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RESEARCH ARTICLE

Preventing a series of unfortunate events: Using qualitative models to improve conservation

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Abstract

1. Biological organisms are increasingly being introduced and eradicated in an effort to maintain biodiversity and ecosystem function in the face of anthropogenic threats. However, these conservation actions can have unintended consequences to non-target species. Careful vetting of these actions using ecological modelling tools could help predict and avoid unintended consequences.
2. Qualitative modelling tools, such as fuzzy interaction webs (FIWs), allow for qualitative rankings of community properties (e.g. interaction strength = high, medium, low) in combination with quantitative information to predict management outcomes. These tools have lower data requirements than strictly quantitative models, facilitating their use for communities lacking comprehensive parameterization. However, no studies have evaluated the efficacy of FIWs for predicting unintended consequences against empirically documented outcomes. Moreover, there is no process for systematically identifying which species to incorporate in community-level conservation assessments to overcome model structure uncertainty. Finally, there is a need to make qualitative modelling tools more accessible for conservation practitioners.
3. We applied FIWs to the case study of lake trout introduction into Yellowstone Lake, Yellowstone National Park, to assess its ability to predict documented community-level outcomes from an intentional species introduction. Next, we used the case study of the intentional red squirrel introduction to Newfoundland to show how a community assessment framework can help define the community interaction web needed for applying a FIW. Lastly, we introduced a user-friendly web interface (https://matrix.mpgranch.com/#/) for applying FIWs to conservation questions.
4. We found that the FIW predicted previously documented directional changes in the abundance of community components relatively well in the Yellowstone Lake case study, even with minimal knowledge of the system. The community

assessment framework provided a formal process for identifying community components for the Newfoundland case study, and the resulting FIW predicted documented unintended consequences. The user interface predicts realistic outcomes in our study system and allows managers to build and apply FIWs for conservation planning.

5. *Synthesis and applications*. Our community assessment framework and user interface can be used to apply FIWs to identify and avert potential unintended outcomes of species introductions and eradications for improved conservation management.

KEYWORDS

assisted migration, biological control, fuzzy cognitive map, fuzzy interaction web, gene drive, rewilding, species removal, translocations

1 | INTRODUCTION

Intentionally introducing and eradicating species for conservation can cause negative, unintended consequences to non-target species that permeate through entire ecosystems (e.g. Bergstrom et al., 2009; Doak et al., 2008; Pearson & Callaway, 2006; Simberloff & Stiling, 1996). A recent global review found unintended outcomes in 36% of management cases evaluated across a range of conservation actions, including assisted migration, rewilding, invasive species removal, gene drives and biological control (Pearson et al., 2021). Importantly, 93% of these unintended outcomes arose from direct or simple indirect interactions with the target species that could potentially be predicted using ecological theory. These findings suggest that many unintended outcomes could be avoided by applying ecological modelling tools to vet management actions prior to execution.

Ecological modelling has advanced from simple models with a few species (e.g. Holt, 1977; Lotka, 1925; Rosenzweig & MacArthur, 1963; Tilman, 1980; Volterra, 1926) to more complex models capable of projecting community-wide outcomes (e.g. Adams et al., 2020; Geary et al., 2020; Godoy et al., 2018; Sauve & Barraquand, 2020). However, these quantitative approaches often require precise data for each species and linkage in the system, and such data are commonly unavailable to conservation practitioners. Nonetheless, compelling arguments exist for introducing and eradicating species on behalf of conservation (Marvier & Kareiva, 2020), and these actions continue to be executed without sufficient vetting to avoid unintended consequences (Pearson et al., 2021).

Qualitative models offer a promising alternative to data-hungry quantitative models. Fuzzy cognitive mapping is one such approach that was developed to understand and predict qualitative outcomes of interactions among network components in social sciences and engineering (Kosko, 1992; Özesmi & Özesmi, 2004; Papageorgiou, 2011). These tools have much lower data requirements than quantitative models, and they can be applied to ecological systems using basic information on the species involved (i.e. the nodes within a community interaction web), their interactions (i.e. the linkages between species and the direction of the interactions—positive or negative) and qualitative rankings of interaction strength (e.g. high, medium, low) generated from data, literature sources and/or expert opinion (Ramsey & Veltman, 2005). Fuzzy cognitive mapping is increasingly being applied to conservation management, where it is referred to as fuzzy interaction webs (FIWs), to predict and inform management outcomes (Baker et al., 2018; Hobbs et al., 2002; Ramsey et al., 2012; Ramsey & Veltman, 2005). These studies suggest that FIWs could provide a critically needed tool for evaluating both intended and unintended outcomes that might arise from proposed species introductions and eradications. However, no studies to our knowledge have applied these tools to scenarios with known outcomes to test their efficacy for predicting unintended consequences. Beyond the necessity of validating FIWs, there are two additional hurdles to implementing these conservation modelling approaches in practice. First, there is no formal process for systematically identifying which species to incorporate in community-level conservation assessments, a shortfall that can result in missing key species and/or generating unnecessarily complex webs. Second, these tools generally require high-level modelling skills, so they are not accessible to all conservation practitioners.

The first challenge in modelling ecological communities is to determine which species and interactions are necessary to incorporate in order to identify important conservation outcomes (Geary et al., 2020; Ramsey & Veltman, 2005). This type of ambiguity is known as 'model structure uncertainty', and in some cases it can lead to impractical numbers of species and interactions being considered (Geary et al., 2020). For example, in building a FIW for the Lake Erie watershed, Hobbs et al. (2002) incorporated more than 160 variables into their ecosystem model. Most managers will not have enough data to parameterize such complex ecosystem models or be certain which species to include. One solution is to use a community assessment framework (see Pearson et al., 2021) to construct a community interaction web around the species targeted for conservation action. This approach draws from fundamental ecological theory to consider how a species proposed for conservation action interacts with others in the community and how those actions permeate throughout the ecosystem. This tool can be used with a combination of natural history information, literature, and if available, empirical data from the system to assess the possible interactions that may strongly link the target organism to other community members. Through this process, a community interaction web can be developed which highlights potential strong direct and indirect interactions linked to the target species. Because this approach attempts to identify all key species/interactions linked to the target species, in addition to vetting potential unintended outcomes, it can also reveal factors that might undermine the primary conservation objective (e.g. a predator or competitor that may suppress a species targeted for introduction).

Another challenge to applying modelling tools for conservation management is that not all conservation practitioners have the specialized software and coding skills often required to apply such models. Although researchers and conservation groups are increasingly developing software (e.g. Marxan; Ball et al., 2009) and establishing online sites to increase access to science-based modelling tools (e.g. https://www.natureserve.org/conservation-tools), this does not always overcome the challenge of usability. One solution is to develop user-friendly interfaces that bypass the need for the user to code the models to better facilitate practitioners to apply such tools.

In this paper, we address three key objectives. First, we apply a FIW to the well-quantified case study of the lake trout *Salvelinus namaycush* introduction into Yellowstone Lake, Yellowstone National Park, USA (Koel et al., 2019) to assess its efficacy for predicting the community-level outcomes that arose from this intentional (although uncondoned) species introduction. Second, because the community interaction web in the Yellowstone Lake system was largely predefined by its prior research history, we use another case study, that of the intentional red squirrel *Tamiasciurus hudsonicus* introduction to Newfoundland, Canada (Benkman, 2010), to demonstrate how the community assessment framework developed by Pearson et al. (2021) can be used to define the community interaction web requisite for applying a FIW. Lastly, we introduce a web interface called the MPG Matrix (hereafter 'the Matrix'; see https://matrix.mpgranch.com/#/; or search online for 'MPG Matrix') that we developed for applying FIWs. The Matrix integrates the FIW modelling framework with a user-friendly interface that allows users to apply FIWs to conservation questions. The Matrix incorporates the Yellowstone and Newfoundland case studies as examples for users to familiarize themselves with the interface. In sum, we demonstrate the efficacy of FIWs as a viable conservation tool and introduce methods for applying this approach in a user-friendly interface so that conservation managers can better vet potential outcomes of species introductions and eradications for conservation.

2 | MATERIALS AND METHODS

2.1 | An introduction to fuzzy interaction webs

Fuzzy interaction webs resemble food webs and community interaction webs. Species, abiotic resources or other concepts are nodes in the web, and interaction directions and strengths define relationships among nodes (e.g. Figure 1a). Species' abundances can be stored in a vector, **s**, of *n* species, and interaction strengths/directions can be stored in an *n* x *n* matrix, **A**. Each species abundance can take on a value described by a fuzzy set on the unit interval (0,1), which can be related to the quantitative range over which a species' abundance naturally varies within a system over time. Fuzzy set values can also describe qualitative or linguistic memberships of relative abundance as determined by quantitative data, literature and/or expert opinion (Hobbs et al., 2002; Özesmi & Özesmi, 2004). For example, there may be consensus that an elk *Cervus elaphus* herd larger than 100 individuals is considered 'large' or that a herd with fewer than 20 individuals is considered 'small', but there may be less agreement on whether a herd of 50 individuals is 'large' or 'medium–large'. FIWs can incorporate the vagueness in qualitative categorizations, in this case, what defines a 'large' versus 'medium' versus 'small' elk herd by creating fuzzy membership functions across the range of abundance values for assigning outcomes to a particular category (Supplementary Materials 1, Figure 4). Similarly, interaction strengths between nodes (i.e. species or concepts) can take on values between −1 and 1, where −1 would indicate a strong negative effect (i.e. predators on prey), 0 would indicate a negligible interaction, and 1 would indicate a strong positive interaction (e.g. plants to herbivores). These interactions can also incorporate vagueness by creating fuzzy membership functions for the possible interaction strengths (Ramsey & Veltman, 2005). In sum, FIWs allow users to map out and formulate interaction webs based on the community members and/or concepts of interest and incorporate a range of available information about species abundances, interaction types and interaction strengths.

Here, we briefly outline the steps to run a FIW (see Supplementary Materials 1 for details) once the system topology has been mapped the community assessment framework (see following sections). When species abundances and/or interaction strengths/directions have been defined, FIWs can be solved numerically to find the solution for the abundance of each species in a community. The new value for each species abundance is found by multiplying that species abundance vector, **s**, by the interaction strengths matrix, **A**: $\mathbf{s} = f(\mathbf{As})$, where $f()$ is the activation function that maps all abundances to values between 0 and 1, representing the minimum and maximum values for each node (see Supplementary Materials 1). One common activation function in FIWs is the logistic function: $f(x) = 1/(1+\exp[-cx])$, where c defines the shape of the curve. We solve for the equilibrium state using an iterative fixed point method (Baker et al., 2018), commonly sped up to convergence using a Gauss–Seidel algorithm (Hobbs et al., 2002). As an output, we have a vector of final relative species abundances, **s**. All model analyses were run in R (R Core Team, 2021).

2.2 | Assessing the efficacy of FIW using the Yellowstone case study

We assessed the efficacy of a FIW for predicting community responses to species introductions/eradications using the

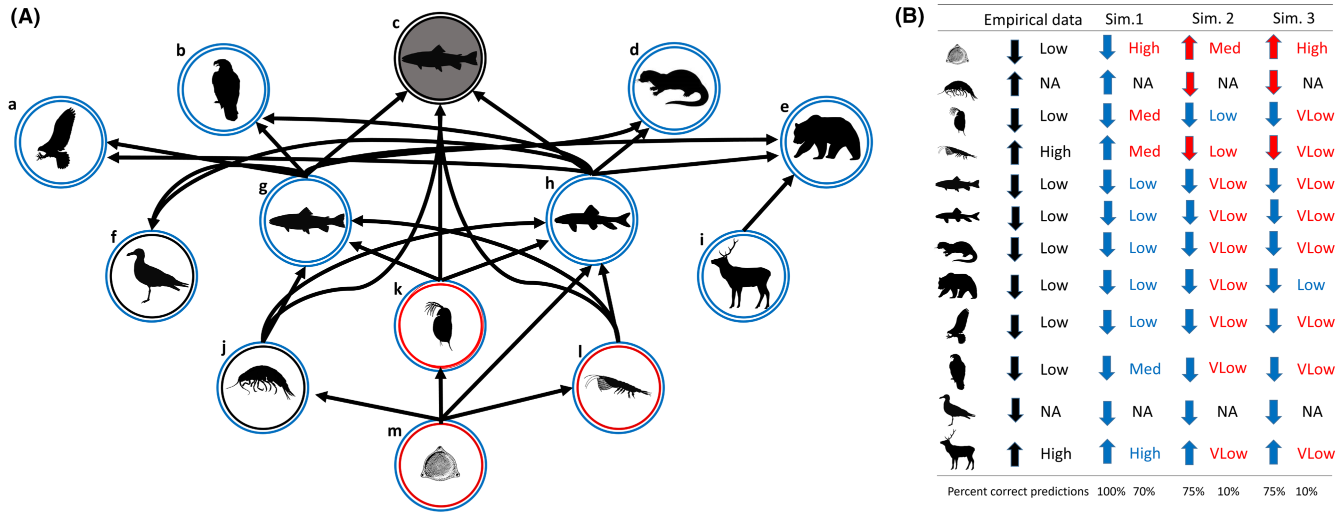

FIGURE 1 (a) Simulated community outcomes from Lake trout introductions to Yellowstone lake based on a fully parameterized FIW using empirical data for pre-introduction to predict post-introduction outcomes. Shaded grey circle shows introduced lake trout (c). Outer circles indicate whether the direction of abundance change post-introduction matched empirical data. Inner circles indicate whether the relative abundance of simulations post-introduction matched empirical data. Blue circles indicate correct predictions, red circles indicate incorrect predictions. Black inner circles indicate species for which empirical abundance data were unavailable. Community includes: Ospreys (a), bald eagles (b), river otters (d), grizzly bears (e), gulls and other fish predators (f), cutthroat trout (g), longnose suckers (h), elk calves (i), amphipods (j), large zooplankton (k), small zooplankton (l) and phytoplankton (m). (b) Simulated community outcomes from lake trout introduction showing the effect of reduced data for predicting direction of species abundance changes and relative species abundance changes. Empirical data column (first column) shows documented results post-introduction. Sim. 1 (second column) includes interaction directions, interaction strengths, species' abundances (depicted in A). Sim. 2 (third column) includes interaction directions and interaction strengths. Sim. 3 (fourth column) includes interaction directions. Arrows indicate the direction of change in species' abundances. Adjacent terms describe the qualitative abundance category post-lake trout introduction. Blue terms indicate simulations matched empirical data, red indicates they did not.

well-quantified case of the intentional (but illegal) introduction of exotic lake trout into Yellowstone Lake, USA (Koel et al., 2019). The introduction of lake trout precipitated a dramatic decline in Yellowstone cutthroat trout *Oncorhynchus clarkia bouvieri*, the top native fish predator, causing rippling effects across multiple trophic levels in the aquatic ecosystem that extended into the adjacent terrestrial ecosystem (Koel et al., 2019). Because the components of this system were quantified before and after lake trout introduction, this case allowed us to build the FIW from only pre-introduction information to predict post-introduction outcomes that could be empirically evaluated.

We first built a fully parameterized FIW by incorporating information on the pre-lake trout food web (Figure 1a), including abundances and interaction strengths for web nodes obtained from Koel et al. (2019) and other literature (Middleton et al., 2013; Wilmot et al., 2016). We identified prospective linkages between lake trout and other species and parameterized their interaction strengths based on literature describing lake trout introduction in Flathead Lake, Montana, U.S.A. (Ellis et al., 2011). We built fuzzy membership functions using five qualitative categories for relative abundance: very low (0%–1%), low (1%–20%, including up to 50%), medium (30%–70%), high (80%–99%, including down to 50%) and very high (99%–100%; see Supplementary Materials 2). We then solved for the equilibrium solution of the species' abundances in the FIW using a Gauss–Seidel algorithm (Hobbs et al., 2002). Classically, FIWs are used to facilitate prediction in patterns or changes in a community structure and how changes in model parameters (i.e. interaction strengths or species abundances) might propagate through the food web (Özesmi & Özesmi, 2004). FIWs involve an iterative process, so running and tuning the model until it converges at equilibrium is generally necessary (Hobbs et al., 2002; Ramsey & Veltman, 2005). Since our first step was to simulate the pre-lake trout abundances in Yellowstone Lake as closely as possible, we iteratively adjusted a few interaction strengths and added a basal resource ('solar radiation') to obtain a FIW that represented the system. Once the model had converged and species' abundances were in the same qualitative category as real-life abundances prior to lake trout introduction (see Koel et al., 2019, table 1), we simulated the effects of lake trout introduction by holding the relative abundance of lake trout at 'high' and finding the new equilibrium of the system (Sim. 1). We recorded the directional change and the qualitative, categorical outcome of all species in the community post-lake trout introduction. We evaluated the results as a categorical comparison to empirically documented species abundance changes in Yellowstone Lake after lake trout introduction.

Because FIWs incorporate expert knowledge and rely on opinions of individuals to build models, appropriate uncertainty analyses are essential to determine if results are robust to parameter uncertainty (Baker et al., 2018). To evaluate the performance of FIW under parameter uncertainty and low data scenarios more commonly experienced by managers in less well-studied systems, we reduced the model information to simulate scenarios where species abundances and interaction strengths were unknown. Accordingly, our second simulation left out all abundance information (i.e. all species' relative abundance pre-lake trout = 0.5) and did not tune interaction strengths during the convergence step (Sim. 2). Our third simulation repeated the second simulation but also left out information on interaction strengths (i.e. only had interaction directions; −1, 0, or 1; Sim. 3). We then repeated the above FIW analysis, evaluating our predictions with what occurred according to empirical evidence in Yellowstone Lake post-lake trout introduction.

2.3 | Defining a relevant interaction web with a community assessment framework

In the Yellowstone Lake case study, the community interaction web was defined by research conducted before and after lake trout introduction. However, in practice, conservation managers must define the community of interest before applying modelling tools to evaluate possible community responses to management actions. Because each species within a community may be linked to many other species through a variety of direct and indirect interactions, defining a community interaction web that encapsulates the components most sensitive to a specified management action can be daunting. However, by invoking a few basic principles of community ecology, a community assessment framework can be systematically applied to map the community interaction web of interest (see Pearson et al., 2021).

This process involves evaluating the fundamental interactions that may link the target species to other community members (Figure 2a) and determining the nature of those interactions (i.e. positive or negative). The focus here should be on interactions potentially strong enough to directly affect other species under the assumption that weak interactions will have limited effects and can be ignored. Interaction strengths may be quantified or qualitatively determined using system data, relevant literature, natural history information and/or expert opinion (Özesmi & Özesmi, 2004). Assigning interaction strengths using imperfect data is inherently subjective, but herein lies the strength of the fuzzification process. As a crude guide, we propose that diet information provides a good metric for trophic interactions, wherein the percentage for prey item A of 90% in a predator's diet might be considered a very strong interaction, whereas a percentage for prey item B of 10% might be coded as a very weak interaction or even ignored. The zones between may rely increasingly on fuzzy membership functions. Available information on species abundances may also be applied in a similar manner. Abundance information may come from sources ranging from censuses to indices because fuzzification relativizes the input (Ramsey & Veltman, 2005). After applying these steps to establish the immediate constellation of web nodes potentially directly influenced by the target organism, this process should be repeated for each species/node deemed to be strongly linked with the target species under the assumption that strong direct effects are most likely to generate indirect effects strong enough to warrant consideration. In this manner, the depth of the web derives from the assumption that interaction strength diminishes as interactions permeate into the web (see Pearson et al., 2021).

2.4 | Applying the community assessment framework and fuzzy interaction web to the red squirrel introduction to Newfoundland

Using the case of the intentional introduction of red squirrels to Newfoundland (Benkman, 2010), we applied the community assessment framework to build a relevant community interaction web. We then parameterized and applied a FIW to assess possible community outcomes arising from this introduction. Red squirrels were introduced to Newfoundland to provide a food subsidy to bolster American marten *Martes americana* populations, but this action led to a serious decline of the endemic Newfoundland red crossbill *Loxia curvirostra percna* via competition for black spruce *Picea mariana* seeds (Benkman, 2010), indicating that at least some unintended outcomes arose from this action. Aside from the above-described interactions, it is unknown to what extent this introduction influenced other community members. Hence, to evaluate the potential range of community outcomes we applied the community assessment to this case study as would be done in a proposed conservation management scenario.

In applying the community assessment framework (Figure 2a) to the red squirrel introduction (Figure 2b), we identified fairly strong 'direct' linkages to predators (two species), competitors (three species/categories) and resources (two species/categories; see Supplementary Materials 2). Note, this was resource-based not interference competition, so these linkages arise through indirect effects and were integrated accordingly. Nodes represented individual species where interactions were fairly explicit (e.g. Newfoundland crossbills specialize on black spruce seeds and red squirrels specialize on conifer seeds including black spruce), but categories were used to represent guilds for weaker, more diffuse interactions (e.g. red squirrels compete with numerous less-specialized seed-eating birds that consume conifer seeds). After establishing the immediate constellation of linkages to the target species, we applied this same process to marten and goshawks because the marten-red squirrel linkage was anticipated to be strong based on the intent of the introduction and the literature indicated that goshawks can specialize on red squirrels (Lewis et al., 2006; Smithers et al., 2005). Given the strong linkage from red squirrels to goshawks, we extended the linkages to include hares and grouse as primary goshawk prey (Lewis et al., 2006, Smithers et al., 2005). We included the linkages to lynx because they are specialists on hares that resort to grouse when hare populations crash (Roth et al., 2007), that is, these are strong interactions indirectly linked to the target species. We linked marten to their primary food resource, microtine rodents (Gosse & Hearn, 2005; Lensink

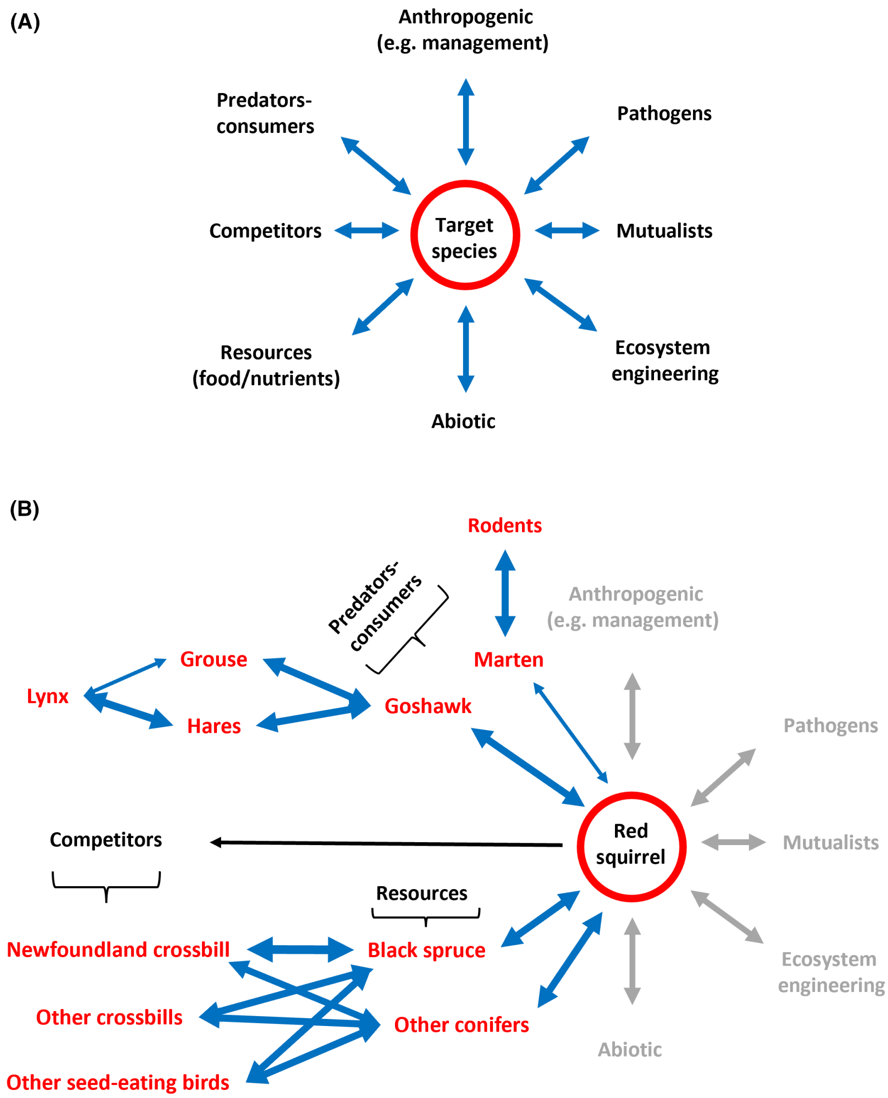

FIGURE 2 (a) Community assessment framework for generating a community interaction web to understand how a target species introduced or eradicated for conservation purposes may influence community outcomes (after Pearson et al., 2021). Interactions included link the target species to other network nodes (species or system components) to identify the species most likely to be affected by the actions, the nature of each interaction linkage (i.e. positive or negative), and the strength of each interaction. There can be multiple sets of interactions in one interaction type (e.g. multiple competitors of the target species) that may need to be considered. The initial community assessment focuses on immediate linkages to the target species likely to be strong enough to substantively alter the abundance or function of other system components. If this assessment indicates the target species is likely to have strong effects on particular community members, then the same process should be applied to the affected species or node to extend the web and include indirect effects, under the assumption that most strong indirect effects derive from strong direct effects. Hence, this approach systematically identifies and follows strong linkages until they become weak, thereby delineating the relevant community of concern. (b) The application of the community assessment to the case of red squirrel introduction to Newfoundland. Heavier lines indicate stronger interactions. All interactions are reciprocal with the nature of the interactions determined by interaction type (e.g. predation = −), so the signs (+, −) are not indicated for simplicity.

et al., 1955). After mapping out the community interaction web, we parameterized the FIW by assigning interaction linkages, directions and qualitative interaction strengths based on natural history information and relevant literature (see Supplementary Materials 2). To illustrate how to conduct parameter uncertainty analyses with FIW, we also performed a parameter uncertainty analysis on the change in Newfoundland crossbill abundance in response to red squirrel introduction (see Supplementary Materials 2).

2.5 | An introduction to the matrix interface for FIWs

The MPG Grassland Matrix was built to understand community interactions and guide management at MPG Ranch, a private conservation area near Missoula, MT, USA (https://matrix.mpgranch.com/#/). The Matrix's user interface (UI) encapsulates R code for applying FIWs in a user-friendly tool for building new matrices to evaluate conservation actions. The steps involve first applying the community assessment framework to the system of interest to identify and parameterize the community interaction matrix (e.g. see Supplementary Materials 1, Table 1) as done for the red squirrel case. Next, this information is used to parameterize each node in the new matrix. Standard fuzzy membership functions (Ramsey & Veltman, 2005) are default in the Matrix, but the user can redefine them if there is a specific justification to do so. Finally, the matrix must be tuned. This is done using any available data from the system and then adjusting unknown parameters until the FIW equilibrates at values approximating known values for the system. For example, in the MPG Grassland Matrix, abundance values (min, max and mean or median) for many organisms were derived from long-term monitoring (18 of 21 nodes), although some values were obtained from the literature (3/21). Most interaction strengths were unknown. Hence, interaction strengths were first approximated using literature and natural history information (Allen et al., 2015; Maron et al., 2012; Pearson et al., 2017; Prugh & Sivy, 2020). Then these values were adjusted until the system equilibrated such that the abundance for each node approximated its known mean (within a few percentage points). Next, the efficacy of the web should be tested by manipulating nodes to see how the system responds. This step helps to highlight interactions for further tuning to finalize the process. Both the Newfoundland red squirrel and Yellowstone Lake cases are built into the Matrix as examples. The UI includes a detailed user's guide.

3 | RESULTS

3.1 | Lake trout introduction to Yellowstone Lake

In the Yellowstone Lake case study for Sim. 1 (the fully parameterized model using data for species' abundance, interaction directions and interaction strengths), the model predicted known outcomes following lake trout introduction for the direction of species changes with 100% success, and it predicted qualitative changes in species' abundances with 70% success (Figure 1a,b, Supplementary Materials 2). When we reduced model information to simulate more common data limitations, we found that the models containing information on only interaction direction and interaction strength (no abundance information = Sim. 2) and only interaction direction (no abundance or interaction strength information = Sim. 3) both predicted the direction of species changes with 75% success, but success in predicting qualitative abundance changes was only 10% (Figure 1b). Even so, 71% of the time, abundance categories were off by only one, such that most differences would not likely jeopardize conservation decisions (e.g. predicted very low when the known category was low).

3.2 | Red squirrel introduction to Newfoundland

Our community assessment of the intentional introduction of red squirrels to Newfoundland identified 11 nodes likely to have sufficiently strong interactions with the target species to warrant evaluations (Figure 2b). We parameterized the web by assigning interaction directions and strengths from the literature. The FIW predicted that all three red squirrel competitors and both of their food resources would decline somewhat (Figure 3). In contrast, the two predators were predicted to increase, with the larger effect on goshawks (Figure 3). Notably, the strongest predicted decline was for the endemic Newfoundland crossbill with only a very modest predicted increase in marten abundance (Figure 3)—outcomes consistent with documented responses (Benkman, 2010). These declines were robust to data uncertainty, with 100% of simulations in our parameter uncertainty analysis showing declines in Newfoundland crossbills with red squirrel introduction (mean decline = −95%, 95% CI = −99.9%, −65.9%).

3.3 | MPG matrix user interface

The Matrix UI generates the same output for the Yellowstone Lake and the red squirrel case studies as derived from the FIWs outlined in Supplementary Materials 2. The FIW for the MPG grassland generates realistic outcomes as validated by extensive study of these semi-arid grasslands (e.g. Maron & Pearson, 2011), and it is currently being used to explain long-term data trends at MPG Ranch. For example, a 10-year vegetation survey shows substantial declines in native and introduced grassland plants at MPG, with the strongest declines in natives. Manipulating the precipitation and ungulate (large herbivores) nodes independently and simultaneously indicates this pattern is most likely explained by both declines in precipitation combined with documented increases in ungulate populations. This model prediction is consistent with the literature (Ortega et al., 2012) and herbivore diet data for this system (P. Ramsey et al., unpublished data). In sum, the current Matrix is a Beta test version (1.0) that will be updated, but it provides a validated user-friendly interface that overlays the requisite R code for applying FIWs to conservation questions.

4 | DISCUSSION

Our evaluation indicates that FIWs show promise as tools for modelling community outcomes of species introductions. In the well-documented case study of lake trout introduction into Yellowstone Lake (Koel et al., 2019), the fully parameterized model predicted known responses to introduction quite well across this complex 12-species system. It even predicted the directional change for all nodes of the most indirect interaction pathway in the system, which extended from the aquatic into the terrestrial ecosystem. In this cryptic pathway, lake trout depleted cutthroat trout abundance, causing grizzly bears to switch from depredating spawning cutthroat to elk calves, thereby depressing elk recruitment (Figure 1; Middleton et al., 2013). Although the less-parameterized models performed more poorly when predicting

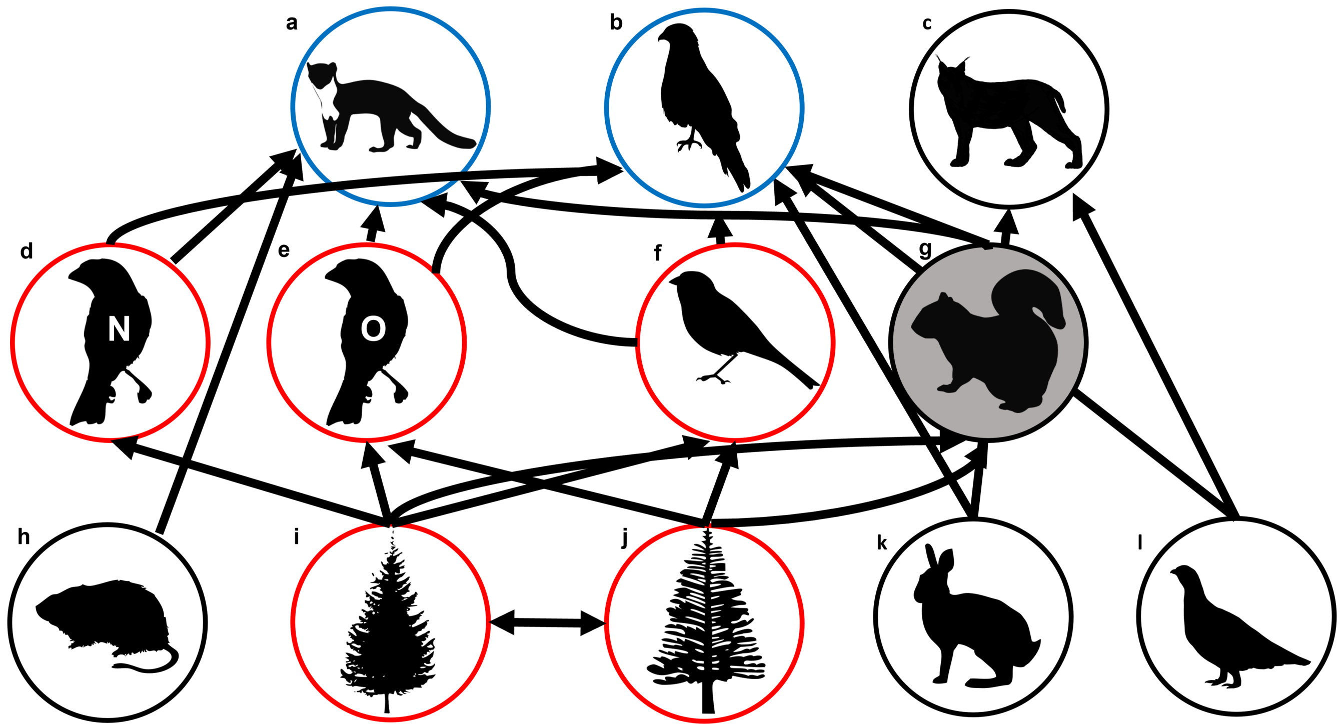

FIGURE 3 Simulated effects of red squirrel (g) introduction into a recipient Newfoundland community where nodes were determined by applying our community assessment framework (see Figure 1). Shaded grey circle shows the manipulated species, red squirrels. Blue circles show predicted increases in abundance, black circles show no predicted changes in abundance, and red circles show predicted decreases in abundance. The community is comprised of martens (a), goshawks (b), lynx (c), Newfoundland crossbills (d), other crossbills (e; i.e. white-winged and red crossbills), other seed-eating birds (f; e.g. purple finch), microtine rodents (h), black spruce (i), other conifers (j), hares (k) and grouse (l). See Supplementary Materials 2 for full results.

categorical changes in species' abundances, they did fairly well at predicting which species would change in abundance and in which direction they would change, with 75% success across the community. Importantly, differences between predicted and real abundance categories often did not differ enough to impede management conclusions. Thus, given relatively minimal information of the type commonly available from the literature and/or natural history understandings, FIWs seem capable of predicting directional changes in species abundances reasonably well. While this example represents a single well-parameterized case study, thorough vetting of FIW in social sciences and other fields has demonstrated that the tool is fairly robust at predicting directional changes in network nodes (Gray et al., 2013; Kosko, 1992; Papageorgiou, 2011). As we discuss below, predicting even directional changes in species abundances would greatly improve the effectiveness of conservation management by identifying potential unintended outcomes prior to implementation.

Whereas the Yellowstone food web was well-quantified prior to lake trout introduction, in most scenarios managers will not have fully parameterized systems. Hence, a community assessment must be conducted to first identify the species most likely to be affected by management actions and determine the nature of their interaction linkages (Figure 2a). Ideally, this assessment will also estimate interaction strengths, at least qualitatively, and include information on species abundances when possible, which may also derive from qualitative inputs. In applying the community assessment to the red squirrel introduction to Newfoundland, we were able to construct a FIW with interaction linkages and strengths derived from natural history information and relevant literature that performed well (Figure 2b). This model successfully predicted that the management objective of substantively increasing marten abundance would not be met, while at least one unintended consequence might be serious—a significant decline of the Newfoundland crossbill (Figure 3). This example illustrates how applying FIW in this case might have warned against unintended outcomes while also indicating the potential for failing to achieve the management objective.

In their global literature review, Pearson et al. (2021) found that 10% of species introductions and eradications did not address any potential effects on non-target species and 39% ignored key interactions like prey or competitors of the target species. Incorporating FIW with the community assessment can formalize the evaluation of directional changes in non-target species for which it provides fairly robust predictions as well as potentially providing information about relative abundance changes. It also may provide a means for identifying more cryptic outcomes linked to density or trait-mediated indirect effects, as demonstrated by the Yellowstone case. While our simulations show that the efficacy of this tool for predicting relative abundance changes is contingent upon the quality of data inputs, even the ability to predict which species might increase or decrease in abundance prior to executing management actions could be helpful. Such predictions could greatly improve conservation management by triggering more detailed assessments of potential unintended outcomes to avoid or mitigate their impacts. We emphasize that our intent here is to provide a heuristic framework, not an exhaustive quantitative assessment of the efficacy of FIWs for conservation management. More advanced applications of FIWs (Baker et al., 2018; Game et al., 2018; Ramsey et al., 2012; Zhang et al., 2013) and other qualitative models (Baker et al., 2019; Baker & Bode, 2021; Dambacher & Ramos-Jiliberto, 2007; Geary et al., 2020; Raymond et al., 2011; Rendall et al., 2021) could be readily adapted to the guidelines we propose.

It is important to acknowledge that FIWs and other qualitative models can be quite sensitive to model structure and parameter uncertainty (Baker et al., 2018; Geary et al., 2020). We dealt with model structure uncertainty by using our community assessment framework (Pearson et al., 2021) to help limit the possible number of nodes included in the FIW. Parameter uncertainty must also be accounted for in more complex models for conservation management, although it is often not (Baker et al., 2018). We incorporated parameter uncertainty analyses in our Yellowstone case, as demonstrated by the change in results under data limited scenarios (Figure 1b). We also outlined how to conduct a parameter uncertainty analysis in the red squirrel case study and found that 100% of the time Newfoundland crossbills declined in response to red squirrel introduction. Despite this success, correctly incorporating expert knowledge into FIWs can be a subjective task, and uncertainty analyses are essential to testing the limits of the constructed FIWs (Geary et al., 2020; Baker et al., 2018; Raymond et al., 2011). Similarly, the importance of including a node (model structure uncertainty) can be analysed using FIWs by adjusting the abundance of a species in a community, akin to the species being introduced in our case studies (i.e. lake trout; red squirrels), and recording the system's response. Here, we caution that excluding a functionally important node is likely more problematic than including noninfluential nodes. Nonetheless, overparameterization can weaken model sensitivity. These methods, in addition to other advances with FIWs (Baker et al., 2018; Ramsey et al., 2012), will help to better address uncertainty in qualitative models.

Scientific efforts to develop, validate and publish new tools for the advancement of conservation are essential and laudable, but such efforts do not always lead to implementation of the new technologies. One major limitation to implementation is making new tools widely accessible to prospective users. Increasingly, scientists are moving beyond simply publishing new tools in scientific journals to establishing these resources on websites where they are more accessible to conservation practitioners. Yet increasing access alone does not necessarily facilitate implementation of tools that require special skills. In vetting FIWs as tools for conservation management and providing the Matrix as a user-friendly interface to apply this tool, we hope to overcome this final hurdle to advancing conservation management.

The many accounts of unintended outcomes from intentional species introductions and eradications (Bergstrom et al., 2009; Courchamp et al., 2003; Pearson & Callaway, 2006; Prior et al., 2018; Simberloff & Stiling, 1996; Zavaleta et al., 2001) indicate that continuing to take such actions without further safeguards is becoming indefensible. Applying a systematic community assessment to vet potential unintended outcomes as proposed by Pearson et al. (2021) is an essential step forward. Our model simulations indicate that complementing this step with qualitative modelling approaches can formalize and further improve on this process and is feasibly done by applying basic ecology and natural history information commonly available to conservation practitioners. Moreover, by creating the user-friendly Matrix interface, we hope to increase the availability and accessibility of a tool that might not otherwise be usable by all conservation practitioners. Finally, we propose that conservation managers apply these guidelines before conducting such actions and measure system responses following management actions to improve the science of species introductions and eradications for conservation.

AUTHORS' CONTRIBUTIONS

T.J.C.-W. and D.E.P. drafted the manuscript; other authors contributed to editing; T.J.C.-W. developed the models and simulations with input from P.G.H. and D.E.P.; B.L. and P.R. obtained and summarized data from MPG Ranch and provided input on the MPG Matrix; E.B., N.H. and J.F. built the UI with input from all. D.E.P. conceived of the initial idea, assembled the team and led the effort.

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CONFLICT OF INTEREST

The authors declare that they have no conflict of interest.

DATA AVAILABILITY STATEMENT

Code needed to reproduce the analysis can be found on Github https://doi.org/10.5281/zenodo.6587882 (Clark-Wolf, 2022).

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SUPPORTING INFORMATION

Additional supporting information can be found online in the Supporting Information section at the end of this article.

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