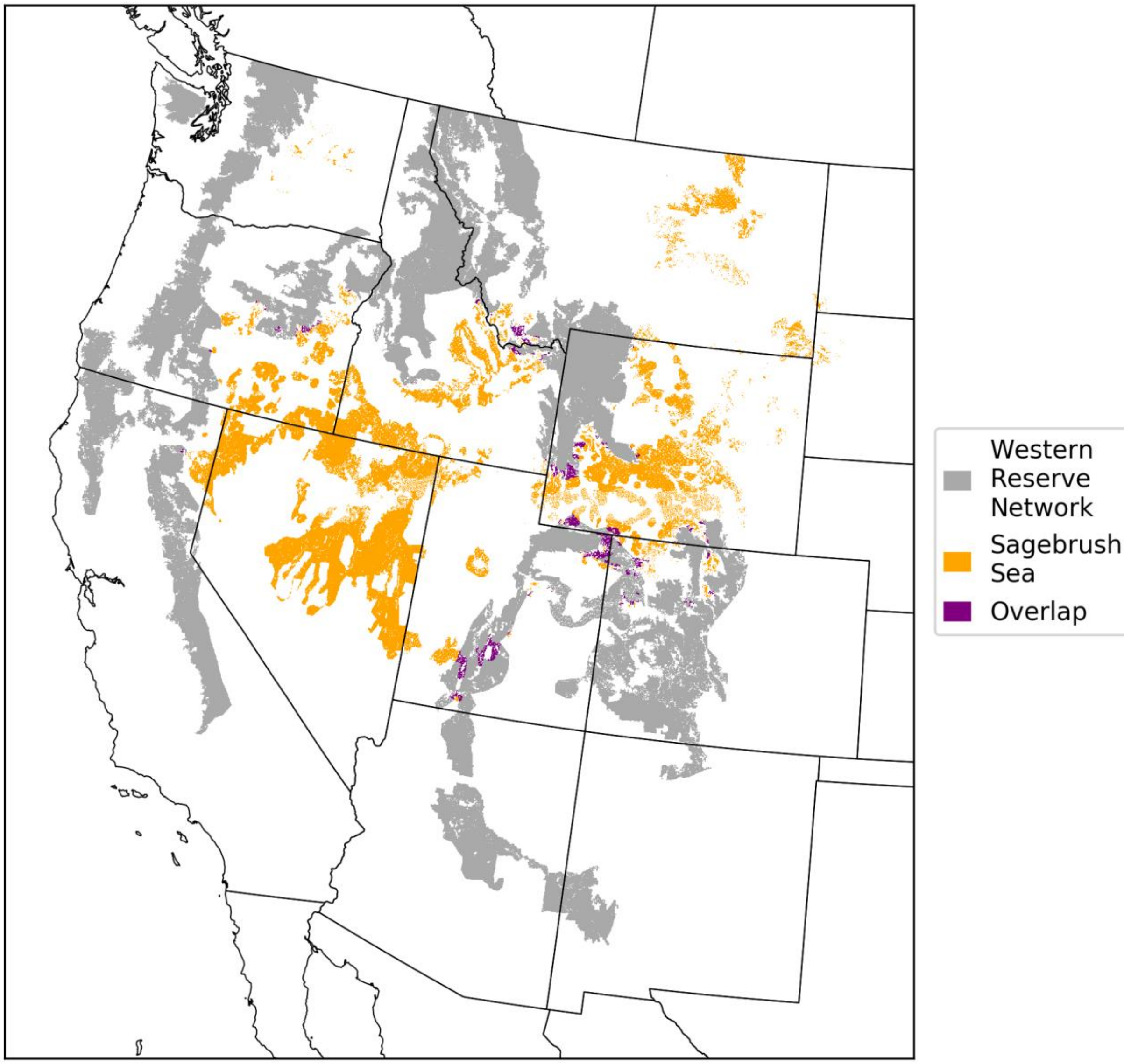

Figure S11. Western Reserve Network and Sagebrush Sea comparison. The 11 potential reserves that comprise the proposed Western Rewilding network Network are shown in gray. The proposed Sagebrush Sea Reserve network is shown in gold. Areas of overlap are shown in purple. Together, the Western Rewilding Network and the Sagebrush Sea Reserve Network make up 683,000 km^2 or approximately 22% of the area in the eleven western states. We obtained the Sagebrush Sea map from Holmer (2022).

Figure S12. Examples of Threatened and Endangered species within the Western Reserve Network that are threatened, at least in part, by livestock grazing. Species and photo credits (left to right): first row - Gunnison sage-grouse (*Centrocercus minimus*; US Department of Interior), Springville clarkia (*Clarkia springvillensis*; US Forest Service), Yellow-billed Cuckoo (*Coccyzus americanus*; Factumquintus, CC BY-SA 3.0); second row - Utah prairie dog (*Cynomys parvidens*; Chin tin tin, CC BY 2.0), Beautiful shiner (*Cyprinella formosa*; Brian Gratwicke, CC BY 2.0), Chihuahua chub (*Gila nigrescens*; Brian Gratwicke, CC BY 2.0); third row - Vernal pool tadpole shrimp (*Lepidurus packardi*; Bill Stagnaro, CC BY-SA 3.0), Dudley Bluffs bladderpod (*Lesquerella congesta*; Clayton Creed - U.S. Fish and Wildlife Service), Lahontan cutthroat trout (*Oncorhynchus clarkii henshawi*; Nevada Fish and Wildlife Office - U.S. Fish and Wildlife Service); fourth row - Brady pincushion cactus (*Pediocactus bradyi*; Rebou, CC BY-SA 3.0), Oregon spotted frog (*Rana pretiosa*; Mid-Columbia River Refuges, CC BY 2.0), New Mexico meadow jumping mouse (*Zapus hudsonius luteus*; Jennifer Frey/USFWS).

Table S1. Recent estimates of wolf population size, by state. Note that estimate types vary; for example, some are based on modeling whereas others are minimum known counts. Thus, care should be used when comparing estimates among states, and the overall total is only intended as an approximate lower bound. See references (listed in the third column) for details.

State	Estimate	Notes and reference for estimate
Arizona	72	2020 survey results based on ground and aerial counts (Maestas et al. 2021)
California	~52[1]	Known wolves only; April 2022 report (California Department of Fish and Wildlife 2022a)
Colorado	~5[2]	Very few wolves; first known breeding pair in decades was detected in June 2021 (Colorado Parks & Wildlife 2021)
Idaho	1,500	(International Wolf Center 2021)
Montana	1,156	Estimate for 2019 based on modeling (Inman et al. 2020)
Nevada	0	Wolves may visit Nevada occasionally (The Wildlife Society 2017)
New Mexico	114	2020 survey results based on ground and aerial counts (Maestas et al. 2021)
Oregon	173	Minimum known count in 2020 (Oregon Department of Fish and Wildlife 2021)
Utah	0	Wolves may visit Utah occasionally (Podmore 2020)
Washington	178	Minimum number in 2020 (Washington Department of Fish and Wildlife et al. 2021)
Wyoming	327	Minimum number of wolves in Wyoming on December 31, 2020 (Wyoming Game and Fish Department et al. 2021)
Total	**3,577**	

[1] This estimate is highly uncertain as it was difficult to obtain a precise count of known wolves

[2] Estimate based on one known breeding pair with three pups. It is likely that several other wolves are present in Colorado, making the actual total higher (Colorado Parks & Wildlife 2021).

Table S2. Summary of potential reserves. For each potential reserve, the first columns show the reserve name, total area, area of Forest Service and Bureau of Land Management grazing allotments (Allot.), average forest carbon density (across the entire reserve), total amount of forest carbon in the proposed reserve, density of roads (highways and primary roads) and streams (orders 2 through 7). The final three columns show the percentage of the proposed reserve that is protected at the GAP 1 level, the percentage at GAP 2, and finally the percentage of all GAP 1 and GAP 2 protected land within the proposed reserve that is designated as livestock grazing allotments (P. Allot.). Carbon data are from Wilson et al. (2013) and protected area data are from PAD-US (2020). This rewilding network, already publicly owned, would make up approximately 496,000 km^2 or 16% of the eleven western states. See Supplemental Methods for other data sources.

Region	Area (km^2)	Allot. (km^2)	mean C (Mg/km^2)	total C (Mt)	Roads (m/km^2)	Streams (m/km^2)	GAP 1 (%)	GAP 2 (%)	P. Allot. (%)
Northern Rockies	104,437	35,417	12,351	1,290	5.0	90.9	24.0%	3.9%	12.9%
Southern Rockies	101,787	88,080	7,103	723	10.5	74.2	15.6%	6.5%	73.1%
Yellowstone	57,860	27,346	7,877	456	15.1	78.2	42.2%	4.0%	14.6%
Southern Cascades	43,788	19,494	19,444	851	15.6	107.8	11.8%	2.8%	11.4%
Sierra Nevada	38,665	24,455	16,133	624	22.1	105.6	28.2%	4.8%	38.8%
Mogollon Plateau	38,387	35,144	5,733	220	16.2	87.2	13.9%	2.9%	73.9%
Northern Cascades	30,867	5,440	21,145	653	11.0	127.2	43.7%	2.8%	5.9%
Wasatch-Kaibab	28,783	24,796	4,702	135	10.6	74.9	2.4%	14.7%	47.8%
Klamath	25,493	8,280	21,777	555	11.6	133.9	23.9%	5.8%	21.8%
Blue Mountains	19,954	16,842	11,272	225	6.6	61.5	8.8%	2.3%	37.1%
Olympics	5,898	0	29,628	175	7.1	173.7	63.0%	0.1%	0.0%

Table S3. Threatened and endangered species in potential reserves. Columns indicate species (or subspecies or DPS) name, common name, initials of potential reserves (see Figure 1 for full names), total range size, and extractive threats ("Li": Livestock, "Lo": Logging, "Mi": Mining", and "O/G": Oil and gas). Footnotes indicate cases where a species is listed across only part of its range. Species are organized by taxonomic group, which is shown in red with the number of associated species in parentheses. Only species with at least 10% of their ranges in potential reserves were considered. Extractive threats were identified using NatureServe Explorer's "Threat Comments" descriptions (NatureServe 2022).

Scientific Name	Common Name	Reserves	Area (km^2)	Li	Lo	Mi	O/G
		Amphibians (5)					
Anaxyrus canorus	Yosemite toad	SN	19,388	*	*		
Rana chiricahuensis	Chiricahua leopard frog	MP	130,535	*		*	
Rana muscosa[3]	Mountain yellow-legged frog	SN	8,871				
Rana pretiosa	Oregon spotted frog	SC NC K	25,149	*			
Rana sierrae	Sierra Nevada Yellow-legged Frog	SN	35,714				
		Birds (5)					
Centrocercus minimus	Gunnison sage-grouse	SR	7,830	*			
Coccyzus americanus[4]	Yellow-billed Cuckoo	NR SR Y SC SN MP NC W-K K BM O	1,216,883	*			
Gymnogyps californianus[5]	California condor	SN MP W-K	167,475				
Strix occidentalis caurina	Northern spotted owl	SC NC K O	178,223		*		
Strix occidentalis lucida	Mexican spotted owl	SR MP W-K	540,042	*	*		
		Crustaceans (2)					
Lepidurus packardi	Vernal pool tadpole shrimp	SC SN K	65,186				

[3] Northern California DPS
[4] Western U.S. DPS
[5] U.S.A. only, except where listed as an experimental population

Scientific Name	Common Name	Reserves	Area (km^2)	Li	Lo	Mi	O/G
Pacifastacus fortis	Shasta crayfish	SC SN	6,556		*		
		Fishes (22)					
Chasmistes brevirostris	Shortnose Sucker	SC K	50,875				
Chasmistes cujus	Cui-ui	SN	7,067				
Cyprinella formosa	Beautiful shiner	MP	18,397				
Deltistes luxatus	Lost River sucker	SC K	28,953				
Gila cypha	Humpback chub	SR Y W-K	198,969				
Gila elegans	Bonytail	SR	110,280				
Gila intermedia	Gila chub	MP	20,208	*		*	
Gila nigrescens	Chihuahua chub	MP	10,274	*	*		
Hypomesus transpacificus	Delta smelt	SC K	12,390				
Lepidomeda vittata	Little Colorado spinedace	MP	9,698	*	*	*	
Meda fulgida	Spikedace	MP	48,442				
Oncorhynchus aguabonita whitei	Little Kern golden trout	SN	1,624	*			
Oncorhynchus apache	Apache trout	MP W-K	7,861	*			
Oncorhynchus clarkii henshawi	Lahontan cutthroat trout	SN	17,820	*	*	*	
Oncorhynchus clarkii seleniris	Paiute cutthroat trout	SN	2,478	*			
Oncorhynchus clarkii stomias	Greenback Cutthroat trout	SR	36,667		*	*	
Oncorhynchus gilae	Gila trout	MP	42,196	*	*	*	
Poeciliopsis occidentalis	Gila topminnow (incl. Yaqui)	MP	23,444				

Scientific Name	Common Name	Reserves	Area (km^2)	Li	Lo	Mi	O/G
Ptychocheilus lucius[6]	Colorado pikeminnow (=squawfish)	SR Y MP	267,942				
Salvelinus confluentus[7]	Bull Trout	NR SC NC BM O	3,331	*	*	*	
Tiaroga cobitis	Loach minnow	MP	47,986				
Xyrauchen texanus	Razorback sucker	SR MP W-K	175,117				
		Flowering Plants (39)					
Arabis macdonaldiana	McDonald's rock-cress	K	14,249			*	
Astragalus applegatei	Applegate's milk-vetch	SC	15,903				
Astragalus cremnophylax var. cremnophylax	Sentry milk-vetch	W-K	5				
Astragalus montii	Heliotrope milk-vetch	W-K	271	*			
Calyptridium pulchellum	Mariposa pussypaws	SN	919				
Clarkia springvillensis	Springville clarkia	SN	1,246	*			
Erigeron rhizomatus	Zuni fleabane	MP	47,270	*			*
Eriogonum pelinophilum	Clay-Loving wild buckwheat	SR	1,337	*			*
Eutrema penlandii	Penland alpine fen mustard	SR	309			*	
Fritillaria gentneri	Gentner's Fritillary	SC K	13,101		*		
Hackelia venusta	Showy stickseed	NC	1,143				
Ipomopsis polyantha	Pagosa skyrocket	SR	600	*			
Ivesia webberi	Webber's ivesia	SN	1,580				
Lasthenia burkei	Burke's goldfields	K	12,784	*			
Lasthenia conjugens	Contra Costa goldfields	K	13,062			*	
Lesquerella congesta	Dudley Bluffs	SR	313	*		*	*

[6] Wherever found, except where listed as an experimental population
[7] U.S.A., conterminous, lower 48 states

Scientific Name	Common Name	Reserves	Area (km^2)	Li	Lo	Mi	O/G
	bladderpod						
Lesquerella tumulosa	Kodachrome bladderpod	W-K	521				
Mirabilis macfarlanei	MacFarlane's four-o'clock	NR	1,104	*			
Orcuttia tenuis	Slender Orcutt grass	SC SN K	19,722				
Packera franciscana	San Francisco Peaks ragwort	MP	24				
Pediocactus (=Echinocactus,=Utahia) sileri	Siler pincushion cactus	W-K	4,648	*		*	
Pediocactus bradyi	Brady pincushion cactus	W-K	725	*			
Pediocactus peeblesianus fickeiseniae	Fickeisen plains cactus	MP W-K	16,130	*		*	
Penstemon debilis	Parachute beardtongue	SR	2,390			*	*
Phacelia argillacea	Clay phacelia	SR W-K	695	*			
Phacelia formosula	North Park phacelia	SR	1,667	*			*
Phacelia submutica	DeBeque phacelia	SR	1,110	*			*
Phlox hirsuta	Yreka phlox	K	2,748	*	*		
Physaria obcordata	Dudley Bluffs twinpod	SR	994	*		*	*
Purshia (=Cowania) subintegra	Arizona Cliffrose	MP	3,831	*			
Ranunculus aestivalis (=acriformis)	Autumn Buttercup	W-K	138				
Schoenocrambe barnebyi	Barneby reed-mustard	W-K	1,870			*	
Schoenocrambe suffrutescens	Shrubby reed-mustard	SR	690	*		*	*
Sclerocactus glaucus	Colorado hookless Cactus	SR	5,825				*
Sclerocactus wetlandicus	Uinta Basin hookless cactus	SR	2,086				

Scientific Name	**Common Name**	**Reserves**	**Area (km^2)**	**Li**	**Lo**	**Mi**	**O/G**
Sidalcea oregana var. calva	Wenatchee Mountains checkermallow	NC	1,953	*	*		
Silene spaldingii	Spalding's Catchfly	NR BM	39,055	*		*	
Townsendia aprica	Last Chance townsendia	W-K	4,057	*		*	*
Trifolium amoenum	Showy Indian clover	K	12,449				
		Insects (5)					
Boloria acrocnema	Uncompahgre fritillary butterfly	SR	4,771				
Bombus franklini	Franklin's bumblebee	SC K	45,866				
Euphydryas editha taylori	Taylor's (=whulge) Checkerspot	O	19,487				
Lednia tumana	Meltwater lednian stonefly	NR	40				
Zapada glacier	Western glacier stonefly	NR Y	679				
		Mammals (11)					
Canis lupus[8]	Gray wolf	SC NC K BM	372,064				
Canis lupus baileyi[9]	Mexican wolf	MP	64,796				
Cynomys parvidens	Utah prairie dog	W-K	22,745	*			
Lynx canadensis[10]	Canada Lynx	NR SR Y SC NC W-K BM	928,154		*		
Martes caurina	Pacific Marten, Coastal Distinct Population Segment	K	57,324		*		
Ovis canadensis sierrae[11]	Sierra Nevada bighorn sheep	SN	10,287	*		*	
Pekania pennanti[12]	Fisher	SN	37,714		*		

[8] U.S.A.: All of AL, AR, CA, CO, CT, DE, FL, GA, IA, IN, IL, KS, KY, LA, MA, MD, ME, MI, MO, MS, NC, ND, NE, NH, NJ, NV, NY, OH, OK, PA, RI, SC, SD, TN, TX, VA,

[9] Wherever found, except where listed as an experimental population

[10] Wherever Found in Contiguous U.S.

[11] Sierra Nevada

[12] SSN DPS

Scientific Name	Common Name	Reserves	Area (km^2)	Li	Lo	Mi	O/G
Urocitellus brunneus	Northern Idaho Ground Squirrel	NR	1,481	*	*		
Ursus arctos horribilis[13]	Grizzly bear	NR Y	143,670	*			*
Vulpes vulpes necator	Sierra Nevada red fox	SN	29				
Zapus hudsonius luteus	New Mexico meadow jumping mouse	SR MP	72,364	*			
			Reptiles (1)				
Thamnophis rufipunctatus	Narrow-headed gartersnake	MP	838	*			
			Snails (2)				
Pyrgulopsis trivialis	Three Forks Springsnail	MP	126	*			
Tryonia alamosae	Alamosa springsnail	MP	1,042	*			

[13] U.S.A., conterminous (lower 48) States, except where listed as an experimental population

Table S4. Summary of high connectivity regions. Each row summarizes connectivity between a different pair of reserves (first two columns). The "Area" column indicates the area of the associated high connectivity region (Figure S3). Subsequent columns indicate the percentages of this region that are livestock grazing allotments, federal lands (National Park Service, Bureau of Land Management, Forest Service, and Fish & Wildlife Service), and potential core gray wolf habitat respectively. Connectivity potential was modeled using the Circuitscape software with a resistance raster derived from maps of federal lands and potential core gray wolf habitat (Anantharaman et al. 2020; Carroll et al. 2021; Esri et al. 2021). See Supplemental Methods for details.

First reserve	Second reserve	Area (km2)	Allotments (%)	Federal (%)	Habitat (%)
Blue Mountains	Northern Rockies	3,692	33.5%	46.6%	83.3%
Blue Mountains	Southern Cascades	11,980	57.1%	75.8%	59.5%
Klamath	Southern Cascades	5,191	9.8%	63.2%	93.5%
Klamath	Sierra Nevada	8,807	28.0%	57.0%	76.6%
Klamath	Olympics	35,954	7.9%	29.1%	79.6%
Northern Cascades	Northern Rockies	15,847	34.8%	60.2%	99.1%
Northern Cascades	Southern Cascades	1,967	29.9%	52.3%	97.7%
Northern Cascades	Olympics	21,224	0.0%	6.1%	69.2%
Northern Rockies	Yellowstone	10,807	67.9%	81.1%	96.7%
Sierra Nevada	Southern Cascades	7,312	35.4%	55.6%	68.8%
Southern Rockies	Yellowstone	15,668	62.2%	69.1%	91.0%
Southern Rockies	Wasatch-Kaibab	1,605	51.7%	55.4%	97.9%

Supplemental Discussion

Successful rewilding will depend on the reversal of state policies that severely limit wolf and beaver abundances. Such policies can impact abundances even within strictly protected areas. For example, more than 500 wolves were recently killed in Idaho, Montana, and Wyoming, which included roughly 20% of the wolves that frequent Yellowstone National Park (Morell 2022). Overall, predator control and recreational wolf hunting are strongly associated with total mortality rates among North American wolf populations (Creel & Rotella 2010) and can disrupt pack social structures, potentially leading to greater livestock depredation risk (Santiago-Avila et al. 2018; Kareiva et al. 2021). In addition, widespread culling of wolves and beavers (and other native mammals) by the U.S. Department of Wildlife Services should be debated and potentially reduced in order to improve connectivity among reserves (Bergstrom et al. 2014).

Federal Status of Wolves in the Western United States

With the exception of the Northern Rocky Mountain population, all gray wolves in the contiguous United States are protected under the Endangered Species Act (U.S. Fish & Wildlife Service 2022a). This is due to a court ruling made on February 10, 2022. As shown in U.S. Fish & Wildlife Service (2022a), the Northern Rocky Mountain population fully covers Idaho, Montana, Wyoming, and covers parts of Washington, Oregon, and Utah. This court ruling does not apply to the Mexican gray wolf.

Given many state wolf management policies (reviewed below), for rewilding to be most effective, wolves should be fully protected federally across the entire contiguous United States (Kareiva et al. 2021).

State wolf policies in the Western US

For each state, excerpts from wolf reports and other sources are shown indicating the listing status of wolves and laws regarding killing wolves.

Arizona

“Legal status: Federal protection, with some exceptions” (International Wolf Center 2022a)

“The Arizona Department of Game and Fish said in a monthly report issued Thursday that a female wolf, a member of the Diamond Pack in Arizona, was “lethally removed” last month following a series of confirmed livestock deaths.” (Lobos of the Southwest 2017)

California

“Gray wolves are listed as endangered under the California Endangered Species Act (CESA) and Species of Greatest Conservation Need in the State Wildlife Action Plan. The "take" of a gray wolf in the state is prohibited, including to hunt, pursue, catch, capture, or kill. This recovering species is in the early stages of establishing itself in California." (California Department of Fish and Wildlife 2022b)

"As of January 2021, the gray wolf is no longer listed under the federal Endangered Species Act" (California Department of Fish and Wildlife 2022b)

Colorado

"On Thursday, February 10th, 2022, the United States District Court vacated the U.S. Fish and Wildlife's (USFWS) 2020 rule delisting gray wolves across the lower 48 states. The ruling returns management authority of gray wolves in Colorado to the U.S. Fish and Wildlife Service." (Colorado Parks & Wildlife 2022a)

"CPW and the Parks and Wildlife Commission will create or modify appropriate regulations to manage the species according to the management plan developed. For example, in January 2022, regulations were passed to permit the use of certain hazing techniques, in part due to the presence of a known pack of naturally migrating wolves in the state. Additionally, a regulation has been passed to take effect in May 2022 that prevents the use of lures to attract wolves." (Colorado Parks & Wildlife 2022b)

Idaho

"Wolves were removed from the ESA endangered species list in 2011. Wolves in Idaho are currently managed under the 2002 Idaho Wolf Conservation and Management Plan and are classified as a big game animal with harvest authorized for both hunting (2009) and trapping (2011)." (Idaho Fish & Game 2017)

"Idaho Code states that wolves molesting or attacking livestock or domestic animals may be controlled (killed) by livestock or domestic animal owners, their employees, agents and animal damage control personnel. No permit from Fish and Game is necessary." (Idaho Fish and Game 2022)

Montana

"Gray wolves are classified as a 'Species in Need of Management' in the state. Montana maintains sustainable hunting and trapping opportunities for wolves that follow the commitments outlined in the state's conservation and management plan." (Montana Fish, Wildlife & Parks 2022)

"At present, Montana Fish, Wildlife and Parks (FWP) implements the 2004 state management plan using a combination of sportsman license dollars and federal Pittman-Robertson funds [...] to monitor the wolf population, regulate harvest, collar packs in livestock areas, coordinate and authorize research, and direct problem wolf control under certain circumstances." (Inman et al. 2020)

Nevada

"Because the court vacated the U.S. Fish and Wildlife Service's 2020 final delisting rule, gray wolves outside of the Northern Rocky Mountain population [...] are now protected under the Endangered Species Act (ESA) as threatened in Minnesota and endangered in the remaining states." (U.S. Fish & Wildlife Service 2022a)

New Mexico

"Legal status: Federal protection, with some exceptions" (International Wolf Center 2022b)

"The U.S. Fish and Wildlife Service surreptitiously authorized the killing of four endangered Mexican gray wolves in New Mexico on behalf of the livestock industry. In response the U.S. Department of Agriculture's Wildlife Services program killed one wolf on March 23 [2020] and three more on March 28 [2020]." (Center for Biological Diversity 2020)

Oregon

"[Oregon Department of Fish and Wildlife] manages wolves in two wolf management zones (West Wolf Management Zone, East Wolf Management Zone). Wolves throughout Oregon were delisted from the state Endangered Species List on November 10, 2015. Wolves are still protected statewide by the Wolf Plan and Oregon statute. Wolves west of Highways 395/78/95 were removed from the federal Endangered Species Act (ESA) on January 4, 2021, then relisted on February 10, 2022." (Oregon Department of Fish and Wildlife 2022a)

"Wolves in eastern Oregon are currently managed under Phase III of the state's Wolf Plan. Wolves in western Oregon are managed under Phase I rules, which provide ESA-like protections, until this area of the state has four breeding pairs of wolves for three consecutive years." (Oregon Department of Fish and Wildlife 2022b).

"The Plan emphasizes use of non-lethal techniques to prevent livestock depredation, but allows implementation of lethal control to address chronic depredation [...]." (Oregon Department of Fish and Wildlife 2019)

Utah

"Due to a recent court ruling, wolves in much of Utah are once again listed as endangered under the federal Endangered Species Act. Wolves are only delisted in a small portion of northern Utah. The delisted zone (highlighted in green on the map) is the only area where the State of Utah has any authority to manage, capture or kill wolves. In the rest of the state, wolves are considered an endangered species and fall under federal control." (Utah Division of Wildlife Resources 2022)

"Although there have been confirmed wolf sightings — and rare instances of wolf-related livestock depredation — there are no known established packs in Utah." (Utah Division of Wildlife Resources 2022)

"Wolves will be controlled or populations reduced when they cause unacceptable impacts to big game. At the UDWR Director's discretion, an emergency management action may be implemented for wolves preying on populations of wildlife that are being re-established, and/or are at low levels. Such an action might include non-lethal control, such as relocation, or lethal control actions." (Utah Division of Wildlife Resources & Utah Wolf Working Group 2005)

Washington

"On Feb. 10, 2022, a U.S. District Judge's order to restore federal protection for gray wolves in certain areas of the U.S. means that wolves in Washington are now federally endangered in the western two-thirds of the state. Wolves in that area were previously listed under the Endangered Species Act until January 4, 2021." (Washington Department of Fish and Wildlife 2022)

"State law specifies that when species are federally listed, [Washington Department of Fish and Wildlife] will recommend they be added to the state's list. Penalties for illegally killing a state endangered species range up to $5,000 and/or one year in jail." (Washington Department of Fish and Wildlife 2022)

"The commission is authorized, pursuant to RCW 77.36.030, to establish the limitations and conditions on killing or trapping wildlife that is causing damage on private property. The department may authorize, pursuant to RCW 77.12.240 the killing of wildlife destroying or injuring property. [...] This section applies to the area of the state where the gray wolf is not listed as endangered or threatened under the federal Endangered Species Act." (Washington state Legislature 2022)

Wyoming

"Wolves in Wyoming were removed from the endangered species list on April 25, 2017. This means management of this species is now led by the State of Wyoming and is subject to state statutes and Commission regulations." (Wyoming Game & Fish Department 2022)

"In 2020, the Wyoming Game and Fish Department implemented a wolf hunting season with the biological objective to stabilize the wolf population at approximately 160 wolves in the [Wolf Trophy Game Management Area]." (Wyoming Game and Fish Department et al. 2021)

“Forty-three wolves were lethally and legally removed by agencies or the public in an effort to reduce livestock losses to wolves.” (Wyoming Game and Fish Department et al. 2021)

Supplemental Methods

Current wolf population

Data on the current wolf population size by state are widely available and likely to be reasonably accurate (Table S1). In total, there are roughly at least 3,520 wolves in the American West (Table S1), although the actual number of wolves could be substantially higher due to some states reporting minimum counts.

Photo credits

We obtained the photos in Figure 2 from the following sources: A) *Removal of Livestock* - left photo from US Fish and Wildlife Service, right from photo Batchelor et al. (2015), B) *Return of Wolves* - left photo from National Park Service, right photo from Robert L. Beschta, C) *Return of Beaver* - left and right photos from US Bureau of Land management.

Data sources and processing

We identified current National Park Service (NPS), Fish and Wildlife Service (FWS), Forest Service (FS), and Bureau of Land Management (BLM) lands using a map of United States federal lands (Esri et al. 2021). The associated data were obtained from federal agencies by Esri and compiled into a single dataset, which was last updated on July 22, 2021. We also obtained a map of FS grazing allotments (U.S. Forest Service 2021), which was last refreshed on September 7, 2021 and is a feature class within the more general Range Management Unit dataset. Similarly, we obtained a map of BLM grazing allotments (Bureau of Land Management 2021). This map was published on July 21, 2021 and indicates the spatial extent of BLM grazing allotments based on data compiled from BLM state offices.

We obtained information on the current gray wolf range and a current distribution map from Curt Bradley and Amaroq Weiss with the Center for Biological Diversity. Note that it includes a small polygon in the extreme northwest Colorado, which may be difficult to see at the regional scale. We modified the map by substituting the more accurate “USFWS Mexican Wolf Project 2020 Occupied Range S of I40” dataset in the American Southwest (U.S. Fish and Wildlife Service & Esri 2022). This dataset shows areas south of I-40 that were occupied by Mexican wolves as of the end of 2020.

We obtained a map showing potential core gray wolf habitat adapted from Carroll et al. (2021) by Curt Bradley with the Center for Biological Diversity (CBD and HSUS 2018).

To estimate forest carbon within potential wolf reserves, we used the "Forest carbon stocks of the contiguous United States (2000-2009)" dataset (Wilson et al. 2013). Specifically, we used the variable "carbon_tot_mg_ha," which reflects the total forest carbon across all stocks at 250 m resolution for the period 2000-2009. Following Law et al. (2021), we masked out non-forested areas using the "Conus Forest Group" dataset from Ruefenacht et al. (2008).

To assess the extent of formal protection we used version 2.1 of the Protected Areas Database of the United States (PAD-US 2020). We considered GAP 1 and GAP 2 protected areas, which are both managed for biodiversity. In GAP 1, natural disturbances proceed normally, whereas in GAP 2, natural disturbances are suppressed (PAD-US 2020).

We obtained road density estimates at 5 arcminute resolution from the GRIP global roads database (Meijer et al. 2018). Specifically, we used the Type 1 (highways) and Type 2 (primary roads) road density rasters.

We obtained a range map showing quaking aspen (*Populus tremuloides*) distribution across North America from Little (1971).

Lastly, we used version 1.0 of the World Wildlife Fund (WWF) HydroRIVERS database as our data source for stream locations (Lehner & Grill 2013). This database is derived from HydroSHEDS data at a 15 arc-second resolution, and is based on defining streams as starting at all pixels with accumulated upstream catchment area greater than 10 km^2 or long-term average natural discharge is greater than 0.1 m/s (Lehner & Grill 2013). We considered only streams with Strahler order between 2 and 7.

We converted all spatial data to 1-km resolution rasters in the USA Contiguous Albers Equal Area Conic projection. We restricted our analysis to the 11 states that make up the Western United States.

Potential reserves

To identify potential wolf reserves, we considered patches (contiguous areas) within core gray wolf habitat on federal lands (NPS, BLM, USFWS, or FS only). We treated raster pixels as connected if they shared a border. So, diagonal connections were not considered. We focused our analysis on patches with an area of at least 5,000 km^2.

We quantified connectivity among potential reserves using the Circuitscape connectivity modeling software (Anantharaman et al. 2020). Circuitscape treats a landscape as a network of resistors and simulates electrical current flow among focal regions across this network. The resistance and current have ecological interpretations, which are described in detail in McRae et al. (2008). In short, resistance can be viewed as the relative difficulty of movement associated with various habitat types and current is related to the relative movement probabilities associated with individuals performing resistance-weighted random walks (McRae et al. 2008). Thus, regions with higher current are likely more important from a connectivity perspective. We used Circuitscape in pairwise mode and mapped the resulting cumulative log current. We considered only nearby pairs of reserves and composited using the maximum function. For the resistance raster, we used 100 plus the following terms:

1. 100 if outside potential core habitat
2. 100 if outside NPS, BLM, and FS lands

For each pair of reserves that we considered (Figure S3), we identified regions with high connectivity using a -6.0 threshold for log current. Such regions are likely particularly important for movement between the pair of reserves. For each of these regions, which could be associated with wildlife corridors, we calculated total area as well as the percentages of the region that were livestock grazing allotments, federal (USFWS, NPS, BLM, and FS) lands, and potential core gray wolf habitat.

In addition, we mapped livestock allotments and forest carbon within potential reserves. For each potential reserve, we also calculated the following statistics:

1. Total reserve area (km^2)
2. Grazing allotment area (km^2)
3. Total forest carbon (Mt)
4. Average forest carbon density (Mg/km^2)
5. Average density of highways and primary roads (m/km^2)
6. Average stream density (m/km2)
7. Percentages protected at GAP 1 and GAP 2 levels (%)
8. Percentage of protected areas (GAP 1 or GAP2) that are also livestock grazing allotments (%)

Threatened and Endangered species

We obtained a list of Threatened and Endangered (T&E) plant and animal species using the USFWS Environmental Conservation Online System (U.S. Fish & Wildlife Service 2022b). To identify T&E species within potential reserves we first rasterized the associated species' range maps (U.S. Fish & Wildlife Service 2022b). We then restricted our analysis to species with at least 10% of their ranges within potential reserves. Note that the quality and methodology associated with the species range maps varies considerably. Thus, our results should be interpreted with this limitation in mind.

We determined the extractive threats faced by these species using NatureServe Explorer's "Threat Comments" descriptions (NatureServe 2022). We considered four threats: Livestock, Logging, Mining", and Oil & Gas. We included threats that were described as historical in nature since they could recur in the future. We did not list threats that were described as "unlikely" or "possible" in cases where little evidence was available.

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