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Predicting community interactions under grizzly bear rewilding and anthropogenic change

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ABSTRACT

Rewilding is increasingly recognized as an impactful conservation strategy, but a key question remains: how do ecological systems respond to the return of species long absent from the landscape? Predicting these responses is challenging due to complex direct and indirect interactions, especially amid anthropogenic changes. The ongoing range expansion of grizzly bears (*Ursus arctos*) in western North America offers a unique opportunity to develop and test predictions about the effects of a large, generalist omnivore returning to its historic range. We developed a priori predictions that grizzly recovery would lead to (1) declines in sympatric large carnivores due to competition, (2) mesopredator release, (3) increased top-down control on large herbivores, and (4) stronger effects under anthropogenic stressors. Our fuzzy interaction webs (FIWs) supported these hypotheses, predicting that in habitats where grizzlies reach high density, black bears (*Ursus americanus*), mountain lions (*Puma concolor*), coyotes (*Canis latrans*), grey wolves (*Canis lupus*), scavenging birds, and ungulates may experience small population reductions through interference competition, exploitation competition, and predation. Small carnivores may increase, while reduced precipitation and human hunting of ungulates may intensify declines in mountain lions and ungulates. While FIWs offer a tractable framework for anticipating community change in complex, data-poor, multitrophic systems, they are still limited by data quality, assumptions of equilibrium dynamics, and the absence of spatial output. Nevertheless, FIWs serve as useful tools for generating testable hypotheses, identifying knowledge gaps, and guiding research and conservation efforts as species recover and ecosystems reorganize under global change.

1. Introduction

Conservation efforts such as increased species protection, habitat restoration, and mitigation of human-wildlife conflicts can enable species to expand and reoccupy parts of their historic ranges (Roman et al., 2015). Resulting changes in species ranges can restructure ecological communities by altering species interactions, which in turn can affect ecological functions and ecosystem services (Fitt and Lancaster, 2017; Jones et al., 2020). An increasingly recognized conservation strategy that seeks to accomplish this is rewilding, the introduction or re-establishment of species to support interactions and ecological functions akin to those in undisturbed ecosystems (Svenning et al., 2016). These efforts often focus on species with unique or strong ecological impacts (Estes et al., 2011) and/or 'flagship' taxa (Lorimer et al., 2015). For example, apex predators, often a public-facing target of conservation, can engage in a variety of important species interactions such as predation on herbivores and regulation of small and large predator populations (Ripple et al., 2014). Rewilding has traditionally involved human-facilitated reintroductions into parts of species' historic ranges (Dobson, 2014; Zimov, 2005) or bolstering existing populations through reinforcement (Seddon et al., 2014). Rewilding can also be achieved through active conservation, such as habitat improvements and facilitating connectivity, which allow extant populations to reinhabit historic ranges and re-establish missing ecological processes and trophic complexity (Perino et al., 2019; Svenning et al., 2016). However, rewilding outcomes have been exceedingly difficult to predict because

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species' population sizes and ecological functions are a product of complex, multi-faceted networks of interactions within communities (Moleón et al., 2014). Moreover, anthropogenic drivers like climate change and hunting pressure are altering systems such that ecological context may differ dramatically from historic conditions (Chen et al., 2011). This raises the challenge of predicting how organisms that have been absent for long periods will affect ecological communities when they return.

An important example of such rewilding is the grizzly bear (*Ursus arctos horribilis*), which was extirpated from much of its native range in the western United States from 1850 to 1970 (Mattson and Merrill, 2002). Efforts to rewild grizzly bears in the region over the last several decades have included active restoration of grizzly bear habitat to facilitate population expansion (Braid et al., 2016), extensive government protections (France and Brister, 2020; Greenwald, 2023), and multiple population augmentations achieved by the translocation of bears to new locations (Drew, 2024; Kasworm et al., 2007). Importantly, grizzly bear extirpation coincided with reductions of other large mammals including elk (*Cervus canadensis*), mule deer (*Odocoileus hemionus*), black bears, mountain lions, and extirpations of grey wolves due to anthropogenic effects (Laliberte and Ripple, 2004). These large mammal species have since recovered, or are still recovering (wolves), in areas throughout the region. Likewise, through conservation efforts, grizzly bears are now expanding into large portions of their historic range, particularly in western North America (Costello et al., 2023, Fig. 1).

Grizzly bears are large-bodied omnivores with the ability to impact populations of prey, scavengers, plants, insects, and a variety of sympatric carnivores through predation, intraguild predation, kleptoparasitsm, carcass-provisioning, herbivory, entomophagy, seed dispersal, and competition (French et al., 1994; García-Rodríguez et al., 2021; Gunther et al., 2014; Milakovic and Parker, 2013; Munro et al., 2006; Murphy et al., 1998; Prugh and Sivy, 2020). These direct and indirect

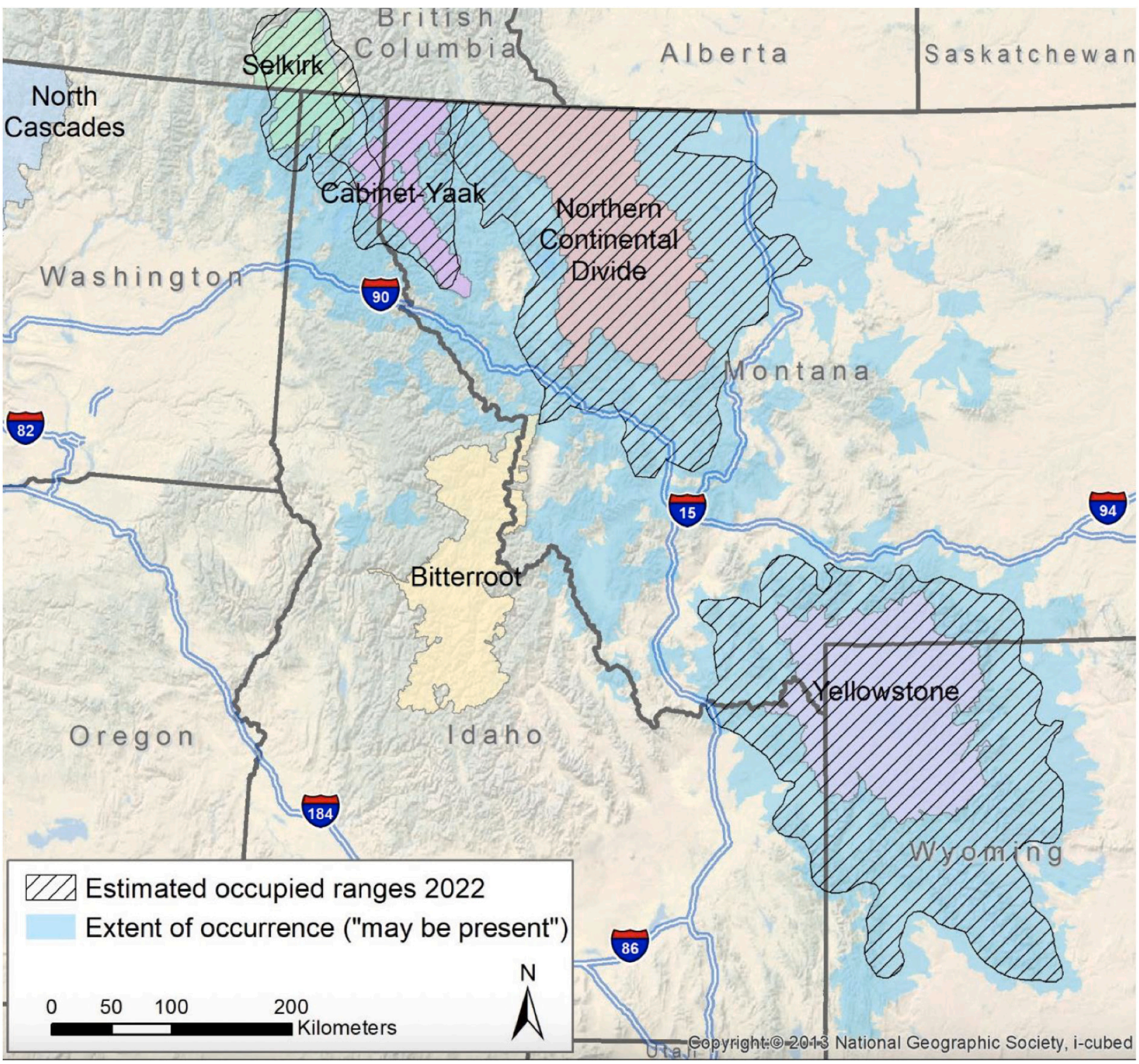

Fig. 1. The current occupied range of grizzly bears in the U.S. Northern Rockies as of 2022, indicated by the hashed area (adapted from Costello et al., 2023). The labeled, colored shapes indicate core target recovery areas in the region, hashed areas indicate currently occupied range, and the blue-green shading (labeled extent of occurrence) indicates areas where occasional observations have been confirmed, but where residency is uncertain. The blue shaded area within the intermountain region (excluding the plains beyond the Rocky Mountain Front which are not part of the recovery zone) coincides with the U.S. portion of the study area for this analysis where grizzly bears are in the process of recovering. Grizzly bears are expanding similarly in the Southern Canadian Rockies. These areas of occupancy are expected to expand further as grizzly bear recovery proceeds. Much of the region is already occupied by the other carnivores and ungulates of interest in this study, except for the grey wolf, which is also still in the process of recovery. Areas of occupied range and occurrence were determined by Costello et al. (2023). (For interpretation of the references to colour in this figure legend, the reader is referred to the web version of this article.)

interactions are often complex. For example, competitive interactions between grizzly bears and other large carnivores have been shown to be season- and system-dependent (Tallian et al., 2022), with consequences for prey species and smaller carnivores via predation and scavenging behavior. Furthermore, novel anthropogenic conditions are leaving a substantial mark on the ecosystems in which grizzlies are returning. Global climate patterns are causing decreased precipitation in this region (Keane and Mahalovich, 2018), potentially reducing primary productivity and leading to cascading ecological consequences (Liu et al., 2021). In addition, hunting, particularly of large ungulates, is prolific in the region (Montana Fish Wildlife and Parks, 2024b), and can alter top-down pressure on ungulates, but also provides additional food sources for some species (Wilmers et al., 2003). Given the potential of this species to broadly influence food webs, as well as the novel anthropogenic conditions of the system, it is important to deploy modeling tools to predict potential community-wide changes to guide system management and monitoring. More broadly, a framework for predicting and vetting how proposed rewilding may alter ecological interactions will be essential for managing many ecosystems but has remained elusive (Clark-Wolf et al., 2022; Pearson et al., 2022).

Fuzzy interaction webs provide a tool for making predictions about the ecological and conservation impacts of re-established populations (Ramsey and Veltman, 2005) in the face of ecological complexity. These models are based on fuzzy set theory and can integrate qualitative and quantitative data from a variety of information sources in a community interaction network (Clark-Wolf et al., 2022) to make general predictions of how populations will respond to a change in the system. This type of analysis is used widely in social sciences and engineering (Aguilar, 2005; Papageorgiou, 2011) and is increasingly applied to conservation and management (Baker et al., 2018; Dexter et al., 2012; Hunter et al., 2015; Pearson et al., 2025; Ramsey and Veltman, 2005; Rooney et al., 2023). Previous research demonstrated that such models could accurately predict the ecological consequences of introduced lake trout (*Salvelinus namaycush*) in Yellowstone National Park and red squirrels (*Tamiasciurus hudsonicus*) in Newfoundland (Clark-Wolf et al., 2022). This approach holds potential to provide critical conservation insights related to the effects of rewilding in complex ecological systems.

Here we use fuzzy interaction webs to predict changes in community dynamics in response to grizzly bear recovery in the Rocky Mountains of the western USA and Canada. Specifically, we seek to develop working hypotheses for how the return of this large omnivore could affect other animal populations in the system under a variety of anthropogenic conditions. We predict that our model will show: 1) declines in sympatric large carnivore populations due to competition, 2) small carnivore release for species that compete less directly with grizzlies, 3) declines in large herbivores due to increased top-down control from grizzlies and other predators, and 4) greater changes under anthropogenic change. Our model outcomes can be compared with actual changes in animal populations as grizzly bear recovery progresses, and aid in our mechanistic understanding of species interactions within the ecosystem. This work is intended to provide a tool that can be evaluated and updated with additional empirical data as it becomes available and is meant to inform and prioritize future research and monitoring efforts. Ultimately, this tool may be broadly applicable for predicting ecological outcomes in instances of species recovery with complex interspecific interactions and environmental change.

2. Methods

2.1. Study area

This study models the effects of grizzly bear rewilding in the U.S. Northern Rocky Mountain ecosystem and Southern Canadian Rockies, where grizzly bears are slowly recovering to historical population densities. The blue shaded area of observation in Fig. 1 coincides with the study area of this analysis, representing areas where grizzly bears are in the process of recovering. The model itself is scale independent, relying on calculations based on mechanistic understandings of network linkages and interaction strengths to predict relative abundance changes of network nodes. Model outputs do not predict specific abundance values for any single population but rather provide general predictions of directional and proportional changes in node abundances that may apply across populations for the modeled region. To ensure our model reflected processes across our large study region, we parameterized our model as described below using data from studies in Montana, Wyoming, Idaho, Colorado, Washington, British Columbia, and Alberta (Appendices S1 and S2) to fully capture regional variation in these ecological parameters.

2.2. Fuzzy interaction webs

Fuzzy interaction webs (hereafter, FIWs) refer to the application of fuzzy cognitive mapping to ecological and conservation studies (Ramsey and Veltman, 2005). Much like a food web or other ecological interaction network, fuzzy interaction webs are composed of nodes representing species within a community connected by bi-directional edges of varying strengths representing species interactions (Pearson and Clark-Wolf, 2023). This type of model is unique in ecological studies in that it can integrate quantitative and qualitative data and also account for asymmetric and bi-directional interactions, that can represent any type of ecological interaction, making it particularly useful for predicting complex systems with variable data sources (Ramsey and Veltman, 2005) and “reciprocal causality” (e.g., where species influence each other), a key feature of ecological communities (Cardinale et al., 2006).

To integrate qualitative and quantitative data, fuzzy interaction webs rely on fuzzy sets - the generalization of ordinary quantitative sets, in which elements can be members of multiple sets to varying degrees (Nguyen et al., 2018). This generalization is described by a membership function in which each element is assigned a value of 0 to 1 for each set it belongs to, representing its relative membership within that set (see Nguyen et al., 2018 for details on membership functions). The degree of an element’s relative membership in each set is determined by qualitative data specific to the element, which can be informed by expert opinion regarding system parameters. In this way, qualitative and quantitative data can be used to model system processes together. Interactions within the FIW are assigned strength values between -1 (strongly negative) and 1 (strongly positive) to indicate the relative strength of interactions, with 0 indicating a non-existent relationship. FIWs use an iterative fixed-point method to solve for an equilibrium state of a community under a given set of constant conditions. Artificially changing population sizes or environmental conditions leads to different equilibrium solutions that can then be compared.

Rather than relying on large amounts of community observation data, FIWs capture the range of potential abundances and interactions of species within a community, and the equilibrium solution identifies the most stable outcome for the system from which it was parametrized (Nguyen et al., 2018). The unique features of FIWs include 1) integration of qualitative and quantitative data as well as uncertainty in data, 2) ability to incorporate bi-directional relationships, and 3) no dependence on large amounts of community observation data (Clark-Wolf et al., 2022). These features differentiate FIWs from methods like structural causal modeling and Bayesian belief networks and make this tool particularly well-suited to predicting qualitative changes in ecological community structure. In this case, our application of FIWs estimates proportional and directional changes of network nodes. See the supplementary materials of (Clark-Wolf et al., 2022) for an in-depth description of fuzzy set theory in application to ecological and conservation studies.

2.3. Model parameterization

The base model used in this study was derived from a fuzzy interaction web developed for MPG Ranch in central west Montana (Clark-Wolf et al., 2022; Pearson and Clark-Wolf, 2023), which lies at the center of our study area (Lat: 46.6808628, Long: −114.0283167) and represents an active area of grizzly expansion (three grizzlies documented with camera traps 2022–2024; P. Ramsey, unpublished data). This model served as a valuable starting point because plant communities and their responses to climate and species interactions have been monitored on the ranch for 12 years, providing parameter estimates of these dynamics. The system also already includes stable populations of mountain lions, black bears, ungulates, and other large animal populations, allowing for strong calibration of the model for these species.

Using this existing fuzzy interaction web as a backbone, we expanded the framework to represent our entire study area within the wider ecosystem of the Rockies. Specifically, we added nodes for grey wolves and grizzly bears to represent the full suite of large carnivorous fauna, which are recovering to historical densities in the region, as well as a node for ungulate carcasses to better clarify processes of predation and scavenging in the system. We also gathered data on densities and interactions of other large and mid-sized mammal species from the broader region to support our model parameterization more regionally. Data related to population densities in the region and species interactions were collected from an extensive literature search and are outlined in the Appendices S1 and S2. Species interactions were assigned values between −1 (strongly negative effect) and 1 (strongly positive effect) to indicate the relative strength and direction of interactions as determined from multiple literature sources (see Appendix 1). For example, to approximate the effect of grasses on grizzly bears, we compiled multiple grizzly bear diet studies in the region and averaged the proportion of grasses in grizzly bear diets across sexes and seasons. We used this average diet composition as our starting point for the approximate effect of grasses on grizzly bears in our models. For species that have both positive and negative direct effects (e.g. herbivory but also seed dispersal), the interaction value was the summed estimation of all direct effects.

Prior to further analysis, we ran the model with singular interaction values to ensure model convergence (Appendices S3, S4, S5). All interaction strength values in this fuzzy interaction web are inherently subjective and intended to qualitatively approximate interaction strengths between nodes. Our sensitivity analyses included for all model outputs, described below, account for this uncertainty, so that we can estimate how variation in parameter inputs impact our predictions. Direct testing and quantification of these types of interactions between large vertebrates are rare in the literature, given the time and effort required to run controlled experiments for these large and often endangered species. As such, methodologies like FIWs that appropriately account for the approximative nature of this data are necessary to make predictions in these systems.

2.4. Model analysis

To accomplish our study objective, predicting changes in abundance of sympatric vertebrates resulting from grizzly bear expansion, we ran a suite of sensitivity analyses in which the interaction strength of grizzly bears on other nodes (species) in the fuzzy interaction web were drawn from uniform distributions over 10,000 iterations. These uniform distributions were centered around the value of the given interaction strength estimated from the literature, with a minimum of 0 and a maximum of double the estimated interaction value. By looking at the resulting magnitude and variation in species population sizes in these simulations, we were able to predict the potential impacts of rewilded grizzly bears on U.S. Northern Rockies ecosystems while accounting for a wide range of potential interaction strengths beyond the specific values obtained from the literature. These ranges of interaction strength are analogous to natural variation in interactions that we might see between species across space and time. We chose to focus our model analysis on medium-to-large mammal and bird species as they interact most strongly with grizzlies in the system and are potentially the most vulnerable. Our results focused on grey wolves, mountain lions, black bears, coyotes, ungulates (*Cervus canadensis, Odocoileus* spp.), small carnivores (bobcat- *Lynx rufus*, foxes- *Vulpes* spp., martens- *Martes* spp., etc.) and scavenging birds (ravens and crows- *Corvus* spp., turkey vultures- *Cathartes aura*, etc.). Our simulations had two major directions of investigation. First, we were interested in parsing the predicted effects of different direct and indirect interactions with grizzly bears on other key species in the system. Second, we modeled different environmental and anthropogenic conditions related to precipitation and human hunting of ungulates to predict how grizzly bear recovery could interact with drivers of global change to exacerbate or mitigate consequences for the ecosystem.

First, to parse the magnitude of direct and indirect effects of grizzly bears in the region, all grizzly bear effects (indicated by a non-zero interaction strength direct from grizzly bears to another species) in the fuzzy interaction web were broken down into four basic ecological interactions: (1) interference competition, (2) predation, (3) scavenging, and (4) herbivory (Fig. 2). In this case, interference competition refers to direct antagonistic interactions between grizzly bears and competing carnivorous species and can include behaviors like intraguild killing, forcing other carnivores off kills, or kleptoparasitism. Predation includes direct effects of grizzly bears on ungulates, and indirect effects on competing carnivores. Scavenging includes direct effects of grizzlies on carcasses (i.e. grizzly consumption of carcasses, removing them from the ecosystem, but also balanced by some carcass generation which can be used by other species) and herbivory includes direct effects of grizzlies on plants (mostly weakly negative through consumption, but also accounts for some positive effects of seed dispersal for certain plants). For both the scavenging and herbivory models, the only effects that grizzly bears have on the sympatric vertebrates of interest in this study are indirect, which is what is reflected in the model results for these simulations. To predict the relative impact of each of these ecological interaction types, we ran four simulations, one for each interaction category. In each simulation, grizzly bear interaction strength values for the relevant category of interaction were drawn from the uniform distributions as described above. All other grizzly bear effects had interaction strengths set to zero. For example, for the interference competition simulation, interference competition effects of grizzly bears on black bears, coyotes, and mountain lions were drawn from their relevant uniform distributions, while other grizzly bear effects related to predation (effect on ungulates, elk and deer [*Odocoileus* spp.]), scavenging (effect on carcasses) and herbivory (effects on plants) were set to zero. In this way, each of these four simulations measured the predicted impact of only a single category of interaction. As such, indirect effects are not explicitly modeled, they arise as a function of the dynamics of the direct interactions and the network linkages. We ran a final fifth simulation including variation in all grizzly effects to predict the overall impact of the four ecological interaction types combined. The central value for each interaction strength included in these simulations can be found in Appendix S1.

Second, to model the interactions of anthropogenic effects with grizzly bear recovery, we ran multiple simulations of the fuzzy interaction web with three set levels of precipitation and human hunting. For precipitation, we ran three simulations with 1) current levels of precipitation (30.5 cm annually based on the 10-year average), 2) 27.9 cm of precipitation annually, and 3) 25.4 cm of precipitation annually. These values are in line with expected changes in climate for a grassland-forest ecotone in the US Northern Rockies, where drier conditions are expected, particularly in the summer and fall seasons (Keane and Mahalovich, 2018). For cervid hunting by humans, we ran three simulations with (1) current levels of take for deer and elk averaged across the state of Montana Fish Wildlife and Parks Regions 1, 2, and 3 from 2013 to 2023, (2) double current levels in this same area and time period, and (3) no hunting. This represents the mountainous portion of

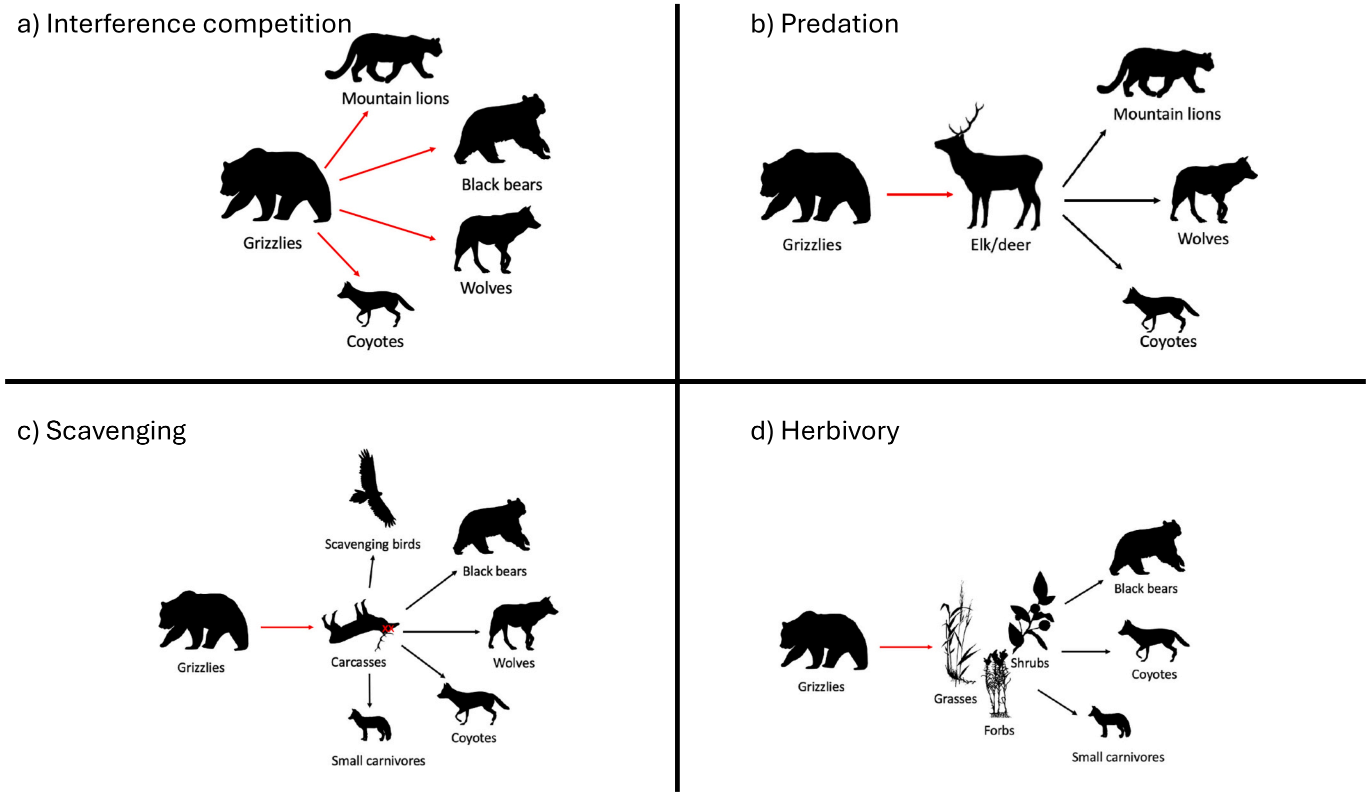

Fig. 2. Graphical representation of the different interaction pathways that are modeled using our sensitivity analysis (see Fig. 3), by which grizzly bears could affect sympatric species in the system. Red arrows represent direct interactions between bears and other nodes in the model, that is, direct interference competition with mountain lions, black bears, wolves, and coyotes in a), direct predation on elk/deer in b), direct scavenging on carcasses in c) and direct herbivory/seed dispersal on vegetation in d). Black lines represent relevant first-order indirect interactions of grizzlies on other nodes in the model, that is, potential impacts on mountain lions, wolves, and coyotes through predation in b), potential impacts on scavenging birds, black bears, wolves, coyotes, and small carnivores through scavenging in c), and potential impacts on black bears, coyotes, and small carnivores in d). These representations are meant to reflect the interactions conceptually to visualize some of the relevant direct and indirect interactions in these models. They are not comprehensive and they do not represent the full breadth of interactions within the models. (For interpretation of the references to colour in this figure legend, the reader is referred to the web version of this article.)

Montana, (Montana Fish Wildlife and Parks, 2024b), and is fairly representative of the hunting take in the wider region. Within the model, effects of hunters are negative on ungulate abundances, and positive on carcass abundances, via the creation of additional food source (i.e. gutpiles). For all simulations, we drew all grizzly bear interaction strengths from the uniform distributions described above for all interaction types. All code and data associated with this project are publicly available on GitHub (https://github.com/DanielGorczynski/Grizzly-rewilding.git, Appendix S7).

3. Results

When considering all grizzly bear interaction types (Fig. 3a), our model predicts that the species most impacted by the recovery of grizzly bears are black bears, with mountain lions, coyotes, ungulates, and wolves also experiencing moderate decreases in population size. Scavenging birds were predicted to exhibit small declines while small carnivores were predicted to undergo small increases in relative population size.

The largest changes in vertebrate populations predicted in response to grizzly recovery were due to both direct and indirect effects associated with interference competition and predation. In our simulation of interference competition by grizzly bears (Fig. 3b), moderate declines were predicted for black bears and coyotes, as well as small declines in mountain lion and wolf populations. These predicted responses were all driven by direct interactions, whereby grizzly bears engage in interference competition with these species. Small predicted increases in relative abundances of scavenging birds, small carnivores, and ungulates were associated with indirect effects of grizzly bear interference competition. In our simulation of predation by grizzly bears (Fig. 3c), moderate declines were predicted for ungulates, and small declines were predicted for wolves and mountain lions. The predicted effect of grizzly predation on ungulates is both direct and indirect due to increased hunting rates of mountain lions in the presence of bears. The predicted effects on mountain lions and wolves are indirect due to competition for ungulates as a food source. Small predicted increases in all other relative species abundances were associated with indirect effects.

Our simulations of scavenging and herbivory by grizzly bears (Fig. 3d–e) predicted less pronounced effects on other large vertebrates than interference competition or predation. The scavenging model predicted small declines in scavenging birds, coyotes, and black bears, very small declines in wolves and small carnivores, and increases in mountain lions and ungulates, all predicted to result from indirect interactions associated with grizzly consumption of carcasses and the effects of this consumption on other species in the system. The herbivory model predicted very small declines in wolves, scavenging birds, mountain lions, ungulates, coyotes, and black bears, and a very small increase in small carnivores.

In general, increases in human hunting of ungulates and decreases in precipitation were predicted to exacerbate population decreases among sympatric species in response to grizzly bears. Under double human hunting of ungulates (Fig. 4b), ungulates and mountain lions showed greater decreases in modeled population size compared with current hunting management. All other populations showed no obvious decline in population size with increased hunting, potentially due to their ability to better use alternative food sources. Under reduced precipitation

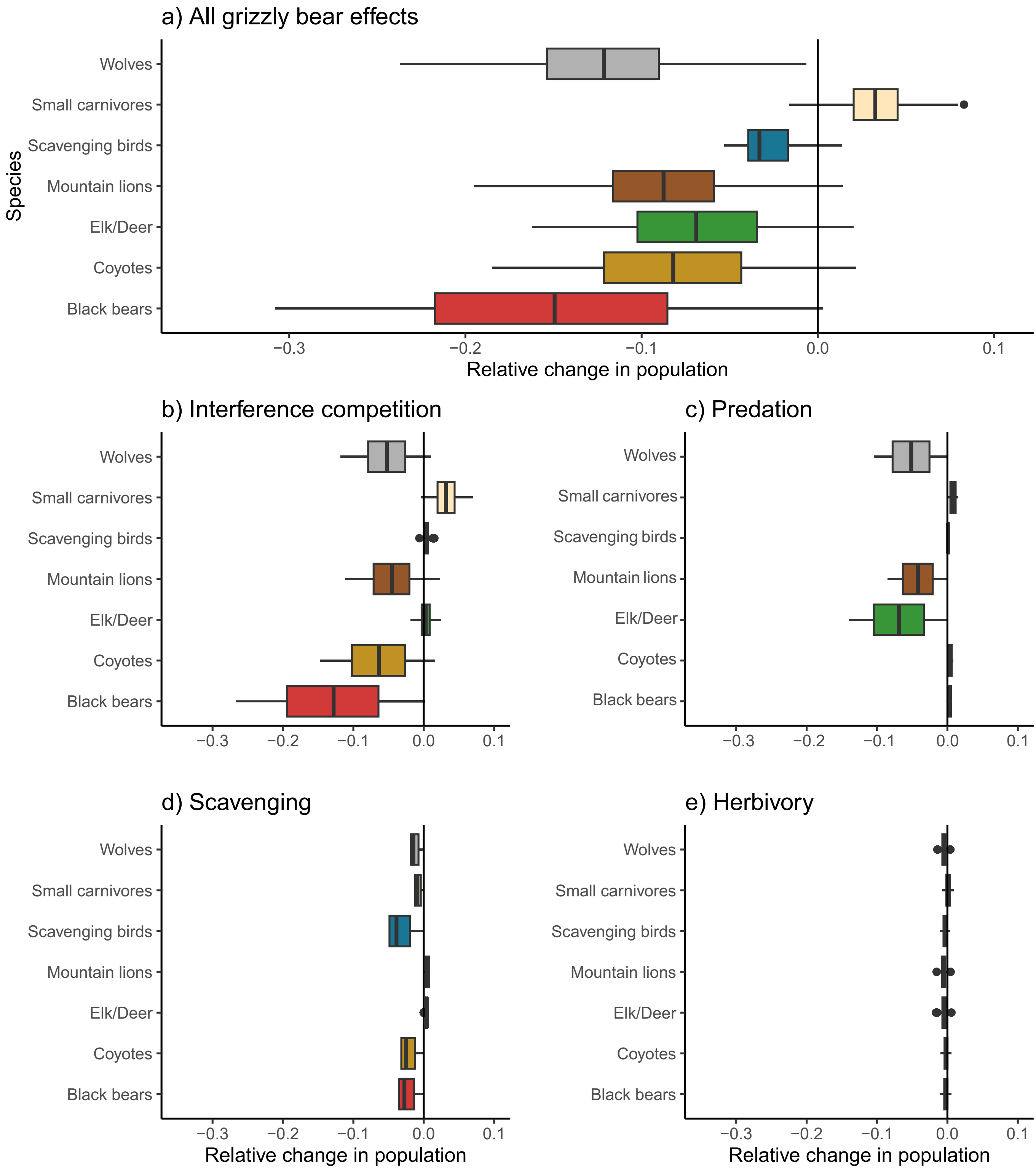

Fig. 3. Relative change in population size of large vertebrate species in response to grizzly bear rewilding, as predicted by fuzzy interaction web models. Panel a shows the total predicted changes in abundances combining all ecological interaction types, while panels b–e show the changes in abundances in response to each interaction type individually. Asterisks indicate species that are directly affected by the specified interaction of grizzly bears; species without asterisks are indirectly affected. An alternative version of this figure with a free x-axis is available in Appendix S6.

(25.4 cm of annual precipitation), black bears, coyotes, ungulates, mountain lions, and wolves all showed greater predicted decreases in population size than under the current average annual precipitation of 30.5 cm (same values as above). Scavenging birds did not show much change, while small carnivores showed a predicted increase in population size.

4. Discussion

Rewilding can have complex effects on communities and ecosystems,

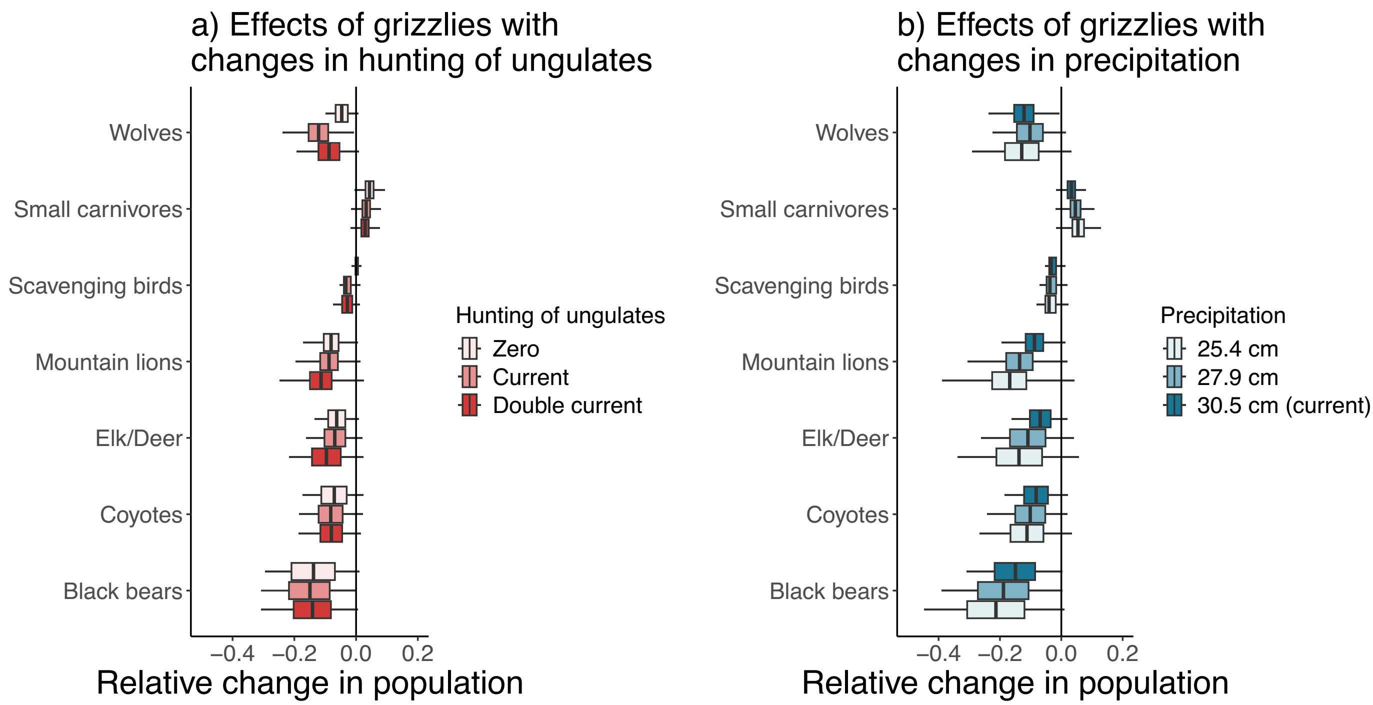

Fig. 4. Relative change in population size of vertebrates in response to grizzly bear rewilding under various levels of human hunting pressure and precipitation regimes.

particularly if systems have undergone extensive anthropogenic change since key functional groups were lost (Svenning et al., 2016). Much of western North America, as well as parts of Europe and Asia, provide critical examples of this, given that key large mammal predators, including bears and wolves, were functionally or completely extirpated from the regions and have been re-expanding to their historical ranges over the past several decades. Developing these predictive hypotheses for how the recovery of grizzlies will affect this system is essential for understanding the ecological dynamics and evaluating ecological outcomes as recovery progresses. In addressing our initial predictions, our model outcomes found support for 1) small declines in sympatric carnivores due to competition, 2) a small increase in small carnivores, and 3) a decline in large herbivores, as well as partial support for 4) greater populations declines under greater anthropogenic change. Changes in climate and hunting regimes present novel conditions unlike those experienced by the ecosystem before large predators were extirpated. Hence, predicted changes in species populations may indicate a no-analogue ecological state with substantive ramifications for future trajectories (Williams and Jackson, 2007). Importantly, other factors like winter severity, disease, and land protection status are likely more impactful on species population size than grizzly bear recovery, yet this model still predicts clear differences in systems with and without grizzlies.

Some of these modest population declines are aligned with current wildlife management goals in the region, particularly in Western Montana where species including wolves (Eggert, 2025), elk (Bealer, 2024), and mountain lions (Montana Fish Wildlife and Parks, 2019) are at least partially being targeted for reduction. As such, grizzly bear recovery can potentially aid in these management goals. However, in other locations, conservation efforts should focus on making sure these species have the resources and protection necessary to persist as grizzly bear recovery proceeds. Overall, rewilding efforts wherein habitat quality and connectivity are improved to facilitate the recovery of ecological and trophic processes have the potential to provide myriad ecological benefits and costs beyond those addressed in this manuscript and can be further explored using this model framework. This work is intended to aid in directing future research and conservation efforts to best quantify the ecological effects of grizzly bear recovery, as well as ensure populations stability for large sympatric species.

One of the primary ways our model predicts that grizzly bears are expected to affect sympatric carnivores is interference competition. This refers to the direct interaction between two individuals in which one is physically harmed or prevented from obtaining resources by the other (Birch, 1957). In this modeled ecosystem, grizzly bears engage in interference competition with black bears, coyotes, wolves, and mountain lions. Because of their overlap in habitat and resource requirements (Apps et al., 2006; Murphy et al., 1998), grizzly bears will naturally encounter these sympatric large predators, particularly while obtaining resources such as at carcasses (Cristescu et al., 2014). As a result of their large size, direct competitive interactions with other predators almost always favor the grizzly, except in the case of wolves where interaction outcomes can vary (Tallian et al., 2022). For black bears and coyotes, these interactions often take the form of intraguild killing by grizzlies (Klauder, 2018; Prugh and Sivy, 2020), directly reducing population sizes of the smaller carnivores. This interference competition is the primary mechanism by which grizzly bears are predicted to affect both black bears and coyotes, with the effects of exploitative competition being relatively minimal, likely due to the high diet flexibility of these smaller species. For mountain lions, interference competition can occur through grizzly bear displacement of mountain lions from their kills, which can occur at over 18 % of mountain lion kills (Rabe et al., 2025), potentially resulting in greater energy expenditure and lost nutrition for mountain lions (Allen et al., 2021; Murphy et al., 1998). Interference competition by grizzlies and resulting decreases in black bear, coyote, wolf, and mountain lion population sizes can also result in smaller, indirect effects on other key species. Notably, ungulates, mammalian small carnivores, and scavenging birds were all predicted to increase to a small extent, likely due to an indirect easing of top-down controls for prey species (Elmhagen et al., 2010), and a competitive release of smaller carnivores and scavengers (Levi and Wilmers, 2012) who compete with and avoid species like coyotes (Parsons et al., 2022; Prugh et al., 2023) that are partially suppressed by the grizzlies.

Another major avenue by which rewilded grizzly bears were predicted to affect key vertebrate species was through predation. Although grizzly bears are generalists with a wide range of diet components including grasses, forbs, berries, roots, nuts, invertebrates, fish, and small vertebrates (Gunther et al., 2014; Munro et al., 2006), ungulates are frequently eaten and can make up a large proportion of grizzly bears' diets in some areas and seasons (Milakovic and Parker, 2013). In the U.S. Northern Rockies, elk and deer are already frequently predated on by other carnivores including wolves, mountain lions, and coyotes (Lodberg-Holm et al., 2021; Singer et al., 1997). According to our model, rewilded grizzly bear populations may further increase top-down effects by predators on these ungulates, and potentially reduce their population size. Likely because of this decrease in ungulate population size, our model predicts that grizzly bear predation also has an indirect effect on other large carnivore species that predate on ungulates, particularly wolves and mountain lions, resulting in small population declines.

Regarding scavenging, as dominant predators in the ecosystem, grizzlies compete with many other scavengers for carcasses left by hunters and other predators. This exploitative competition is predicted to result in small or very small population declines in other scavengers (black bears, coyotes, etc.). Finally, although vegetation can make up a substantial proportion of grizzly bear diets (Gunther et al., 2014; Mattson, 1997; Munro et al., 2006; Schwartz et al., 2006), the relatively low population density of grizzlies prevents them from substantially altering vegetation populations, and therefore, likely results in relatively weak indirect interactions with other species engaging in herbivory. Nevertheless, recent work has posed omnivores as critical determinants of ecological stability in a changing world (Gutgesell et al., 2022). Thus, as anthropogenic changes continue to alter ecosystems, these omnivorous pathways by which grizzlies and other omnivores can impact other species may become more ecologically significant.

Hunting is a major recreational activity in western North America, with thousands of hunters participating each year. In this region, deer and elk are by far the most hunted big game species, and hunting is closely regulated. In our model, the effects of deer and elk hunting in conjunction with grizzly bear recovery are predicted to be variable, with the most obvious predicted changes being declines in ungulates and mountain lions. The lack of decline of some species with increasing ungulate hunting could be due to the supplementary resources provided by gutpiles and carrion remains, which is shown to be an important food source for many scavengers (Wilmers et al., 2003), and is included as a component of the model. As grizzly bear recovery continues in western North America, and as political landscapes change, it is likely that grizzlies will eventually be hunted (Montana Fish Wildlife and Parks, 2024a), instigating a new interaction that the current model does not account for. Our framework provides the flexibility to model the effects of grizzly bear hunting to inform harvest objectives moving forward.

Finally, global climate change is expected to drastically alter ecological communities worldwide with rising temperatures and changes in precipitation regimes (Chen et al., 2011). In the U.S. Northern Rockies and Canadian Southern Rockies, droughts are expected to increase in frequency and precipitation is expected to decrease, especially in summer and fall (Keane and Mahalovich, 2018). This has the strong potential to reduce primary productivity (Liu et al., 2021), and hence available forage for herbivores and omnivores like the grizzly bear (Fortin et al., 2013). Our models predict that this will have a particularly strong effect on animals that engage in herbivory and their associated predators. In conjunction with grizzly bear recovery, all the most affected species (black bear, coyote, mountain lion, ungulates, and wolves) have exacerbated population declines with decreasing annual precipitation. These predictions are consistent with large-scale experiments indicating stronger bottom-up than top-down control in this system (Maron and Pearson, 2011). In general, more information is needed to understand the effects of climate change on terrestrial mammal populations (Paniw et al., 2021), but evidence in North America does indicate that large species alter their space use and occupancy in response to changing climate conditions (Tourani et al., 2023). Yet under these shifting conditions, omnivores have been posited to play a key role in stabilizing complex communities through diet variability and adaptability under varying conditions (Gutgesell et al., 2022). As such, brown bears could play an even more important role in supporting community-wide functions under these conditions. This analysis predicts that climate change may indeed have substantial effects on large mammal populations. It also emphasizes the need to understand the interaction between global climate change and other anthropogenic factors on a local scale, and to find the best ways to predict and mitigate community-level consequences.

Fuzzy interaction webs, like the one presented in this study, hold the potential to predict community responses in complex, multitrophic, bidirectional, ecological networks. However, several limitations of fuzzy interaction webs require that their outputs be interpreted as general, directional predictions rather than precise estimates. The use of qualitative data is one of the strengths of FIWs, but also limits the precision of its outputs, while the lack of spatial components prevents the model from incorporating any sort of spatial heterogeneity or specificity. In addition, FIWs' assumption of equilibrium population dynamics does not account for temporal variability and stochasticity that could be a driving force in the system. Finally, given the complexity of the system and limited data availability, additional ecological interactions were not included in the model, such as grizzly kleptoparasitim of red squirrel middens (Mattson and Reinhart, 1997). Yet, FIWs and similar tools may become increasingly useful as global change progresses, with biological, environmental, and anthropogenic drivers changing in tandem. This is particularly true in situations like this where large, wide-ranging vertebrates make experimental testing and quantification of species interactions extremely difficult. FIWs can provide a rough understanding of these effects in the absence of these data, help identify gaps in the literature and suggest future avenues for research and conservation strategies.

Our predictions suggest that, as grizzly bear populations re-expand into their historical range, the ensuing ecological change may result in modest population declines of sympatric predators and ungulates. These predicted changes are a result of multiple direct and indirect effects, mostly related to interference competition and predation. Concurrent changes in human hunting and climate change may exacerbate population declines, but directed management holds the potential to reduce declines and prevent more serious, long-lasting effects like loss of ecological function. Importantly, our models predict species population responses to the highest grizzly bear densities found in the region. As a result, in non-optimal grizzly habitats where grizzly bear carrying capacity is lower, observed population declines may be on the lower end of our model predictions. This type of predictive model may be highly relevant in other regions where carnivore populations, including brown bears in Europe and Asia, are recovering, and additional models could be developed that can accommodate the unique biological communities and environmental conditions in these regions.

We emphasize that while predictive modeling approaches like FIWs provide opportunities for assessing potential outcomes of conservation actions, model predictions vetting is necessary to evaluate model efficacy, improve modeling approaches for the future, and increase ecological understanding of the system. Accomplishing this requires on the ground data from areas pre and post grizzly bear recovery to measure relative changes in sympatric vertebrate population size comparable to the outputs produced by this FIW. Study sites with long-term, comprehensive biological data collection like MPG Ranch offer a great opportunity to perform this type of cross-validation once grizzly bear recovery is complete, and data collection related to this question is currently ongoing. Previously, cross-validation had been used to compare FIW model predictions to community-level changes in Yellowstone Lake following the introduction of lake trout, and in Newfoundland following the introduction of red squirrels. Changes predicted from FIW models have been found to be consistent with actual community changes in these instances (Clark-Wolf et al., 2022). Success in predicting community effects of grizzly bear recovery would go a long way to validating the effectiveness of FIWs for ecological modeling, given the complexity of the system. As species ranges shift globally in instances of rewilding and other conservation actions (Pearson et al., 2022), it is critical to understand the way species' effects propagate across ecological networks in order to direct conservation efforts in a way that will give the entire biological community the best chance of long-term sustainability.

CRediT authorship contribution statement

Daniel Gorczynski: Writing – review & editing, Writing – original draft, Visualization, Methodology, Investigation, Formal analysis, Data curation, Conceptualization. **T.J. Clark-Wolf:** Writing – review & editing, Writing – original draft, Supervision, Methodology, Data curation, Conceptualization. **Jedediah F. Brodie:** Writing – review & editing, Writing – original draft, Supervision, Methodology, Conceptualization. **Dean Pearson:** Writing – review & editing, Writing – original draft, Supervision, Methodology, Investigation, Data curation, Conceptualization.

Declaration of competing interest

I have nothing to declare.

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Appendix A. Supplementary data

Additional supporting information may be found in the online version of the article at the publisher's website. The MPG model upon which the model presented in this manuscript is based can be found at (https://matrix.mpgranch.com/#/). The code used to run the models in the manuscript can be found at (https://github.com/DanielGorczynski/Grizzly-rewilding.git). Supplementary data to this article can be found online at https://doi.org/10.1016/j.biocon.2025.111455.

Data availability

All data and code are included in the supplementary materials.

References

Aguilar, J., 2005. A survey about fuzzy cognitive maps papers (invited paper). Int. J. Comput. Cogn. 3 (2), 27–33.

Allen, M.L., Elbroch, L.M., Wittmer, H.U., 2021. Can't bear the competition: energetic losses from kleptoparasitism by a dominant scavenger may alter foraging behaviors of an apex predator. Basic Appl. Ecol. 51, 1–10. https://doi.org/10.1016/j.baae.2021.01.011.

Apps, C.D., McLellan, B.N., Woods, J.G., 2006. Landscape partitioning and spatial inferences of competition between black and grizzly bears. Ecography 29 (4), 561–572. https://doi.org/10.1111/j.0906-7590.2006.04564.x.

Baker, C.M., Holden, M.H., Plein, M., McCarthy, M.A., Possingham, H.P., 2018. Informing network management using fuzzy cognitive maps. Biol. Conserv. 224, 122–128. https://doi.org/10.1016/j.biocon.2018.05.031.

Bealer, N., 2024. Elk Habitat Management in Montana W-179-R Annual Interim Report (December 2024).

Birch, L.C., 1957. The meanings of competition. Am. Nat. 91 (856), 5–18. https://doi.org/10.1086/281957.

Braid, A.C.R., Manzer, D., Nielsen, S.E., 2016. Wildlife habitat enhancements for grizzly bears: survival rates of planted fruiting shrubs in forest harvests. For. Ecol. Manag. 369, 144–154. https://doi.org/10.1016/j.foreco.2016.03.032.

Cardinale, B.J., Weis, J.J., Forbes, A.E., Tilmon, K.J., Ives, A.R., 2006. Biodiversity as both a cause and consequence of resource availability: a study of reciprocal causality in a predator–prey system. J. Anim. Ecol. 75 (2), 497–505. https://doi.org/10.1111/j.1365-2656.2006.01070.x.

Chen, I.-C., Hill, J.K., Ohlemüller, R., Roy, D.B., Thomas, C.D., 2011. Rapid range shifts of species associated with high levels of climate warming. Science 333 (6045), 1024–1026. https://doi.org/10.1126/science.1206432.

Clark-Wolf, T.J., Hahn, P.G., Brelsford, E., Francois, J., Hayes, N., Larkin, B., Ramsey, P., Pearson, D.E., 2022. Preventing a series of unfortunate events: using qualitative models to improve conservation. J. Appl. Ecol. 59 (9), 2322–2332. https://doi.org/10.1111/1365-2664.14231.

Costello, C.M., Dellinger, J., Fortin-Noreus, J., Haroldson, M.A., Kasworm, W.F., Tiesberg, J.E., van Manen, F.T., 2023. A summary of grizzly bear distribution in Montana: application of consistent methods in 2022, Montana Fish, Wildlife and Parks. https://pubs.usgs.gov/publication/70247700.

Cristescu, B., Stenhouse, G.B., Boyce, M.S., 2014. Grizzly bear ungulate consumption and the relevance of prey size to caching and meat sharing. Anim. Behav. 92, 133–142. https://doi.org/10.1016/j.anbehav.2014.03.020.

Dexter, N., Ramsey, D.S.L., MacGregor, C., Lindenmayer, D., 2012. Predicting ecosystem wide impacts of wallaby management using a fuzzy cognitive map. Ecosystems 15 (8), 1363–1379. https://doi.org/10.1007/s10021-012-9590-7.

Dobson, A.P., 2014. Yellowstone wolves and the forces that structure natural systems. PLoS Biol. 12 (12), e1002025. https://doi.org/10.1371/journal.pbio.1002025.

Drew, M., 2024. Wildlife officials relocate two montana grizzlies to yellowstone ecosystem, Flathead Beacon. https://flatheadbeacon.com/2024/08/06/wildlife-officials-relocate-two-montana-grizzlies-to-yellowstone-ecosystem/ (August 6).

Eggert, A., 2025. Two bills seeking to roughly halve Montana's wolf population pass out of committee, Montana Free Press. http://montanafreepress.org/2025/01/24/two-bills-seeking-to-roughly-halve-montanas-wolf-population-pass-out-of-committee/ (January 25).

Elmhagen, B., Ludwig, G., Rushton, S.P., Helle, P., Lindén, H., 2010. Top predators, mesopredators and their prey: interference ecosystems along bioclimatic productivity gradients. J. Anim. Ecol. 79 (4), 785–794. https://doi.org/10.1111/j.1365-2656.2010.01678.x.

Estes, J.A., Terborgh, J., Brashares, J.S., Power, M.E., Berger, J., Bond, W.J., Carpenter, S.R., Essington, T.E., Holt, R.D., Jackson, J.B.C., Marquis, R.J., Oksanen, L., Oksanen, T., Paine, R.T., Pikitch, E.K., Ripple, W.J., Sandin, S.A., Scheffer, M., Schoener, T.W., Wardle, D.A., 2011. Trophic downgrading of planet earth. Science 333 (6040), 301–306. https://doi.org/10.1126/science.1205106.

Fitt, R.N.L., Lancaster, L.T., 2017. Range shifting species reduce phylogenetic diversity in high latitude communities via competition. J. Anim. Ecol. 86 (3), 543–555. https://doi.org/10.1111/1365-2656.12655.

Fortin, J.K., Schwartz, C.C., Gunther, K.A., Teisberg, J.E., Haroldson, M.A., Evans, M.A., Robbins, C.T., 2013. Dietary adjustability of grizzly bears and American black bears in Yellowstone National Park. J. Wildl. Manag. 77 (2), 270–281. https://doi.org/10.1002/jwmg.483.

France, T., Brister, D., 2020. Bringing back the great bear: challenges and opportunities of grizzly restoration in the Northern Rockies. Pub. Land Res. Law Rev. 42, 15.

French, S.P., French, M.G., Knight, R.R., 1994. Grizzly bear use of army cutworm moths in the Yellowstone ecosystem. In: Bears: Their Biology and Management, vol. 9, pp. 389–399. https://doi.org/10.2307/3872725.

García-Rodríguez, A., Albrecht, J., Szczutkowska, S., Valido, A., Farwig, N., Selva, N., 2021. The role of the brown bear *Ursus arctos* as a legitimate megafaunal seed disperser. Sci. Rep. 11 (1), 1282. https://doi.org/10.1038/s41598-020-80440-9.

Greenwald, N., 2023. Recovery of the grizzly bear at the intersection of law and science. Front. Conserv. Sci. 4. https://doi.org/10.3389/fcosc.2023.1142991.

Gunther, K.A., Shoemaker, R.R., Frey, K.L., Haroldson, M.A., Cain, S.L., van Manen, F.T., Fortin, J.K., 2014. Dietary breadth of grizzly bears in the greater Yellowstone ecosystem. Ursus 25 (1), 60–72. https://doi.org/10.2192/URSUS-D-13-00008.1.

Gutgesell, M.K., McCann, K.S., Gellner, G., Cazelles, K., Greyson-Gaito, C.J., Bieg, C., Guzzo, M.M., Warne, C.P.K., Ward, C.A., O'Connor, R.F., Scott, A.M., Graham, B.C., Champagne, E.J., McMeans, B.C., 2022. On the dynamic nature of omnivory in a changing world. BioScience 72 (5), 416–430. https://doi.org/10.1093/biosci/biab144.

Hunter, D.O., Britz, T., Jones, M., Letnic, M., 2015. Reintroduction of Tasmanian devils to mainland Australia can restore top-down control in ecosystems where dingoes have been extirpated. Biol. Conserv. 191, 428–435. https://doi.org/10.1016/j.biocon.2015.07.030.

Jones, N.T., Symons, C.C., Cavalheri, H., Pedroza-Ramos, A., Shurin, J.B., 2020. Predators drive community reorganization during experimental range shifts. J. Anim. Ecol. 89 (10), 2378–2388. https://doi.org/10.1111/1365-2656.13289.

Kasworm, W.F., Proctor, M.F., Servheen, C., Paetkau, D., 2007. Success of grizzly bear population augmentation in Northwest Montana. J. Wildl. Manag. 71 (4), 1261–1266. https://doi.org/10.2193/2006-266.

Keane, R.E., Mahalovich, M.F., 2018. Effects of Climate Change on Forest Vegetation in the Northern Rockies Region.

Klauder, K., 2018. Between a Risk and a Hard Place: Scavenging Patterns and Habitat Selection of Carnivores in the Subarctic (Master of Science). University of Washington.

Laliberte, A.S., Ripple, W.J., 2004. Range contractions of north American carnivores and ungulates. BioScience 54 (2), 123–138. https://doi.org/10.1641/0006-3568(2004)054[0123:RCONAC]2.0.CO;2.

Levi, T., Wilmers, C., 2012. Wolves-coyotes-foxes: a cascade among carnivores. Ecology 93, 921–929. https://doi.org/10.2307/23213740.

Liu, X., Ma, Q., Yu, H., Li, Y., Li, L., Qi, M., Wu, W., Zhang, F., Wang, Y., Zhou, G., Xu, Z., 2021. Climate warming-induced drought constrains vegetation productivity by weakening the temporal stability of the plant community in an arid grassland ecosystem. Agric. For. Meteorol. 307, 108526. https://doi.org/10.1016/j.agrformet.2021.108526.

Lodberg-Holm, H.K., Teglas, B.S., Tyers, D.B., Jimenez, M.D., Smith, D.W., 2021. Spatial and temporal variability in summer diet of gray wolves (*Canis lupus*) in the Greater Yellowstone Ecosystem. J. Mammal. 102 (4), 1030–1041. https://doi.org/10.1093/jmammal/gyab060.

Lorimer, J., Sandom, C., Jepson, P., Doughty, C., Barua, M., Kirby, K.J., 2015. Rewilding: science, practice, and politics. Annu. Rev. Environ. Resour. 40 (1), 39–62. https://doi.org/10.1146/annurev-environ-102014-021406.

Maron, J.L., Pearson, D.E., 2011. Vertebrate predators have minimal cascading effects on plant production or seed predation in an intact grassland ecosystem. Ecol. Lett. 14 (7), 661–669. https://doi.org/10.1111/j.1461-0248.2011.01633.x.

Mattson, D.J., 1997. Use of ungulates by Yellowstone grizzly bears *Ursus arctos*. Biol. Conserv. 81 (1–2), 161–177. https://doi.org/10.1016/S0006-3207(96)00142-5.

Mattson, D.J., Merrill, T., 2002. Extirpations of grizzly bears in the contiguous United States, 1850–2000. Conserv. Biol. 16 (4), 1123–1136. https://doi.org/10.1046/j.1523-1739.2002.00414.x.

Mattson, D., Reinhart, D., 1997. Excavation of red squirrel middens by grizzly bears in the Whitebark pine zone. J. Appl. Ecol. 34, 926. https://doi.org/10.2307/2405283.

Milakovic, B., Parker, K.L., 2013. Quantifying carnivory by grizzly bears in a multi-ungulate system. J. Wildl. Manag. 77 (1), 39–47. https://doi.org/10.1002/jwmg.434.

Moleón, M., Sánchez-Zapata, J.A., Selva, N., Donázar, J.A., Owen-Smith, N., 2014. Inter-specific interactions linking predation and scavenging in terrestrial vertebrate assemblages. Biol. Rev. 89 (4), 1042–1054. https://doi.org/10.1111/brv.12097.

Montana Fish Wildlife & Parks, 2019. Montana Mountain Lion Monitoring and Management Strategy. Montana Fish Wildlife & Parks.

Montana Fish Wildlife & Parks, 2024a. 2024 Statewide Grizzly Bear Management Plan, p. 15. https://fwp.mt.gov/binaries/content/assets/fwp/conservation/bears/grizzly-management/record-of-decision.pdf.

Montana Fish Wildlife & Parks, 2024b. Harvest estimates, Montana Fish Wildlife & Parks. https://myfwp.mt.gov/fwpPub/harvestReports.

Munro, R.H.M., Nielsen, S.E., Price, M.H., Stenhouse, G.B., Boyce, M.S., 2006. Seasonal and diel patterns of grizzly bear diet and activity in West-Central Alberta. J. Mammal. 87 (6), 1112–1121. https://doi.org/10.1644/05-MAMM-A-410R3.1.

Murphy, K.M., Felzien, G.S., Hornocker, M.G., Ruth, T.K., 1998. Encounter competition between bears and cougars: some ecological implications. Ursus 10, 55–60.

Nguyen, H.T., Walker, C., Walker, E.A., 2018. A First Course in Fuzzy Logic, 4th ed. Chapman and Hall/CRC https://www.taylorfrancis.com/books/mono/10.1201/9780429505546/first-course-fuzzy-logic-hung-nguyen-carol-walker-elbert-walker.

Paniw, M., James, T.D., Ruth Archer, C., Römer, G., Levin, S., Compagnoni, A., Che-Castaldo, J., Bennett, J.M., Mooney, A., Childs, D.Z., Ozgul, A., Jones, O.R., Burns, J.H., Beckerman, A.P., Patwary, A., Sanchez-Gassen, N., Knight, T.M., Salguero-Gómez, R., 2021. The myriad of complex demographic responses of terrestrial mammals to climate change and gaps of knowledge: a global analysis. J. Anim. Ecol. 90 (6), 1398–1407. https://doi.org/10.1111/1365-2656.13467.

Papageorgiou, E.I., 2011. Review Study on Fuzzy Cognitive Maps and Their Applications During the Last Decade, pp. 828–835.

Parsons, A.W., Kellner, K.F., Rota, C.T., Schuttler, S.G., Millspaugh, J.J., Kays, R.W., 2022. The effect of urbanization on spatiotemporal interactions between gray foxes and coyotes. Ecosphere 13 (3), e3993. https://doi.org/10.1002/ecs2.3993.

Pearson, D., Clark-Wolf, T., 2023. Predicting ecological outcomes using fuzzy interaction webs. Ecology 104, e4072. https://doi.org/10.1002/ecy.4072.

Pearson, D., Clark, T.J., Hahn, P.G., 2022. Evaluating unintended consequences of intentional species introductions and eradications for improved conservation management. Conserv. Biol. 36 (1), e13734. https://doi.org/10.1111/cobi.13734.

Pearson, D.E., DePuy, A.L.W., Kuhlman, M.P., 2025. Inspiring citizens and municipalities to initiate pollinator conservation: the urban pollinator matrix modeling tool. Urban Ecosyst. 28 (2), 91. https://doi.org/10.1007/s11252-025-01703-9.

Perino, A., Pereira, H.M., Navarro, L.M., Fernández, N., Bullock, J.M., Ceaușu, S., Cortés-Avizanda, A., Van Klink, R., Kuemmerle, T., Lomba, A., Pe'er, G., Plieninger, T., Rey Benayas, J.M., Sandom, C.J., Svenning, J.-C., Wheeler, H.C., 2019. Rewilding complex ecosystems. Science 364 (6438), eaav5570. https://doi.org/10.1126/science.aav5570.

Prugh, L.R., Sivy, K.J., 2020. Enemies with benefits: integrating positive and negative interactions among terrestrial carnivores. Ecol. Lett. 23 (5), 902–918. https://doi.org/10.1111/ele.13489.

Prugh, L.R., Cunningham, C.X., Windell, R.M., Kertson, B.N., Ganz, T.R., Walker, S.L., Wirsing, A.J., 2023. Fear of large carnivores amplifies human-caused mortality for mesopredators. Science 380 (6646), 754–758. https://doi.org/10.1126/science.adf2472.

Rabe, J.W., Binder, W.J., Anton, C.B., Meyer, C.J., Metz, M.C., Smith, B.J., Ruth, T.K., Murphy, K.M., Bump, J.K., Smith, D.W., Stahler, D.R., 2025. Prey size mediates interference competition and predation dynamics in a large carnivore community. Commun. Biol. 8 (1), 424. https://doi.org/10.1038/s42003-025-07779-5.

Ramsey, D., Veltman, C., 2005. Predicting the effects of perturbations on ecological communities: what can qualitative models offer? J. Anim. Ecol. 74 (5), 905–916. https://doi.org/10.1111/j.1365-2656.2005.00986.x.

Ripple, W.J., Estes, J.A., Beschta, R.L., Wilmers, C.C., Ritchie, E.G., Hebblewhite, M., Berger, J., Elmhagen, B., Letnic, M., Nelson, M.P., Schmitz, O.J., Smith, D.W., Wallach, A.D., Wirsing, A.J., 2014. Status and ecological effects of the world's largest carnivores. Science 343 (6167), 1241484. https://doi.org/10.1126/science.1241484.

Roman, J., Dunphy-Daly, M.M., Johnston, D.W., Read, A.J., 2015. Lifting baselines to address the consequences of conservation success. Trends Ecol. Evol. 30 (6), 299–302. https://doi.org/10.1016/j.tree.2015.04.003.

Rooney, R.C., Daniel, J., Mallory, M., Hedd, A., Ives, J., Gilchrist, G., Gjerdrum, C., Robertson, G., Ronconi, R., Wilcox, K., Wong, S., Provencher, J., 2023. Fuzzy cognitive mapping as a tool to assess the relative cumulative effects of environmental stressors on an Arctic seabird population to identify conservation action and research priorities. Ecol. Solut. Evid. 4 (2), e12241. https://doi.org/10.1002/2688-8319.12241.

Schwartz, C.C., Haroldson, M.A., White, G.C., Harris, R.B., Cherry, S., Keating, K.A., Moody, D., Servheen, C., 2006. Temporal, spatial, and environmental influences on the demographics of grizzly bears in the Greater Yellowstone Ecosystem. Wildl. Monogr. 161 (1), 1–8. https://doi.org/10.2193/0084-0173(2006)161[1:TSAEIO]2.0.CO;2.

Seddon, P.J., Griffiths, C.J., Soorae, P.S., Armstrong, D.P., 2014. Reversing defaunation: restoring species in a changing world. Science 345 (6195), 406–412. https://doi.org/10.1126/science.1251818.

Singer, F.J., Harting, A., Symonds, K.K., Coughenour, M.B., 1997. Density dependence, compensation, and environmental effects on elk calf mortality in Yellowstone National Park. J. Wildl. Manag. 61 (1), 12–25. https://doi.org/10.2307/3802410.

Svenning, J.-C., Pedersen, P.B.M., Donlan, C.J., Ejrnæs, R., Faurby, S., Galetti, M., Hansen, D.M., Sandel, B., Sandom, C.J., Terborgh, J.W., Vera, F.W.M., 2016. Science for a wilder Anthropocene: synthesis and future directions for trophic rewilding research. Proc. Natl. Acad. Sci. 113 (4), 898–906. https://doi.org/10.1073/pnas.1502556112.

Tallian, A., Ordiz, A., Metz, M.C., Zimmermann, B., Wikenros, C., Smith, D.W., Stahler, D.R., Wabakken, P., Swenson, J.E., Sand, H., Kindberg, J., 2022. Of wolves and bears: seasonal drivers of interference and exploitation competition between apex predators. Ecol. Monogr. 92 (2), e1498. https://doi.org/10.1002/ecm.1498.

Tourani, M., Sollmann, R., Kays, R., Ahumada, J., Fegraus, E., Karp, D.S., 2023. Maximum temperatures determine the habitat affiliations of north American mammals. Proc. Natl. Acad. Sci. USA 120 (50), e2304411120. https://doi.org/10.1073/pnas.2304411120.

Williams, J.W., Jackson, S.T., 2007. Novel climates, no-analog communities, and ecological surprises. Front. Ecol. Environ. 5 (9), 475–482. https://doi.org/10.1890/070037.

Wilmers, C.C., Stahler, D.R., Crabtree, R.L., Smith, D.W., Getz, W.M., 2003. Resource dispersion and consumer dominance: scavenging at wolf- and hunter-killed carcasses in Greater Yellowstone, USA. Ecol. Lett. 6 (11), 996–1003. https://doi.org/10.1046/j.1461-0248.2003.00522.x.

Zimov, S.A., 2005. Pleistocene Park: return of the mammoth's ecosystem. Science 308 (5723), 796–798. https://doi.org/10.1126/science.1113442.