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Defining ecological and socially suitable habitat for the reintroduction of an apex predator

Mark A. Ditmer [a,b,*], George Wittemyer [a], Stewart W. Breck [c], Kevin R. Crooks [a]

[a] Department of Fish, Wildlife, and Conservation Biology, Colorado State University, 115 Wagar, Fort Collins, CO 80523, USA
[b] USDA. Forest Service, Rocky Mountain Research Station, 324 25th Street, Ogden, UT, 84401, USA
[c] USDA National Wildlife Research Center, 4101 LaPorte Avenue, Fort Collins, CO, USA

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ABSTRACT

Reintroducing native carnivores risks creating conflict with people and consequently reducing support for coexistence and conservation efforts. Determining the interface between areas of ecological suitability and conflict risk can help enhance success of carnivore restoration, but this is often difficult because accurate data on risks and tolerance are lacking. Gray wolves (*Canis lupus*), a focus of reintroduction efforts in the US, require tolerance to persist in human-dominated landscapes but also catalyze societal-level conflicts throughout their global range. Via an unprecedented process to restore an apex predator, in November 2020, citizens in the state of Colorado, USA voted to reintroduce wolves to the state where they had been extirpated ~70 years prior. We leveraged voting records of over three million citizens to quantify and map an index of tolerance for wolves and combined it with spatially explicit data on livestock distributions and land ownership to create predictions of direct conflict risk between wolves and humans. Conflict risk was juxtaposed with estimates of wolf ecological suitability developed using seasonal prey densities along with environmental and anthropogenic features that influence wolf habitat use. Our social-ecological modeling approach predicted that ~56 % of the West Slope of Colorado contained ecologically suitable habitat and relatively low conflict risk. Our models also delineated possible conflict hotspots where ecological suitability and conflict risk converge, thus facilitating targeted proactive management. We demonstrate how voting patterns can provide unique, spatially explicit insight on tolerance that can be integrated with other information to help facilitate human-carnivore coexistence and carnivore restoration success.

1. Introduction

Defaunation of the world's carnivore species throughout vast portions of their ranges (Wolf and Ripple, 2017) have led to efforts to restore populations (Johns, 2019). In some areas, carnivores can play important roles in ecological communities through top-down interactions (Ripple et al., 2017), both directly (e.g., predation) and indirectly (e.g., behavioral modification of prey species and mesocarnivores). This can result in cascading effects on ecosystems such as reductions of prey populations and habitat alterations (Estes et al., 2011; Peterson et al., 2014). Humans can derive benefits from carnivores such as existence and aesthetic values and revenue from tourism or hunting (Duffield, 2019), and indirectly from alterations to prey behavior and abundance (Ripple et al., 2014;

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* Correspondence to: U.S.D.A. Forest Service Rocky Mountain Research Station, 324 25th Street, Ogden, UT, 84401,USA.
E-mail address: mark.ditmer@usda.gov (M.A. Ditmer).

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Gilbert et al., 2017; Raynor et al., 2021). However, carnivores also can incur costs to people, including threats to human safety and depredation of domestic animals, which can inflict substantial economic losses and emotional grief (Muhly and Musiani, 2009). Such conflict can result in strong negative attitudes, especially among those incurring costs most frequently (Naughton-Treves et al., 2003). For reintroduction efforts of carnivores to succeed, efforts must consider ways of reducing conflict and determining where tolerance will allow for long-term human-carnivore coexistence (Lute et al., 2018).

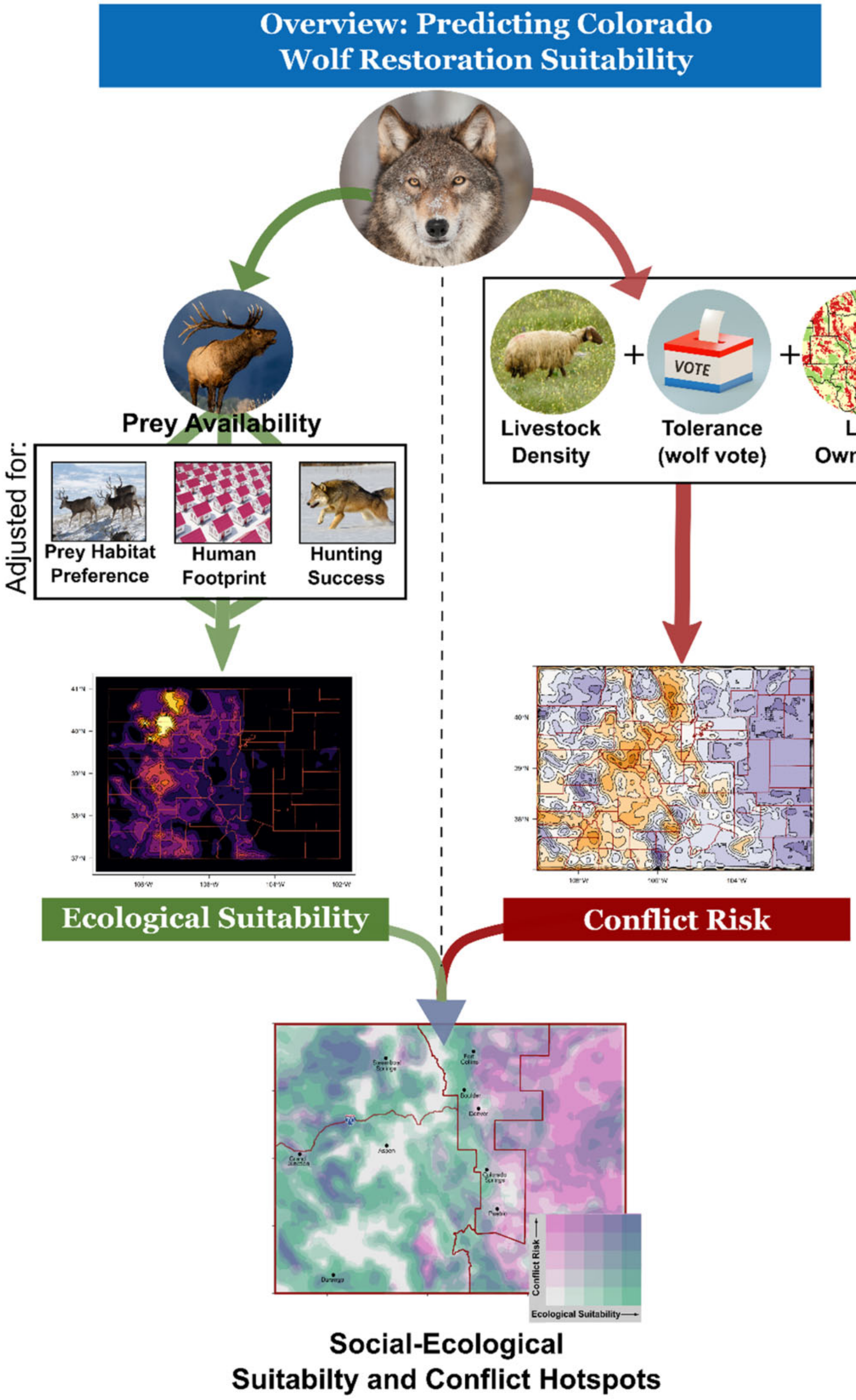

Fig. 1. Methodological flow chart that provides a general overview of the approach of delineating suitable habitat for wolf restoration in Colorado, USA, integrating ecological suitability with conflict risk to predict social-ecological suitability and conflict hotspots.

The expansive human footprint leaves few areas where carnivores can exist, or be restored, without co-occurring with humans (Theobald et al., 2020). As such, carnivore habitat increasingly overlaps with humans, necessitating tolerance of carnivores to enable them to persist in human-dominated landscapes (Carter and Linnell, 2016). Consequently, integrating social and ecological information to develop social-ecological models that account for human tolerance can be especially useful for predicting and managing human-carnivore conflict (Struebig et al., 2018). Tolerance, considered here as the passive acceptance of carnivores (Bruskotter and Wilson, 2014), can be shaped by numerous factors, including perceived risks (Houston et al., 2010), politics (Eeden et al., 2021), and emotional responses (Jacobs et al., 2014). As with many large carnivores, tolerance is often the determining factor for efforts to restore gray wolves (Mech, 2012, 2017), because wolves evoke strong passion (Bangs et al., 1998) and engender broader conflicts over unresolved social debates such as land use and governmental intervention in conservation (Nie, 2001). Improperly assessing human-wolf conflict and failing to mitigate it can lead to high levels of poaching or retaliatory killing (Liberg et al., 2012) and weakening of institutional oversights and policies required for protecting recovering populations (Olson et al., 2015). Additionally, human-wolf conflict can spillover to negatively impact other fauna within the ecosystem (Mateo-Tomás et al., 2012). As such, this comprehensive integration of cross disciplinary data is foundational for the discipline.

In November 2020, citizens in the US state of Colorado voted on a ballot initiative that would require the state wildlife agency to reintroduce gray wolves in the western portion of the state starting by the end of the year 2023. Wolves are native to Colorado, but given perceived threats to livestock and game, were extirpated by the mid-1940′s by government-sponsored predator control (Carhart, 2017). Although a few wolves have dispersed to Colorado from the Greater Yellowstone Ecosystem, where wolves were reintroduced in the 1990′s, most individuals have been killed or simply disappeared (Smith et al., 2010; Colorado Parks and Wildlife, 2020c). Past surveys of Coloradans suggested a high-level of support for wolf reintroduction (Meadow et al., 2005; Niemiec et al., 2020; Pate et al., 1996), but the November 2020 ballot initiative passed by a slim margin (50.9% support). Voting results from the ballot initiative provide a unique opportunity to index tolerance of wolves by providing a near population-level assessment (72.4% of eligible Coloradans cast ballots in the measure).

Here, in advance of their reintroduction to the state, we used the results from the wolf restoration ballot initiative as proxy for tolerance and combined them with maps of land ownership and livestock density to estimate the seasonal potential for direct conflict risk between wolves and humans (including livestock). Depredation of livestock by wolves is the primary source of conflict and public intolerance globally (Mech, 2017). Indeed, an analysis of media coverage in Colorado prior to the ballot initiative showed the most commonly reported negative impact discussed was livestock depredation (51.4% of articles; Niemiec et al., 2020). By quantifying and mapping the spatial convergence of conflict risks and our estimates of ecological suitability, we were able to identify areas more likely to support viable wolf populations ("high social-ecological suitability"), along with potential conflict hotspots. These social-ecological components, which are more commonly modeled in disjunct efforts, suggest locations which may be more optimal for restoration efforts and where to target proactive management to reduce conflict. We discuss the implications of our results for human-carnivore coexistence with the aim of refining the process of carnivore restoration.

2. Methods

Our overall methodology (Fig. 1) for developing a social-ecological suitability model and mapping relative habitat suitability in Colorado was based on quantifying two primary factors for the long-term persistence of wolves: 1) ecological habitat suitability based on a sufficient prey base and preferred environmental features and conditions, and 2) limited direct mortality and minimized conflict potential with humans. Here we define conflict as areas with higher probabilities of direct impacts to people (including livestock and pets) and wolves. Although we incorporate an index of social tolerance to delineate the attitudes of the public about wolf presence, we do not attempt to model social conflict (conflict among stakeholders about wolves). Our aim was to incorporate both ecological suitability and direct conflict risk to provide predictions of relative social-ecological suitability at a broad spatial scale. We assume areas with the highest socio-ecological suitability provide better locations for establishing viable populations of wolves on the landscape with less risk of conflict. Where possible, we relied on findings from studies conducted in mosaics of public and private lands (e.g., outside of National Parks) in the Intermountain West of the United States.

Below we describe how we estimated ecological suitability for wolves by mapping the abundance of their primary prey, and then refined those estimates using seasonal distributions and factors that influence the relative likelihood of space use for both wolves and prey within those areas. Estimates of direct conflict risk were developed using information on livestock density, an index of social tolerance, and land ownership. Although wolves will be initially reintroduced on the Western Slope, our goal was to assess places that could potentially create human-wolf conflicts anywhere in the state of Colorado, given wolves can disperse long distances. As such, we overlaid independently developed statewide seasonal estimates of both ecological suitability and conflict risk to determine their convergence and divergence in space seasonally. We considered areas of high convergence to be potential "conflict hotspots" since those locations contain high quality wolf habitat and high potential conflict. Regions with the relatively highest ecological suitability and lowest conflict risks were defined as areas of "high social-ecological suitability". Areas with low ecological suitability and high conflict risk, as well as areas with converging low values for each component, are of least interest because it is unlikely wolf populations would establish in such areas. We note that our model estimates are considered relative values because we scaled and centered our mapped values due to different units among the inputs used for calculating both ecological suitability and conflict risk.

2.1. Ecological suitability

2.1.1. Prey abundance

We developed wolf prey density estimates for Colorado using the 2019 elk (*Cervus canadensis*), mule deer (*Odocoileus hemionus*), and white-tailed deer (*O. virginianus*) population estimates from Colorado Parks and Wildlife (2020a). Elk and deer (mule deer primarily in the Western Slope & Front Range, white-tailed deer in the Eastern Plains) are critical prey species for wolves in the Northern Rockies (Smith et al., 2004) and are the potential prey species with the highest densities in Colorado (Colorado Wolf Management Working Group, 2004; Fig. S1; Fig. S2). CPW estimates annual population sizes at the herd-level and provides these herd-level boundaries for the state. Population density for elk and deer were calculated using the 2019 population estimates divided by the area (km^2) of each herd-level boundary. We created seasonal spatially explicit estimates of prey availability by combining density estimates with CPW range delineations by species and season.

Range delineations provided approximate regions for overall seasonal range, seasonal concentration areas, and resident population. We overlaid each range map onto the corresponding species' prey density maps by season to refine the locations of prey availability. Seasonal concentration areas were defined by CPW as representing areas where "densities are 200% higher than the surrounding area during a specific season" (Colorado Parks and Wildlife, 2020b). Consequently, for each season, we multiplied the associated prey density that overlapped with concentration areas by 200% to better approximate the increased seasonal prey density. For seasonal ranges outside concentration areas, we multiplied the underlying density values by 50%. For resident ranges, we used the raw prey density estimates (i.e., 100%, no multiplier). For all areas within a species' density map that did not overlap seasonal or resident ranges, we assigned a prey density of zero. While this assumption of no prey outside of these seasonal and resident population ranges is likely incorrect, it was meant to help discern areas where prey density is reduced to a point unlikely to support a resident population of wolves.

For each season, we summed the elk and deer density maps to create estimates of total prey density for both species during summer and winter in Colorado. To reduce the artifact of assuming there were no prey outside of seasonal ranges, and to assess prey density at a scale more ecologically relevant to wolf packs, we used a moving window to smooth the total prey density maps (Fig. S3). See Section 2.3, "Identifying social-ecological suitability and conflict hotspots", for more details about smoothing of all primary layers. We made the assumption that more prey availability supports wolf persistence although the exact number of prey required for a wolf pack is not well documented (Fuller et al., 2003) and not considered here.

2.1.2. Landscape variables influencing prey space use

The locations of prey within seasonal ranges will depend on environmental conditions and available resources that can vary dramatically seasonally (Singleton, 1995). For winter, we assumed prey species would seek out access to vegetation with less snow cover (Paquet et al., 1996). We used satellite-derived estimates of snow cover over the months of December through March during 2019 (Fig. S4). Each 500 m^2 cell provided the average daily snow cover for that location during the 2019 winter (Hall and Riggs, 2016). During winter, wolves living in mountainous regions can alter their behavior to better track migratory prey, often moving into valley bottoms where snow conditions and terrain are optimal for hunting high densities of prey (Singleton, 1995; Kunkel and Pletscher, 2001; Nelson et al., 2012).

As a proxy for prey resource use during the summer months, we used average NDVI from NASA's MODIS products (MOD13Q1 v006; (Didan, 2015), which provides a 16-day composite at a 250 m^2 resolution of vegetative greenness. Carroll et al. (2006) used a similar approach when estimating summer wolf resource use in Colorado, assuming that prey densities will be higher in areas with more vegetative greenness (specifically, tasseled-cap greenness). Vegetative greenness is an important driver of ungulate space use in Colorado (Northrup et al., 2016). We averaged NDVI values from the summers (July through September) of 2015 – 2019 to create an average NDVI map.

2.1.3. Hunting success

To further refine spatial maps relative to where wolves can successfully hunt, we incorporated landscape and environmental factors shown to influence vulnerability to wolf predation. Wolves are coursing predators and avoid steep terrain to maximize kill rate success (Paquet et al., 1996), and the core home ranges of wolves in the Northern Rocky Mountains contained areas with significantly fewer steep slopes than the surrounding areas (Oakleaf et al., 2006). We used a digital elevation model to estimate slope as a proxy for prey vulnerability/hunting success. We assumed that steeper slopes would generally be avoided by wolves due to greater movement resistance and reduced hunting success.

2.1.4. Landscape variables influencing space use by wolves

Carroll et al. (2003) considered areas with greater road density to be detrimental for wolf recovery in Colorado because roads can increase mortality risk via increased access by humans. Wolf-vehicle collisions also cause direct mortality for wolves (e.g.,Wydeven et al., 2001). In general, wolves tend to avoid establishing packs in areas with higher road density (Mladenoff et al., 1995; Houts, 2000). Oakleaf et al. (2006) found that higher road density areas were less common within wolf pack core and home ranges relative to areas without established packs, and the difference was much greater for high traffic volume relative to low traffic volume roads. To create a road density layer, we considered only highways and other paved roads that are classified as "major" arterial routes (i.e., have greater traffic volume) by the Colorado Department of Transportation, and we converted these to rasters representing road density at a 500 m^2 resolution (length of road/area). Lower volume roads, and particularly unpaved roads, while sometimes still considered a factor in reducing the likelihood of establishment of a wolf pack, can also be used by wolves as conduits for movement and hunting

(Dickie et al., 2017; Whittington et al., 2004). Consequently, the relationship between wolf space use and low volume roads was not as clear, and therefore, not included in our analysis. Wolves also tend to avoid areas of higher housing density (Zimmermann et al., 2014; Carricondo-Sanchez et al., 2020) and even areas within National Parks with relatively few isolated human structures (Malcolm et al., 2020). To incorporate the potential avoidance of development by wolves, we used estimated housing density for 2010 (National Park Service, 2010) at a sub-census block unit (100 m^2) using data modeled from the United States Census Bureau (see details in Theobald 2005). Housing density estimates were aggregated to a 500 m^2 resolution and added to the road density layer.

2.1.5. Combining prey abundance with likelihood of space use

Our seasonal estimates of ecological suitability rely on the abundance data for the primary prey of wolves as the main factor for determining broad ecological suitability. We then refined ecological suitability within those areas based on aspects of prey (snow cover) and wolf space use (road and housing density), and wolf hunting success (slope). In order to incorporate the more fine-scale

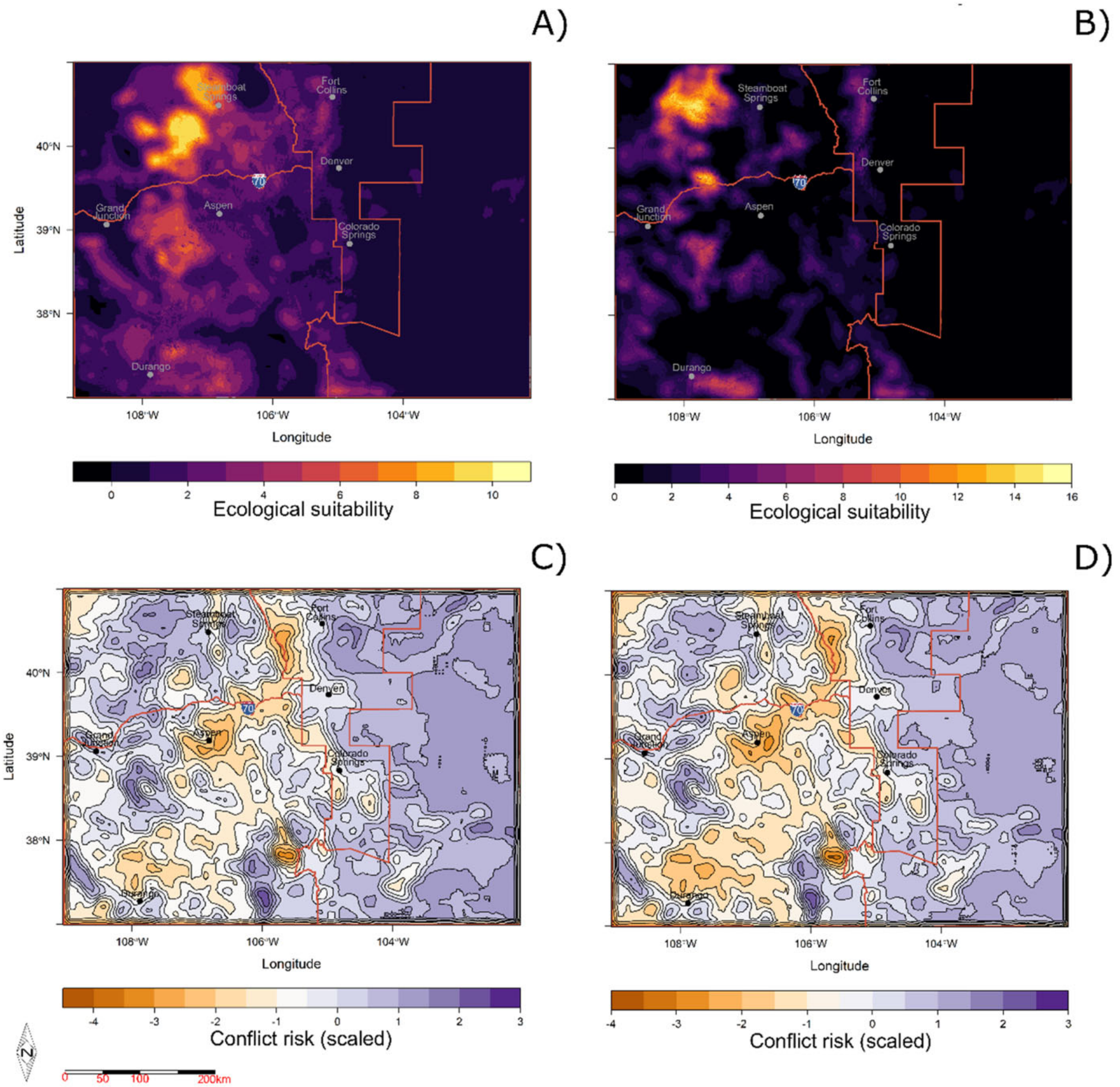

Fig. 2. Maps of wolf ecological suitability for A) summer and B) winter within the entire state of Colorado, USA resulting from multiplying the smoothed estimates of total seasonal prey density (based on populations size and ranges of elk and deer) by the wolf space use likelihood (values: 0–1; see methods). Panels C) and D) show the smoothed and scaled estimates of human-wolf conflict risk (see methods for definition) in summer and winter, respectively. Regions within the state are delineated in red (Western Slope – north of Interstate 70 [northwest], Western Slope – south of Interstate 70 [southwest], Front Range [central, includes the city of Denver], Eastern Plains [east]).

factors into our winter prey density estimates, we first normalized slope using the maximum slope in Colorado (values: 0–1) and multiplied it by snow cover proportion. We normalized the resulting values by the maximum value to create a spatially explicit layer representing relative winter prey space use and hunting success for wolves (larger values represented less likely prey space use and accessibility for hunting). Second, we combined and then normalized the road and housing density by the maximum combined value to represent areas of space generally avoided by wolves. We added the values from these two derived layers and then normalized it by the maximum value to provide a 0–1 scaled map of these combined landscape factors, where high values indicated landscape factors assumed to reduce the likelihood that a location is suitable for wolves regardless of overall prey abundance. We repeated the same process for summer, but instead of using snow cover proportion to reduce our estimates of prey space use, we used summer NDVI to increase it (Fig. S4B). To do so, we classified average NDVI into 10 quantile groups from the least amount of vegetative greenness to the areas with the most. We took the inverse of the quantile classification (i.e., less vegetative greenness was assigned a higher value, range 0–1) and multiplied it by the normalized slope, again adding the road and housing density estimates such that high values were associated with factors thought to be detrimental to wolf occupancy. Finally, we multiplied the seasonal prey density estimates by the inverse of the corresponding seasonal layer of wolf space use (Fig. S5; larger values represent higher likelihood of space use) to further refine our maps of ecologically suitable wolf habitat in Colorado (Fig. 2A & B).

2.2. *Human-wolf conflict risk*

2.2.1. *Livestock depredation*

Due to the potential for conflict associated with livestock depredation (Mech, 2017), especially in public land grazing allotments managed by U.S. Forest Service (USFS) and the Bureau of Land Management (BLM) during summer (Hanley et al., 2018), we created maps of livestock density at the allotment level for 2019 (Bureau of Land Management, 2020; USFS data provided by request). Estimating the density of livestock per allotment is important for ascertaining conflict risk because the likelihood of wolf depredation increases with livestock abundance (DeCesare et al., 2018). Each permit was associated with an allotment and we summed the total permitted head of livestock per allotment. We removed permits associated with horses, bison, and mules with the assumption that they are less vulnerable to wolf predation than are cattle and sheep. We then created density values used in our final mapping by dividing the total head of livestock by the area (acres) of each allotment. The combined density estimates (for USFS and BLM), smoothed by 540 km^2 to represent availability to a wolf pack, based on the territory sizes for wolf packs in other areas of the northern Rocky Mountains (Rich et al., 2012), delineates the estimated risk of livestock depredation on public land in the summer **(**Fig. S6A**)**. Colorado state agricultural experts informed us that many grazing allotments below ~2000 m in elevation are frequently used during the winter months. We also examined the relationship between snow cover and the elevation of grazing allotments and found that allotments with an elevation $<$ 2000 m had less than 10% snow coverage during the 2019 winter. Resultingly, we developed a layer for winter public livestock risk by assuming any allotment located $<$ 2000 m in elevation still had livestock present during the winter months (Fig. S6B**)**.

Fine-scale data on the spatial distribution of livestock on private lands are not publicly available. However, for western Colorado counties, we examined data from the National Agriculture Statistics Service (NASS; USDA) and found a strong correlation between log county-level production of cattle and sheep and the area of each county used for the production of hay and alfalfa**,** quantified with remotely sensed data using NASS's Cropscape at a 30 m resolution ($R^2 = 0.70$; USDA National Agricultural Statistics Service Cropland Data Layer 2020). We used the close correlation between area used for hay and alfalfa and livestock production to represent areas with more winter and summer private livestock holdings (Fig. S6C**)**.

2.2.2. *Land ownership*

We used data that classified land ownership in Colorado from the Colorado State University Natural Resource Ecology Laboratory collated from several state agencies (Colorado Ownership, Management and Protection, Theobald et al., 2010). Research shows private lands increase the potential for human-wolf conflict relative to public (Houts, 2000; Mladenoff et al., 1995), and wolf survival is generally much higher in protected areas (Smith, 2010; Hebblewhite and Whittington, 2020), especially designated wilderness (Barber-Meyer et al., 2021). We further categorized ownership status to reflect the relative risk of wolves being killed based on different levels of on-the-ground management, protection and/or enforcement as such: private lands = 0% protection; local (city, county) lands = 50% protection; lands with active natural resource management (BLM, USFS, state parks) = 70% protection; designated wilderness areas = 90% protection; and National Park Service lands = 100% protection (Fig. S7A).

2.2.3. *Tolerance*

To derive a spatially explicit index of the relative tolerance for wolves, we used the proportion of voters that voted in support of Proposition 114 by precinct using results from the Colorado Secretary of State's website **(**Fig. S7B**)**. Precinct boundary delineations were based on efforts by the New York Times to determine 2020 boundaries; although the official boundaries for CO were not yet released (New York Times - The Upshot, (Watkins et al., 2021). We assume that areas with higher voting percentages in favor of wolf restoration equates to generally greater tolerance regarding sharing the landscape with wolves relative to areas with less support for the ballot initiative, but language in the ballot measure and general political context during the vote may affect this assumption.

2.2.4. *Combining conflict risk layers & conflict layer weighting*

For the livestock component of the summer conflict risk map, we added the normalized values representing livestock density estimates on public lands and areas of hay/alfalfa production on private lands. The winter map depicting livestock risk included only areas of hay/alfalfa production with the assumption that most livestock are not on public lands in the winter. Separately, we developed one map that summed the inverse of the land protection values (0–1; Step 2) and the inverse of the index of wolf restoration support (0–1; Step 3). The combined values were then normalized and added to both the summer and winter livestock risk maps separately to create seasonal conflict potential maps (Fig. 2C & D). We created seasonal maps of wolf conflict risk by combining the spatially explicit estimates using the following weighting: 50% livestock depredation, 25% land ownership and 25% tolerance. For the primary model (*see sensitivity analyses below*) we assumed that livestock would be the main source of direct human-wolf conflict. Within the livestock depredation layer, we weighted public land allotments × 2 the private land livestock proxy values because of heightened vulnerability of livestock in public grazing allotments relative to private land in closer proximity to human settlements. The combined livestock risk values were then normalized and added to both the summer and winter conflict risk maps separately. The two maps were then scaled, centered, and smoothed by 540 km^2 (Fig. 2C & D).

2.3. *Identifying social-ecological suitability and conflict hotspots*

We used a 540 km^2 window that represents territory sizes for wolf packs in other areas of the northern Rocky Mountains (Rich et al., 2012) to smooth both our seasonal layers for ecological suitability and conflict risk to represent the conditions wolves would experience within their range. As such, the values capture the conditions to which a potential wolf pack whose range is centered at each location would be exposed, with the assumption that the pack has a similar home range size to our moving window area. For example, if we assume an area that may be occupied by a pack has low tolerance for wolves, the social tolerance index values contributing to conflict risk from that location will reflect this sentiment for any location that is within the smoothed area.

We combined our centered and scaled relative estimates of both ecological suitability and human-wolf conflict risk into season-specific maps that quantified the correlations between the two input types. This approach of mapping the correlation of quantile values allowed us to highlight areas of divergence and convergence of these opposing aspects of wolf recovery using bivariate choropleth plots. Colors depicting the ecological suitability and conflict risk were derived by placing the values of each distribution into ten groups based on quantiles and then assigning each location a value based on the level of divergence or convergence of the quantiles for each component throughout Colorado. We mapped and quantified the areal coverage in our maps by examining overlap between areas estimated to have the best social-ecological suitability, defined here as areas with overlap of the 60th quantile values (i.e., 60th quantile to maximum) of ecological suitability and the lowest 40th quantile values of conflict risk (i.e., 40th quantile value to minimum) by season. These thresholds mark relative levels of interest and are not strictly biologically based. Areas with more extensive overlap between the two seasons may provide better year-round habitat stability because wolves would be less likely to have to shift their range between seasons or potentially switch their diet to livestock in areas where prey density changes markedly between the seasons. In addition, we identified conflict hotspots, the relatively riskiest locations for wolf recovery, by extracting areas with the highest 60th quantile values of ecological suitability (i.e., 60th quantile to maximum) and the highest 60th values of conflict risk (i.e., 60th quantile to maximum). Research suggests that areas with high natural prey, considered high quality wolf habitat, may also increase the likelihood of wolf-livestock conflicts despite ample wild prey as wolves learn to hunt the relatively more vulnerable livestock (e.g., Nelson et al., 2016). To better assess differences in our sensitivity analyses (*see below*), we calculated the areal coverage of the best social-ecological suitability and conflict hotspots for four regions of the state: a) the Western Slope – north of Interstate 70, b) the Western Slope – south of Interstate 70, c) the Front Range, and d) the Eastern Plains.

2.4. *Sensitivity scenarios*

We conducted six sensitivity analyses to determine the variability in the areal coverage of social-ecological suitability and conflict hotspots within the four regions of Colorado. The first three scenarios altered inputs for the ecological suitability model while keeping the same conflict risks, while the last three scenarios changed conflict risks but not ecological suitability inputs. The (1) “minimum prey population” and (2) “maximum prey population” used historical elk and deer population estimates for each herd’s population size over the last 10 years of monitoring (2009 – 2019) by CPW; we assigned each herd-area the minimum or maximum historical population size, respectively. In the (3) “all prey species available” scenario, we incorporated not only the 2019 population estimates for elk and deer, but spatially explicit estimates for all ungulate species monitored by CPW (Fig S2); moose (*Alces alces)*, Rocky Mountain and desert bighorn sheep (*Ovis canadensis, O. c. nelson),* and pronghorn (*Antilocapra americana*). We then altered the weightings of the conflict risk inputs from the primary model of 50% livestock, 25% ownership, and 25% tolerance to (4) 80%, 10%, 10% respectively in the “high livestock conflict weight”, and (5) 33.33% each in the “equal conflict weights” scenario. Lastly, in the “high sheep vulnerability” scenario, we multiplied the sheep count per grazing allotment by 6.4 before creating livestock density estimates based on findings by (Muhly and Musiani, 2009) that estimated 6.4 sheep are killed per wolf attack for every one cattle in northern Rocky Mountain states. Cattle remained at their associated head counts.

3. Results

Outputs from our habitat suitability model (Fig. 1) predicted the relative ecological suitability for wolves in Colorado was highest in the Western Slope region north of Interstate 70 for both summer (Fig. 2A) and winter (Fig. 2B), given this region contains the highest densities of elk (*Cervus canadensis)* and deer (both mule [*Odocoileus hemionus*] and white-tailed [*O. virginianus*]; Fig. S1), with terrain suitable for wolves to hunt (i.e., slope as a proxy) and relatively low housing and road densities (Fig. S4D). As a result, this northwestern region had higher estimated relative weight of wolf space use (Fig. S5). However, this same region contains a large area with high conflict potential (Fig. 2C & D) driven by high densities of livestock on public lands during both seasons (Fig. S6A & S6B), relatively little protected lands compared to the southern Western Slope, and lower tolerance for wolf reintroduction (Fig. S7B). The strong spatial convergence of ecological suitability and conflict risk (Fig. 3) in the northern Western Slope resulted in similar proportion of areas considered high social-ecological suitability (38.4%; Fig. 4 A) and areas designated as conflict hot spots (26.9%). Conflict hot spots were predicted throughout much of the area in both seasons (Fig. 4B).

Relative to the northern Western Slope, the Western Slope region south of Interstate 70 contained less area with high values of ecological suitability, due to lower prey base density (Fig. S3), more areas of high elevation that seasonally limit prey access to forage resources, and steep slopes that reduce wolf hunting success (Fig. S4C). These factors resulted in relatively lower estimated relative weight of wolf space use, particularly in the winter season (Fig. S5A). However, this southwestern region generally has low road and housing density, especially compared to the Front Range (Fig. 4D), and its prey abundance, although less than the northern Western Slope, is still high. Critically, the region contains markedly less high conflict risk area (Fig. 2C & D) aside from a few, localized places

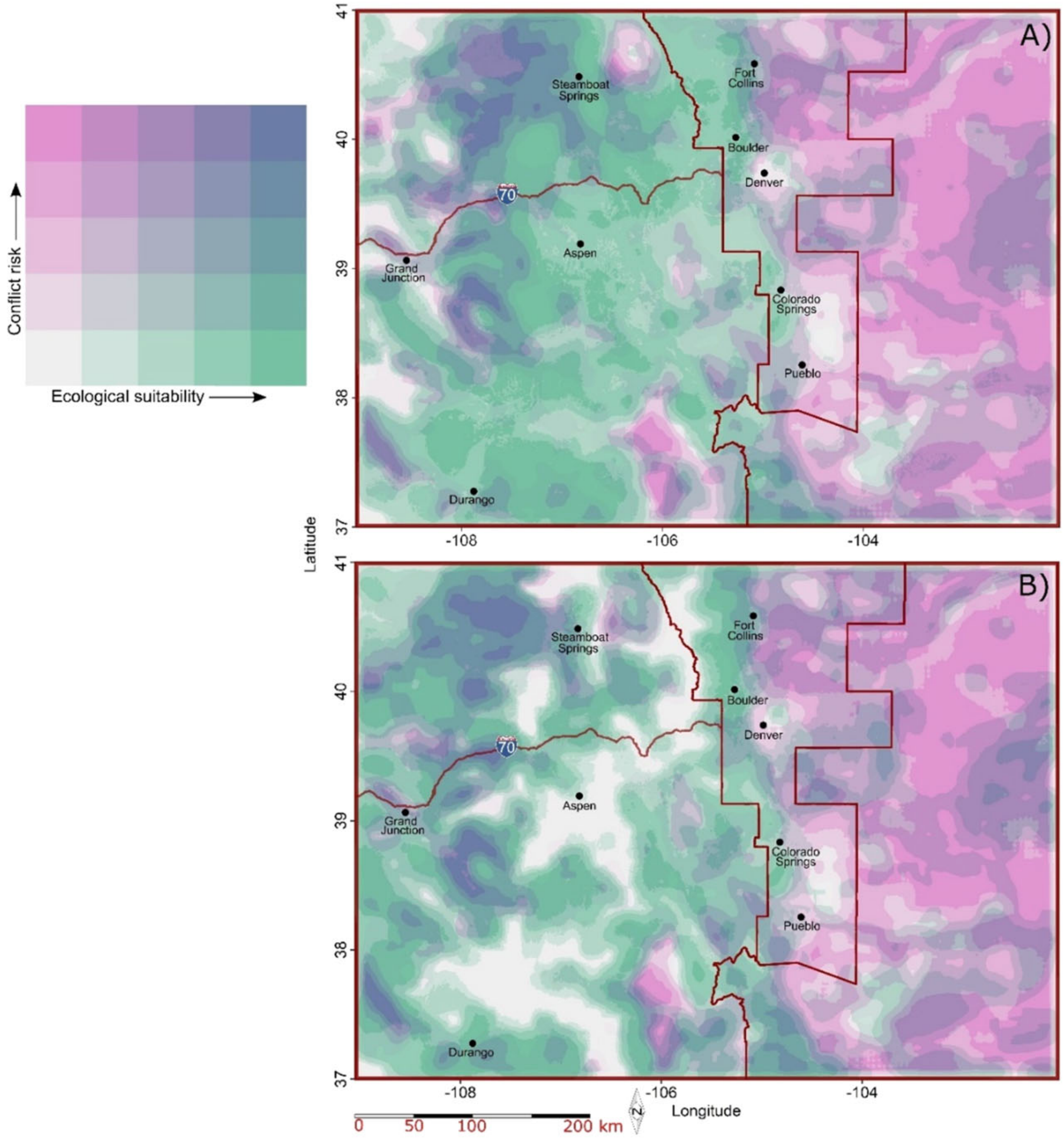

Fig. 3. Bivariate choropleth map of Colorado using ecological suitability and conflict risk (see Fig. 2) for A) summer and B) winter. Locations where the relative values of ecological suitability are high and conflict risk are low are colored with darker shades of green, representing areas of high social-ecological suitability. Locations where the relative values of both ecological suitability and conflict risk are high are colored dark purple, represent conflict hotspots. Bright pink areas show where conflict risk is high but ecological suitability is low. White colored areas contain relatively low ecological suitability and conflict risk. Regions within the state are delineated in red (Western Slope – north of Interstate 70 [northwest], Western Slope – south of Interstate 70 [southwest], Front Range [central, includes the city of Denver], Eastern Plains [east]).

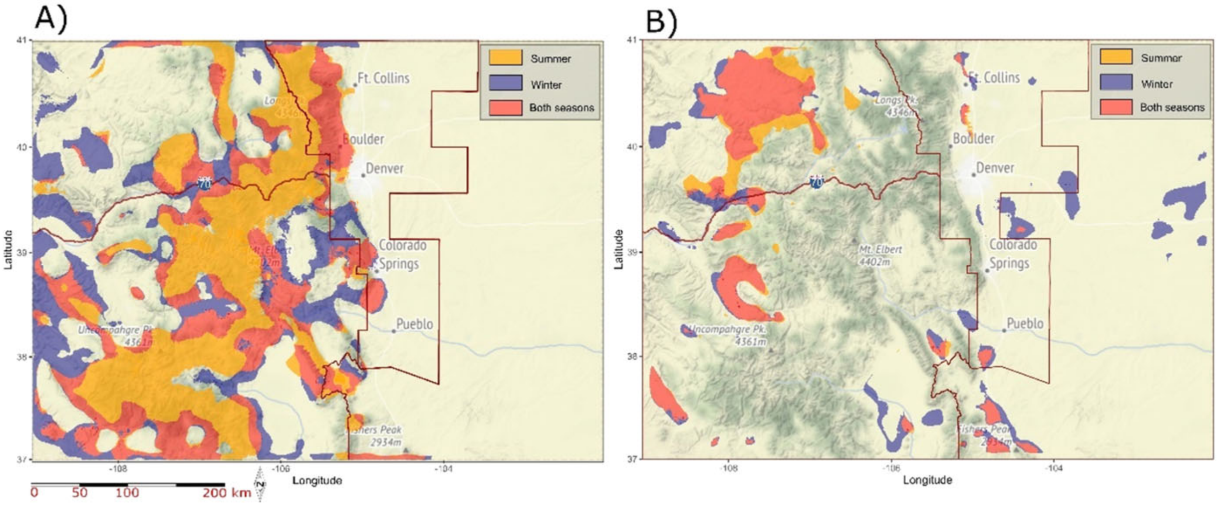

Fig. 4. A) Areas within Colorado where seasonal values with the highest 60th quantile values for ecological suitability and the lowest 40th quantile for conflict risk; such areas represent high social-ecological suitability for wolves. Areas that met this criterion for both seasons are shown in red. Conflict hotspots B**)** were defined by seasonal values with the highest 60th quantile values for ecological suitability and the highest 60th quantile for conflict risk. Conflict hotspots that overlapped both seasons are shown in red. Regions within the state are delineated in red (Western Slope – north of Interstate 70 [northwest], Western Slope – south of Interstate 70 [southwest], Front Range [central, includes the city of Denver], Eastern Plains [east]).

with high livestock density (Fig. S6**)**. The region also contains areas of connected protected lands (Fig. S7A) along with higher tolerance for wolf reintroduction, especially in the resort regions of Aspen and Vail and around the southwestern city of Durango (Fig. S7B). Conflict risk was generally low in areas of high ecological suitability (Fig. 3), resulting in 65.3% of the region considered high social-ecological suitability, albeit some of it highly seasonal (**Fig. 7A**), versus just 7.6% considered potential conflict hotspots (**Fig. 7B**). Additionally, unlike the northern Western Slope, where livestock production and low tolerance were spatially aligned, the southern Western Slope contained several large patches of high tolerance within areas of public livestock grazing or private land livestock production (Fig. S8).

The Front Range contained a low percentage of areas considered conflict hotspots (3.4%; Fig. 4**B**), but its urban areas (Fig. S4D) and relatively low prey base resulted in few areas considered to be high social-ecological suitability (21.6%; Fig. 2A & B; Fig. 4A). Finally, the Eastern Plains contains the lowest ecological suitability in the state (Fig. 2A & B), due to low prey base density and low tolerance (Fig. S7B) resulting in areas with the highest potential conflict risk for wolves (Fig. 2C & D). As such, conflict hotspots (4.7% of the area; Fig. 4D) and areas of high social-ecological suitability (2.1% of the area; Fig. 4A) were rare. These conditions are less likely to support resident wolf populations.

Sensitivity analysis results of our model input layers demonstrated that social-ecological suitability and conflict hotspots in the southern Western Slope were robust to variation among the six plausible scenarios, based on the low variability of percentages classified as social-ecological suitability (61.9 – 65.5%) and conflict hotspots (6.4 – 18.7%) within the region (Table 1). Increasing the weighting of livestock conflict (i.e., increase from 50% to 80%) had the greatest influence on model results; conflict hotspot coverage increased 11.1% and social-ecological suitability decreased by 3.4% compared to the base model results. Although social-ecological suitability was also generally consistent among scenarios for the northern Western Slope region (range: 34.3–41.6%), the percentage of conflict hotspots increased by 16.8% relative to the base model estimates under the high livestock conflict weight scenario (range: 20.9–43.8%). Social-ecological suitability remained consistently low in the Front Range (range: 18.8–23.9%) and the Eastern Plains (range: 1.6–3.5%) irrespective of changes in model inputs. The "all prey species available" scenario resulted in the largest increase in conflict hotspots in the Front Range (+7.5%; resulting from pronghorn availability, Table 1), which contained higher relative variability of conflict hotspots (2.5–10.9%) compared to the Eastern Plains (3.2–6.4%; largest increase in conflict hotspots in the "maximum prey population scenario" relative to base model results).

4. Discussion

Increasingly, social-ecological systems approaches are used to develop conservation and species management plans (Dickman, 2010). Social-ecological models can provide novel inference into the drivers of human-wildlife conflicts and predictions of conflict hotspots (Lischka et al., 2018). Integration of social and ecological data is critical for developing management actions to reduce conflict, especially when considering the reintroduction or recolonization of controversial carnivore species (Behr et al., 2017). Previous work on wolf restoration in Colorado focused on either ecological habitat suitability (Carroll et al., 2003, 2006) or tolerance (Meadow et al., 2005; Niemiec et al., 2020; Pate et al., 1996) primarily in isolation as the spatial and temporal resolution of these data sources are often not matched. By aggregating spatially explicit data on social and ecological processes, including precinct level vote

Table 1
Results from the sensitivity scenarios where we compared the percentages of areal coverage within the four regions of Colorado considered either high social-ecological suitability or a conflict hotspot relative to the primary (base) model output. The first row of data shows the percentages of the area within the of the four regions for the primary model described in the main text, while the subsequent rows show the difference relative to the primary model value for each column, for each of the six considered sensitivity scenarios. See Fig. 4 for the mapped results of the primary model and associated regions. The area for each region is listed in the last row.

		WESTERN SLOPE - North		WESTERN SLOPE - South		FRONT RANGE		EASTERN PLAINS	
Model name	Description	Social-ecological Suitability	Conflict Hotspot	Social-ecological Suitability	Conflict Hotspot	Social-ecological Suitability	Conflict Hotspot	Social-ecological Suitability	Conflict Hotspot
Primary model	Primary model described in Methods	38.4%	26.9%	65.3%	7.6%	21.6%	3.4%	2.1%	4.7%
Minimum prey population	Elk & deer min. population values over previous 10 years	+ 1.6%	-6.0%	-0.1%	-0.7%	-2.8%	+ 1.1%	-0.4%	-0.3%
Maximum prey population	Elk & deer max. population values over previous 10 years	+ 3.2%	-5.5%	-1.4%	-0.7%	-2.3%	-0.9%	-0.2%	+ 1.7%
All prey species available	Prey base included all 6 CO ungulates	+ 1.4%	-6.0%	-0.5%	-0.6%	-1.2%	+ 7.5%	-0.5%	+ 1.3%
High livestock conflict weight	Conflict layer weighted 80% livestock conflict (20% ownership & vote)	-4.1%	+ 16.8%	-3.4%	+ 11.1%	+ 2.3%	-0.1%	+ 1.3%	-1.4%
Equal conflict weights	Equal weighting for conflict among livestock, vote, ownership	+ 2.3%	-4.7%	-0.5%	-1.2%	-1.5%	0.0%	-0.6%	+ 0.4%
High sheep vulnerable	Counts of sheep on public lands weighted 6.4X	+ 0.3%	+ 1.4%	+ 0.2%	-0.1%	-0.3%	+ 0.1%	-0.1%	+ 0.1%
	Area (km^2)	80,755		154,030		68,954		143,568	

data on the November 2020 ballot initiative to restore wolves to Colorado, our analysis integrated the two approaches, mapping and quantifying the convergence and divergence of both ecological suitability and conflict risk for wolves in Colorado. The Western Slope of Colorado, the target for wolf restoration, is expansive, with over 58 million acres containing a variety of habitats, land uses, and opinions on carnivore reintroduction (Niemiec et al., 2020). Our social-ecological models identified nearly 56% of the combined northern and southern Western Slope (ca. 32.5 million acres) as relatively suitable seasonal wolf habitat with areas of high ecological suitability and low conflict risk, consistent with prior studies suggesting that Colorado still supports suitable habitat for wolves (Carroll et al., 2003, 2006; Mech, 2012). However, 14% of the Western Slope (ca. 8.3 million acres) was identified as potential conflict hotspots that would benefit from proactive management and outreach efforts to reduce conflict in advance and during the wolf restoration process. The majority of the area where high conflict risk and ecological suitability converged were aggregated in the northern Western Slope (Fig. 4).

Although tolerance is a critical determinant of the ability of carnivores to persist in human-dominated systems, accurate, fine-resolution, spatially explicit data on tolerance is difficult to obtain (Carter et al., 2020). The Colorado ballot initiative, where over 3 million voters cast ballots on whether to restore gray wolves to the state, provided an unprecedented opportunity to measure a proxy of tolerance for wolves. Colorado contains vast areas of ecologically suitable wolf habitat, but the vote data provided a spatially explicit index that enabled both broad- and fine-scale (precinct level) assessments of support for wolf reintroduction. Without developing this index of tolerance and combining it with livestock and land ownership in our conflict risk model, only ecological suitability would have served as the basis of our habitat assessment. The highest area of ecological suitability was the northern Western Slope of the state, but integration of potential conflict hotspots into our ecological models identified other regions (e.g., the southwest part of the state) that provide greater social-ecological suitability for wolves with less predicted conflict. Specifically, whereas livestock density and tolerance generally converge in the northern Western Slope, resulting in high levels of conflict risk in the region even without the vote data, the information on elevated tolerance levels for wolf reintroduction increased our predictions of social-ecological suitability in the southern Western Slope. Attempting carnivore reintroductions in areas with low tolerance can exacerbate a variety of societal-level conflicts, resulting in increased poaching and retaliatory killing of carnivores (Skogen and Krange, 2020). Interestingly, the voting patterns in Colorado clearly display high variability within the Western Slope, with more support around mountain resort towns, such as Vail, Aspen, and Durango (Fig. S7B). This pattern demonstrates that the passage of the proposition, and wolf tolerance in general, was not simply split between the more populated Front Range and the western part of the state where reintroduction will occur. In addition, the vote data offers a precise way to identify communities with relatively high tolerance, even if they contain large percentages of private land and livestock presence, such as areas around Durango, which may be more amenable to engagement work on wolf conflict intervention or mitigation strategies (Fig. S8).

Livestock depredation can quickly diminish tolerance and lead to persecution of carnivores (Weise et al., 2015), thus creating ecological traps and reducing functional connectivity (Ghoddousi et al., 2021). As such, we focused on integrating both land ownership (e.g., protection from poaching based on enforcement/management presence) and livestock depredation risk into our index of tolerance (i.e., the vote data) to predict potential conflict risks. Delineating the spatiotemporal conflict risk associated with livestock presence is especially important in Colorado because large areas of public lands with little human presence contain grazing allotments where free-ranging livestock might be vulnerable to wolf predation. It is important to note that increasing the model weight of the livestock variable from 50% to 80% resulted in the largest change in conflict risk estimates among the regions; conflict hotspots increased in both regions of the Western Slope and social-ecological suitability was reduced. These results suggest locations where proactive management could be targeted to reduce livestock depredation, for example through non-lethal methods such as fladry and carcass management (Musiani et al., 2003; Lance et al., 2010; Wilson et al., 2017). Other methods like range riding, alteration to the locations or timing of public land grazing, and livestock husbandry that are being used in practice may also help reduce the likelihood of depredation in such areas but have not been a focus of much research to date.

Since gray wolves were restored into the Greater Yellowstone Ecosystem (GYE) in the mid-1990′s, a few wolves have dispersed south through Wyoming into Colorado; however, most of these wolves have been killed or have disappeared without establishing a viable population (Smith et al., 2010; Colorado Parks and Wildlife, 2020c). Our models predict that wolves that do immigrate to Colorado from Wyoming, typically into the northwest corner of the state, arrive in an area with high conflict potential (Figs. 2–4). For instance, in 2021 wolves naturally immigrated to northern Colorado in an area with high livestock density that our model predicted to have some of the highest conflict potential in the state. In subsequent months, and at the time of publishing this article, several cattle have been confirmed killed by these wolves, supporting our model results indicating this was an area with high potential for conflict. The active reintroduction mandated by the ballot initiative would provide more flexibility as to where to initially restore wolves, preferably in regions with relatively lower risk of conflict with people. Restoring and managing a population of wolves in Colorado both greatly expands the occupancy within their historical range and establishes another viable protected population that could be managed within a regional framework in the Rocky Mountains (Smith et al., 2016; Mech, 2017).

In addition to limited conflict with humans, the persistence of wolf populations requires abundant prey populations (Oakleaf et al., 2006; Mech, 2017). Colorado supports sufficient prey for wolves, including the largest elk population of any U.S. state (+280,000 individuals; Lukacs et al., 2018; Colorado Parks and Wildlife, 2020b) as well as abundant deer (~400,000; Bergman et al., 2015), primarily located in the Western Slope where wolves will be reintroduced. Importantly, our sensitivity scenarios demonstrated that even in scenarios that considered the lowest and highest population estimates for elk and mule deer herds over the last 10 years, the predicted locations and amounts of the best social-ecological suitability with minimal conflict were similar to our primary model using 2019 prey estimates. Prey densities throughout much of Colorado exceed those of many other Western states that support viable wolf populations. As such, our estimates of ecological suitability may be conservative and habitat capable of supporting wolf populations may extend further geographically.

Although most elk populations in Colorado exceed population objectives set by the state wildlife agency, some are under objective, particularly in the southwest portion of the state (Colorado Parks and Wildlife, 2020a). While our analysis suggested that southwest Colorado may have the best opportunity for viable wolf reintroduction efforts (i.e., high ecological suitability and low conflict risk), wolf introduction into an area where elk populations are below population objectives may raise concerns for hunters and wildlife managers. In hunting units where wolves will be restored, managers could provide information to hunters to reduce the probability that wolves are not mistaken for coyotes, and to remind individuals that the reintroduced wolves are currently protected as an endangered species under Colorado state law. Other areas that merit management focus are regions with a high overlap of prey and livestock density, as our model outputs show in northwestern Colorado, given some wolves may opportunistically switch from natural prey species to more vulnerable domestic animals (Nelson et al., 2016).

Our analyses quantified and examined the spatial convergence and divergence of ecological suitability and conflict risk estimates throughout the state of Colorado, thus offering insight into planning for wolf reintroduction. Additional finer scale analyses would help identify more localized areas to target site-specific conflict reduction measures, including actions to minimize livestock depredation. Further consideration of the growing human footprint in Colorado would also be useful especially after wolves expand their geographic expansion from the initial reintroduction sites. A study published in 2006 predicted that, after forecasting increased human population growth and road development, Colorado could support at least 400 wolves by 2025 (Carroll et al., 2006). However, the study did not incorporate any estimates of wolf tolerance. Most people in Colorado reside in the rapidly growing Front Range, where our model predicts relatively small amounts of high social-ecological suitability. Despite a rapidly growing human population, Colorado also has over 24 million acres of public land (Colorado Natural Heritage Program, 2020), a key component for suitable wolf habitat that helps to minimize human-wolf conflict (Mladenoff et al., 1995; Houts, 2000). Nonetheless, continued urban and exurban development in the western part of the state will reduce habitat for both wolves and prey (Johnson et al., 2017).

Given the projected human population growth and changing climatic conditions within Colorado, evaluating both the current and future carrying capacity of wolves in the state will require incorporating both ecological and social considerations for long-term planning. Our social-ecological suitability model did not forecast future climate and human development and their impacts on habitat suitability and connectivity for wolves; such analyses would be valuable next steps. Future research also should consider connectivity among seasonal high-quality habitat and potential routes for dispersing wolves and how such movement may influence conflict risks in ecologically suitable habitat in Colorado that may eventually become occupied. Additionally, more sophisticated prey space use models should be developed to better predict prey distribution post-reintroduction. Our study had to rely on numerous assumptions because some data were limited, such as the presence of livestock on private lands near associated crop fields. We also had to make assumptions about what quantile thresholds of the convergence and divergence of conflict and ecological suitability constituted a “conflict hotspot” or “high socio-ecological” designation (although all quantile values are mapped in Fig. 3). Importantly, our estimates of social tolerance were potentially biased low given that a vote for wolf restoration is suggestive of high tolerance, but a vote against the initiative does not necessarily imply that an individual is against the concept of wolf restoration in Colorado. Voters may have voted against the initiative for a variety of reasons, such as media reports of naturally recolonizing wolves, concerns about the cost of reintroduction, uncertainty about support from managing agencies, the ballot initiative process itself (Niemiec et al., 2020) or the politicization of the issue (Ditmer et al., 2022). Similarly, our ecological suitability thresholds were assigned relative to prey density in Colorado, which holds the highest densities of wolf prey species in the western United States (Bergman et al., 2015; Lukacs et al., 2018). As such, what we considered relatively low prey density in Colorado likely overlaps with what is considered higher prey densities in some regions in other states with wolves.

In some locations large carnivores are expanding to parts of their geographic ranges where they were extirpated (e.g., Chapron et al., 2014). However, in many areas, carnivores remain absent from their historic range and disconnected by physical barriers, land use change, or anthropogenic resistance (Wolf and Ripple, 2017; Ghoddousi et al., 2021). Restoring native carnivores to historic ranges is increasingly being considered in conservation strategies (Carver et al., 2021). Over the past several decades, value conflicts among the general public have increasingly resulted in citizen-initiated ballot measures to directly influence wildlife management policy, including initiatives focused on carnivore management and restoration (Manfredo et al., 2017, 2020). Resulting voting patterns can provide unique, spatially explicit insight on tolerance towards carnivores that can be integrated with other social and ecological information to reduce potential conflict and improve the success of carnivore restoration efforts.

Declaration of Competing Interest

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

Data Availbility

All data used in this analysis, aside from livestock grazing allotment data provided by the USFS, are available publicly. Many of the intermediate maps are available in the supplemental materials.

Appendix A. Supporting information

Supplementary data associated with this article can be found in the online version at doi:10.1016/j.gecco.2022.e02192.

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