

Predicting ecological outcomes using fuzzy interaction webs

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Abstract

The past 100 years of empirical research in ecology have generated tremendous knowledge about the component interactions that structure ecological communities. Yet, we still lack the ability to reassemble these puzzle pieces to predict community responses to perturbations, a challenge that grows increasingly urgent given rapid global change. We summarize key advances in community ecology that have set the stage for modeling ecological systems and briefly review the evolution of ecological modeling efforts to identify critical hurdles to progress. We find that while Robert May demonstrated that quantitative models could theoretically predict community interactions nearly 50 years ago, in practice, we still lack the ability to predict ecological outcomes with reasonable accuracy for three reasons: (1) quantitative models require precise data for parameterization (often unavailable) and have restrictive assumptions that are rarely met; (2) estimating interaction strengths for all network components is extremely challenging; and (3) determining which species are essential to include in models is difficult (model structure uncertainty). We propose that fuzzy interaction webs (FIW), borrowed from the social sciences, hold the potential to overcome these modeling shortfalls by integrating quantitative and qualitative data (e.g., categorical data, natural history information, expert opinion) for generating reasonably accurate qualitative predictions sufficient for addressing many ecological questions. We outline recent advances developed for addressing model structure uncertainty, and we present a case study to illustrate how FIWs can be applied for estimating community interaction strengths and predicting complex ecological outcomes in a multitrophic (plants, herbivores, predators), multi-interaction-type (competition, predation, facilitation, omnivory) grassland ecosystem. We argue that incorporating FIWs into ecological modeling could significantly advance empirical and theoretical ecology.

KEYWORDS

community interaction web, ecological modeling, fuzzy cognitive map, fuzzy cognitive web, fuzzy set theory, interaction strength, network, perturbation, prediction, qualitative models

A NEED FOR PREDICTIVE ECOLOGICAL MODELS IN THE ANTHROPOCENE

Prediction is the ultimate goal of any science (Houlahan et al., 2017). In ecology, it has long been debated whether prediction is a reasonable objective, or even feasible, given the degree of idiosyncrasy in natural systems (Lawton, 1999; Maris et al., 2018). Yet, now more than ever, there is a need for ecological advances in prediction to understand how anthropogenic perturbations like climate change, overexploitation, pollution, and biological invasions that are driving change today will affect ecological systems and the services they provide humans tomorrow (Landi et al., 2018). Herein, we highlight key advances in community ecology that have both set the stage for modeling ecological systems and revealed the complexity that must be overcome to predict ecological outcomes. We then briefly review the evolution of ecological modeling efforts to predict community interactions and outline the challenges continuing to stall progress. We propose that fuzzy cognitive maps, qualitative models developed in the social sciences and engineering fields, may help to overcome key hurdles inhibiting ecological modeling. Finally, we provide a case study to illustrate how fuzzy interaction webs (FIW) can be used to develop multitrophic, multi-interaction-type models that provide reasonable predictions of complex community responses to natural and anthropogenic perturbations.

EVOLUTION OF ECOLOGY: DEFINING THE PUZZLE PIECES

Over the last several decades, ecologists have used reductionist approaches to disassemble communities into their component parts to understand fundamental ecological interactions. These efforts have generated tremendous advances in our knowledge and conceptualizations of ecological systems. Early representations of communities were dominated by food pyramids that emphasized energy flow through bottom-up trophic pathways (Lindeman, 1942) (Figure 1). However, in 1960, Hairston, Smith, and Slobodkin introduced the “Green-world Hypothesis” (Hairston et al., 1960) which turned these ideas upside down by arguing that predators may control primary productivity by moderating consumer effects on primary producers. These ideas transitioned conceptualizations from simple bottom-up systems to systems capable of feedback between bottom-up and top-down processes. The power of these consumer effects was empirically validated by Robert Paine’s discovery of the keystone species concept (Paine, 1966), reinforced by Jim Estes’s work with sea otters and kelp beds (Estes & Palmisano, 1974), and experimentally demonstrated by Carpenter and Kitchell’s studies showing how top predators could control productivity and water clarity in freshwater lakes (Carpenter & Kitchell, 1988). Yet, as noted by Polis and Strong (1996), these new models remained

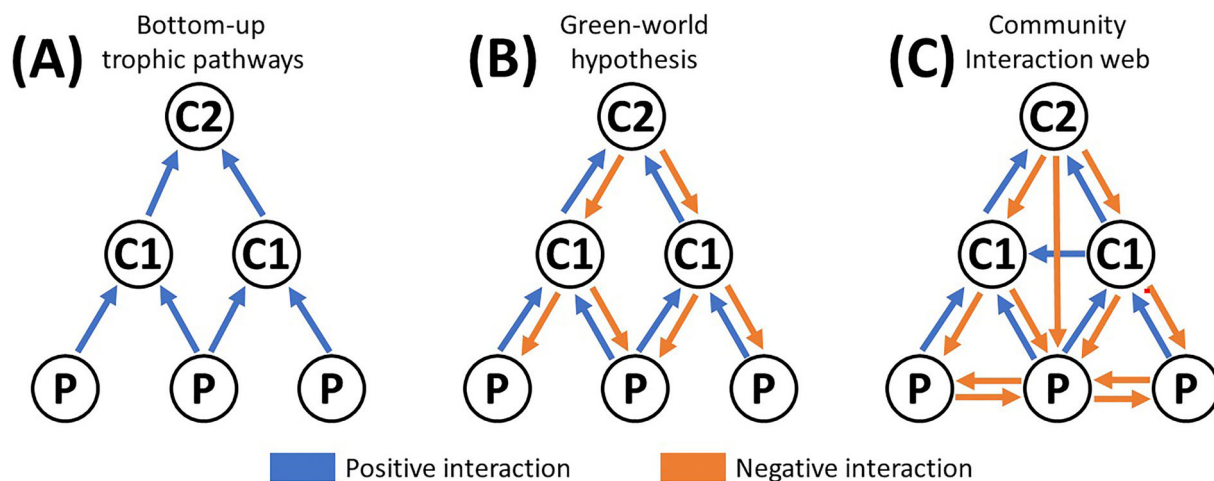


FIGURE 1 Evolution of community conceptualizations. (A) Early depictions of communities were dominated by concepts of energy flow through bottom-up trophic pathways from primary producers (P) to primary consumers (C1), secondary consumers (C2), and so on, with inefficiencies in energy flow resulting in reduced abundance of organisms at progressively higher trophic levels (e.g., [Odum, 1957]). (B) The Green-world Hypothesis (Hairston et al., 1960) turned these ideas upside down by proposing that predators (C2) could exert controls over plants (P) and system energetics by suppressing herbivores (C1) sufficiently to release producers from consumer control. This depiction reflects a basic food web with interaction linkages directed both up and down but restricted to trophic interactions. (C) The community interaction web (Wootton, 1994) allows for nontrophic interactions including competition (shown between the Ps), facilitation (shown between the C1s), and omnivory (shown by the C2 linked to both C1s and Ps). Such webs provide more realistic depictions of ecological systems because they can incorporate all manner of ecological interactions.

overly simplistic because they continued to misrepresent communities as discrete tiers of ecological interactions instead of complex webs. Research since has established that food webs in any form are far too simplistic because they fail to incorporate powerful nontrophic interactions like competition (Connell, 1961), facilitation (Bertness & Callaway, 1994), ecosystem engineering (Jones et al., 1994), and interaction modifications (where one species modifies the interaction strength between two other species; Werner & Peacor, 2003). Community interaction webs (*sensu* Wootton, 1994) ultimately emerged as a way to encapsulate this breadth of complex interactions in a manner sufficient to set the stage for predicting community responses to perturbations (Figure 1). Yet, models reflecting the full complexity of real-world communities are markedly rare (e.g., Kéfi et al., 2016; Landi et al., 2018; Novak et al., 2011).

EVOLUTION OF ECOLOGICAL MODELING: QUANTITATIVE APPROACHES AND MAJOR HURDLES

Paralleling empirical efforts to understand the component interactions underlying ecological networks, early modeling efforts introduced Lotka–Volterra style differential equations to conceptualize and predict basic pairwise interactions like competition and predation (Lotka, 1925; Volterra, 1926). These efforts established the foundation for building more complex three-species modules like apparent competition (Holt, 1977) and community-level models (Levins, 1968; May, 1973). In 1973, Robert May demonstrated that a community matrix, built on these mathematical principles, could theoretically predict the effect of perturbing one species within a community on all other community members (May, 1973). Yet, despite this invaluable proof of concept, in practice, these quantitative models have proven impractical because: (1) key underlying assumptions are rarely met; (2) the models are highly sensitive to web topology and the accuracy of parameter inputs (especially interaction strengths); and (3) sufficient high-quality empirical data are rarely available for all elements of a community matrix (Montoya et al., 2009; Novak et al., 2011; Wootton, 2002; Yodzis, 1988). Moreover, applying such models to complex communities with multiple trophic levels and diverse trophic and nontrophic interactions requires that highly accurate data are gathered on the same scales for many distinct taxa. Hence, even though the problem of predicting community outcomes was theoretically solved nearly 50 years ago, ecologists continue to struggle to predict outcomes of community perturbations (Adams et al., 2020; Godoy et al., 2018; Novak et al., 2011).

Despite these practical constraints, this theoretical work was foundational in establishing the five essential elements of a community interaction web necessary to predict community outcomes. Examining these elements highlights two critical challenges for ecological modeling. The first three elements are the nodes or species in the web, the linkages between the nodes, and the nature or direction of the linkages (i.e., are the interactions positive or negative). These elements define the web topology and can, in theory, represent all the types of interactions described above. Importantly, they are essentially qualitative and largely defined from natural history information. Nonetheless, assuring that all critical nodes and linkages are accounted for presents a serious modeling challenge, referred to as “model structure uncertainty,” that must be addressed in real-world systems (Dambacher et al., 2002; Geary et al., 2020). The last two elements, species abundances and interaction strengths (the strength of the interaction assigned to each linkage), are quantitative and more challenging to obtain. While species abundances can be approximated using field-based indices and/or population estimation, interaction strengths are difficult to obtain without complicated pairwise experiments (Wootton & Emmerson, 2005). Moreover, pairwise experiments cannot detect some higher-order interactions (defined here as interactions manifested through >2 species which cannot be determined from pairwise interactions, see Kleinhesselink et al., 2022). Hence, even with the best modeling techniques, correctly defining web topology and obtaining reasonable estimates of interaction strengths, especially for complex systems, present significant hurdles. Because of these issues, well quantified webs are taxonomically and ecologically biased toward trophic interactions and smaller-scale ecosystems or subsystems such as bipartite webs that are more tractable (e.g., Kéfi et al., 2016; Landi et al., 2018; Novak et al., 2011).

Beyond the tradition of deterministic models, stochastic time-series models offer a means for using large datasets to estimate elusive parameters, such as interaction strengths, from empirical data (Auger-Méthé et al., 2021; Ives et al., 2010; Ovaskainen & Meerson, 2010). For example, autoregressive moving average (ARMA) models have been successfully used to estimate interactions between species within a community (Downing et al., 2020; Ives et al., 2003, 2010; Ziebarth et al., 2010). ARMA models are useful because they give a flexible structure that can incorporate stochasticity, measurement error, and species interactions. These parameters can be estimated using common frequentist approaches such as maximum-likelihood estimation (Ives et al., 2010). However, these models have yet to be applied to a wide range of communities because they are difficult to fit to short- or medium-length ecological

datasets (Ives et al., 2010). For example, Ziebarth et al. (2010) suggested that datasets of <60 years may be too short to characterize population dynamics. Other statistical modeling frameworks, such as state-space models (and its subset, Hidden Markov models), represent key advances because they can allow users to model ecological processes separately from observation error and other sources of variability, and can be done flexibly within a Bayesian framework (Auger-Méthé et al., 2021; McClintock et al., 2020). Similar to the issues encountered with ARMA models, fitting state-space models to ecological communities are likely to involve estimating dozens to hundreds of species interactions, possibly leading to parameter identifiability problems (Sauve & Barraquand, 2020). In summary, because of the data length necessary to fit these models and the number of parameters needed to be fit, these models present unlikely routes to broadly understand interactions in ecological communities.

QUALITATIVE MODELS: AN ALTERNATIVE APPROACH

While ecology has historically focused on quantitative models that make precise predictions (Godoy et al., 2018; Novak et al., 2016), for many questions, qualitative predictions are sufficient for advancing both ecology and conservation (Dambacher et al., 2002; Levins, 1974; Ramsey & Veltman, 2005). For example, simply knowing which species in a web are likely to respond to a perturbation, in which direction, and by relatively how much (i.e., a little or a lot) is adequate to provide qualitative feedback on many ecological processes and to address many conservation questions (Clark-Wolf et al., 2022; Ramsey & Veltman, 2005). Qualitative models, designed for this purpose, were introduced into ecological modeling early on (Levins, 1974) but have yet to achieve mainstream status. Qualitative modeling can trace its origins to community ecology theory where species interactions can be described by the following dynamical system (May, 1973):

$$\frac{dN_i}{dt} = f_i(N_1, N_2, \dots, N_n)N_i. \quad (1)$$

where N_i is the abundance of species i , and f_i describes the per-capita population growth rate of species i as a function of its own abundance (N_i) and some set of other species in the n -species community. In community ecology theory, interaction strengths between species i and j are calculated as the effect of species j 's abundance on the per-capita growth rate of species i at equilibrium. The matrix of all interaction strengths between species i and

j is the “interaction matrix” (sensu Novak et al., 2016) also referred to as the community matrix, with elements:

$$A_{ij} = \left. \frac{\partial f_i}{\partial N_j} \right|_*. \quad (2)$$

where $*$ denotes evaluation at equilibrium. The interaction matrix A_{ij} (hereafter A) quantifies the direct effect of one species, at equilibrium, on all other species to which it is directly linked in a community (Figure 2).

Often in community ecology, quantitatively defined species' interaction strengths are unavailable due to the challenges associated with their estimation noted above. Qualitative models allow for the estimation of community responses to perturbation, even using poorly studied nodes lacking information on interaction strengths or abundance, by leveraging qualitative information (Dambacher et al., 2002; Levins, 1974; Ramsey & Veltman, 2005). These models are created solely by knowing the nodes within a community and the signs and linkages between those nodes (e.g., positive, negative, or neutral) (Levins, 1974). With qualitative models, the interaction matrix A now comprises -1 , 0 , and 1 s (now known as $^\circ A$) instead of nonbinary numbers (Figure 2B). Loop analysis (Levins, 1974) evaluates the response of $^\circ A$ by quantifying the direct and indirect effects (effect of one species on another via an intermediate species) resulting from perturbation by calculating the adjoint matrix of $-^\circ A$ (Figure 2C). Despite these advances, qualitative models have been less well received in community ecology, probably due to the historic focus on quantitative models combined with concerns over loss of information on interaction strengths and the all-or-nothing nature of their predictions (Ramsey & Veltman, 2005). However, more advanced qualitative models hold the potential to address these shortfalls.

An important problem with qualitative modeling that must be overcome for practical application is that qualitative predictions become unreliable as the number of nodes and linkages increase and communities become complex (Dambacher et al., 2002). For example, in Figure 2, we highlight an example of qualitative modeling using loop analysis for herbivore–plant–nitrogen interactions in an old-field food web (Schmitz, 1997), showing that large numbers of linkages and nodes in the system create sign indeterminacy, leading to poor understanding of community responses to perturbations. Moreover, assuming no knowledge of interaction strengths besides directionality limits prediction. For example, Novak et al. (2011) found that quantitatively specified community matrices using poorly estimated parameters provided better qualitative predictions than qualitatively specified community matrices using loop analysis. One proposed solution to this problem is running simulations where randomly chosen

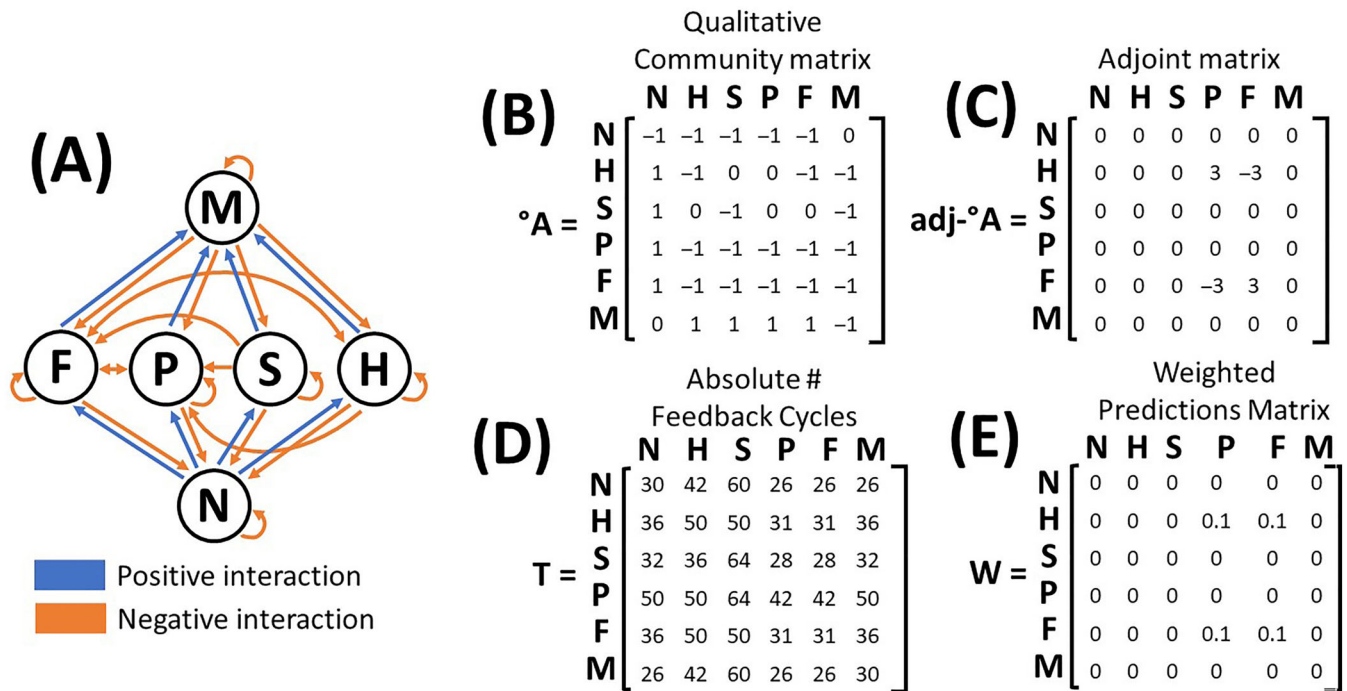


FIGURE 2 Qualitative modeling using loop analysis. (A) Community matrix for herbivore-plant-nitrogen interactions in an old-field food web specified by Schmitz (Schmitz, 1997). M = grasshopper, F, P, S, H = perennial plants, and N = soil nitrogen. (B) The qualitative community matrix, $^{\circ}A$, where interactions consist of -1 , 0 , or 1 s. (C) The adjoint matrix of $^{\circ}A$, which quantifies the net number of positive and negative direct and indirect effects (hereafter, “feedback cycles”) resulting from perturbation. (D) T , the absolute number of feedback cycles, and (E) W , the weighted predictions matrix, which indicates the degree of ambiguity, or sign indeterminacy, in a species’ response to a perturbation. Please see Dambacher et al. (2002) for more details on how matrices are calculated mathematically. The low or zero values found in this matrix indicate that it is highly unlikely to predict the response to perturbation due to high indeterminacy, which we suggest could be resolved using FIWs.

interaction strengths are generated for the community matrix and assessed based on ecological criteria (e.g., if predicted behavior makes sense based on our understanding of the system’s ecology) (Baker et al., 2019; Dambacher et al., 2003; Raymond et al., 2011). Yet we believe such fixes reflect a deeper flaw in purely qualitative models, which is that there is a loss in potentially valuable information about interaction strengths in the process of building these models that could be gleaned from imperfect quantitative data, natural history information, and expert opinion (Ramsey & Veltman, 2005; Roberts, 1986). Here, we propose that one qualitative modeling technique, FIW, which represents a middle ground between quantitative and qualitative modeling approaches that can improve predictions of community perturbations when quantitative information is unavailable.

FUZZY INTERACTION WEBS: A NOVEL FORM OF QUALITATIVE MODELS

Fuzzy cognitive maps are a form of qualitative models developed in the social sciences and engineering (Kosko,

1992; Papageorgiou, 2011) which have an advantage over other qualitative models in that they allow for a relatively seamless merging of high-quality quantitative information with qualitative approximations of model parameters, including interaction strength (Clark-Wolf et al., 2022; Ramsey & Veltman, 2005; Roberts, 1986). These models are increasingly used for predicting outcomes of conservation actions, and referred to as FIWs (Ramsey & Veltman, 2005). Their efficacy for predicting complex outcomes has recently been demonstrated using empirically documented case studies (Clark-Wolf et al., 2022). FIWs are more robust for large community interaction networks than other qualitative ecological models (e.g., loop analysis) because they can incorporate information about interaction strengths (Ramsey & Veltman, 2005). These models hold great potential for advancing ecology, but they are currently underutilized by ecologists.

FIWs use a branch of mathematics known as fuzzy set theory, where elements of a fuzzy set (i.e., a qualitative category) can have partial membership instead of bivalent membership, that is, elements only belong or do not belong. This means that values can be assigned according to the degree of confidence that a value falls within a set/category. For example, using a fuzzy set, we can

partially assign membership using qualitative or linguistic values, according to the degree to which we are confident in a value using categories like “low,” “medium” or “high” (Kosko, 1992). For example, we could be mostly confident that an interaction between two species is “high,” so we assign much membership to that category. But we also allow for some membership in the “medium” category to account for low confidence in that interaction.

FIWs use fuzzy membership functions to code this level of fuzziness into models of community dynamics (Ramsey & Veltman, 2005). For example, let us say we are modeling lake trout in a food web. In Appendix S1: Figure S1, lake trout abundance between 0 and 200 would have a “low” membership value of 1, but as lake trout abundance increases, the membership value for “low” decreases and the membership value for “medium” increases. The degree of overlap should represent the level of fuzziness or uncertainty in the decision-making process (Ramsey & Veltman, 2005). For example, if we think there are around 400 lake trout, the resulting fuzzified value would be: “low = 0.4, medium = 0.6, high = 0.” This vector represents the fuzzy membership values for use in the FIW model. These values are standardized so that all values are on the same scale, allowing for comparison across disparate species/ecosystems.

FIWs can be used to predict community responses to perturbations (we focus on press perturbations as they emulate many anthropogenic impacts on ecological systems) where values like species abundances or interaction strengths can be varied to explore community outcomes. The FIW uses a discrete variant of the dynamical equation (Equation 1), the Gauss–Seidel algorithm, to speed up convergence to equilibrium (Baker et al., 2018):

$$N_{t+1} = \lambda f(AN_t) + (1 - \lambda)N_t. \quad (3)$$

where N is a vector of species abundances, A is an interaction matrix, t is the iteration number, λ is a relaxation parameter used to accelerate convergence, and $f()$ is an activation function that maps abundance values to values between 0 and 1, representing the minimum and maximum for each species (Clark-Wolf et al., 2022). The equilibrium solution of FIW can be found using fuzzified species abundance or interaction strengths. Once the equation is solved, the membership values for each species abundance are found using rescaled fuzzy sets (e.g., low, medium, or high categories), or can be defuzzified for crisp, quantitative results (see Clark-Wolf et al., 2022 for more mathematical detail and instructions for implementing FIWs) which reflect abundances in original measurement scales.

In sum, FIWs may help to overcome numerous shortfalls associated with quantitative models, but these models have yet to be adopted widely in ecology.

However, before quantitative or qualitative ecological modeling efforts can advance, it is necessary to address the fundamental challenges of model structure uncertainty and estimation of interaction strengths that hinder all ecological modeling efforts. Model structure uncertainty must be addressed independently of FIWs, but FIWs may be useful to help address the issue of estimating community interaction strengths as discussed below.

ADDRESSING MODEL STRUCTURE UNCERTAINTY: DEFINING WEB TOPOLOGY

Efforts to define web topology and address model structure uncertainty in qualitative models have focused on quantitative solutions. For example, current methods for addressing model structure uncertainty focus on constraining the number of possible nodes/interactions (e.g., plants cannot consume herbivores) and then generating all alternative model structures (e.g., hundreds of millions of model realizations [Raymond et al., 2011]). More tractable, but less comprehensive approaches include conducting a “scenario analysis” to identify and simulate multiple potential model structures and compare the results of those configurations or building ensembles of models and identifying where they converge on model predictions (Geary et al., 2020). However, web topology is grounded in the natural history of the community and hence is less amenable to a strictly quantitative solution.

To address this challenge, Pearson et al. (2021) proposed a community assessment framework (see Clark-Wolf et al., 2022 for an applied example) derived from ecological theory for identifying the community interaction web. This approach focuses on the target species of interest to systematically evaluate the standard set of interactions (e.g., competition, predation, facilitation, etc.) that might directly, “strongly” link the target or focal species to other components in the community using applicable information from empirical data, literature, and natural history information. In their applications of this approach for conservation, these authors proposed that the community assessment should focus on relatively strong or potentially strong interactions, ignoring very weak interactions based on the assumption that strong direct effects are most ecologically relevant and most likely to propagate substantive indirect effects (see Pearson et al., 2021). This idea is supported by the finding that model efficacy is more sensitive to precisely estimating strong interactions rather than weak one (Novak et al., 2011). After this initial step is applied to determine direct linkages to the target species, this approach is repeated for any species/nodes presumed

to be strongly linked to the target species to determine the depth to which indirect effects might penetrate the web. This method establishes a basic or “null” web by systematically applying community ecology concepts to ensure critical interactions and species are considered while limiting model complexity. This approach is somewhat analogous to models of intermediate complexity (Plagányi et al., 2014), but applies a formal and repeatable ecologically based methodology. This basic web can be evaluated further using sensitivity analyses to determine whether adding/removing nodes makes substantive differences in community responses to perturbations (Baker et al., 2018). Given that some research suggests that weak interactions may play important roles in network stability (e.g., McCann et al., 1998), it is essential to note that the stipulation of focusing on strong interactions can be relaxed when applying the community assessment framework to explore these ideas further (i.e., the roles of strong vs. weak interactions) in ecological modeling.

ESTIMATING SPECIES ABUNDANCE AND INTERACTION STRENGTH

Estimating species abundance and interaction strength also presents a challenge. Many methods have been developed to estimate individual species abundances across divergent taxa. For example, mark–recapture techniques are used for small mammals, point counts for birds, and ocular cover estimates for plants. The greater challenge revolves around integrating disparate metrics to form a community matrix with common denominators and scales for all nodes. This challenge is exacerbated by these divergent metrics being associated with measurement errors that may differ greatly in degree and structure. FIWs provide a solution to this data integration challenge by re-scaling all values to the relative unit interval of [0,1] using piecewise linear transformations (Clark-Wolf et al., 2022; Ramsey & Veltman, 2005).

Estimating interaction strength across such diverse taxa is even more difficult as the standard approach has been to apply manipulative experiments that isolate and quantify each pairwise interaction separately Wootton and Emmerson (2005) for a review, Kleinhesselink et al. (2022). This seemingly impossible task is made more difficult by the fact that interaction strengths in isolation may not reflect interaction strengths within the web due to emergent properties of the web such as higher-order interactions (Kleinhesselink et al., 2022; Wootton & Emmerson, 2005), and poor estimates undermine predictive accuracy (Novak et al., 2011). In theory, one solution to this problem is to apply system dynamics analysis to estimate interaction strengths for all community

interactions in situ (Wootton & Emmerson, 2005). This can be done by quantifying an intact system over time and then perturbing one or more elements of the community to model system responses (e.g., Laska & Wootton, 1998). However, it is possible to derive interaction strengths representative of community-level dynamics by simply monitoring an intact system over time (Downing et al., 2020; Ives et al., 2003; Solow & Sherman, 1997; Wootton & Emmerson, 2005; see also Tikhonov et al., 2020 for general community application of monitoring data). In theory, long-term monitoring of a system at equilibrium could generate the information necessary to assign web topology and species abundances, thereby allowing for the estimation of interaction strengths. While this assumption that a system is at or near equilibrium is questionable, we postulate that, as long as a system is not immediately disrupted by a large pulse perturbation, such monitoring can still capture representative system metrics under slower, steadier, press perturbations that are increasingly ubiquitous like climate change, species loss, nutrification, and so forth. Accordingly, we propose that four of the five essential elements of a community interaction web can be determined by monitoring (nodes, linkages, interaction signs, and species’ abundance) and the fifth element, interaction strengths, can be derived from web topology and dynamical behavior using FIWs (see example below). Such an approach should, in theory, provide interaction strengths that reflect not just pairwise interactions, but the manifestation of pairwise interactions in the context of community dynamics including indirect effects, trait-mediated interactions, and other higher-order interactions (Baker et al., 2016; Ives et al., 2003; Kleinhesselink et al., 2022; Sandal et al., 2022).

INSIGHTS FROM APPLYING A FUZZY INTERACTION WEB TO A CASE STUDY: MPG RANCH

Clark-Wolf et al. (2022) recently demonstrated the efficacy of FIWs for predicting ecological outcomes using documented case studies. They also introduced the web-based user interface, MPG Matrix, for modeling FIWs (<https://matrix.mpg ranch.com/#/>). Here, we apply this interface to demonstrate how FIW can be used to estimate community interaction strengths and to parameterize complex ecological models using qualitative and quantitative data to predict community outcomes in grassland systems in western Montana, USA (Figure 3). The base web reflects key functional groups at a coarse scale that depicts basic energy flows and ecological processes relevant to this system. In this depiction, some

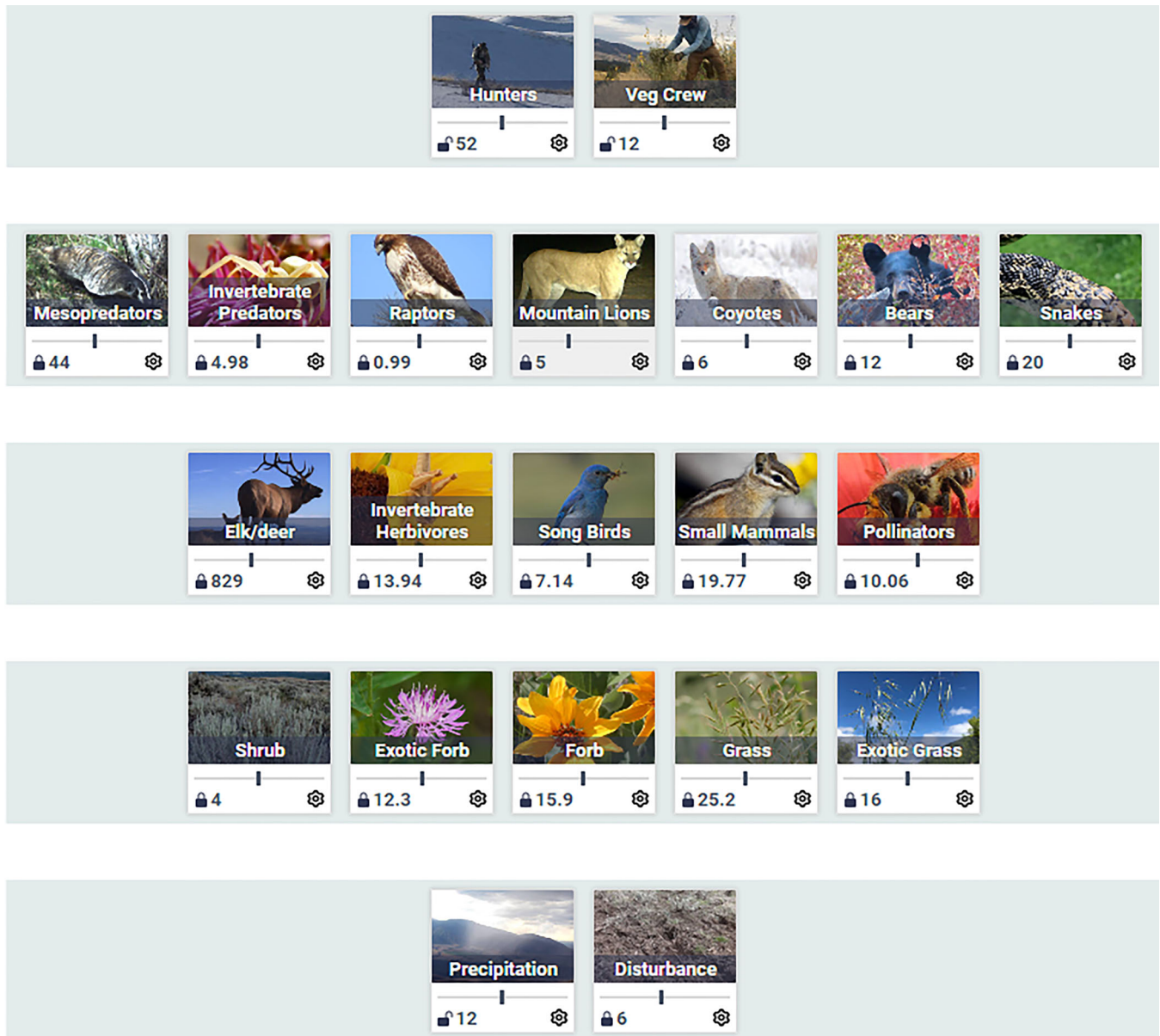


FIGURE 3 Screenshot of the MPG Matrix user interface showing the MPG Ranch Grasslands matrix (<https://matrix.mpgranch.com/#/gallery>) developed by Clark-Wolf et al. (2022). The matrix comprises 21 nodes representing key species/functional groups, critical abiotic inputs (precipitation) and processes (disturbance), and important management actions (hunting and vegetation management). The ability to link concepts like anthropogenic actions into the ecological network is an important attribute for predicting how anthropogenic perturbations affect ecological systems and ecosystem services. The MPG Grasslands matrix includes a full complement of terrestrial taxa and a variety of linkage types including competition (e.g., plant-plant), herbivory, mutualism (pollination), predation, trait-mediated interactions (e.g., negative behavioral response of coyotes to mountain lions), and intraguild predation (e.g., mountain lion depredation of coyotes). The abundance of any node in the matrix interface can be changed to determine its effects on the community. The interface can be used to modify extant matrix templates or create new matrices for applying FIW for ecological and conservation modeling. All photographs were taken by M. P. G. Ranch.

nodes represent individual species of ecological (e.g., mountain lions, *Puma concolor*) or cultural importance (e.g., black bears, *Ursus americanus*, weakly interacting but locally charismatic). Other nodes represent functional species groups analogous to “trophic species” (sensu Pimm et al., 1991), but without restriction to

trophic interactions. Notably, some nodes represent anthropogenic factors (management actions) and abiotic processes (precipitation). This ability of FIWs to expand beyond the traditional concept of nodes as species is essential for modeling anthropogenic perturbations and ecosystem processes. Web topology (nodes, linkages, and

linkage signs) was determined from natural history understandings derived from long-term monitoring. Abundances were derived from up to 10 years of data (depending on the node). Abundance data reflect classical sampling approaches with plants measured as percent cover per 1 m² and songbirds measured via point counts of individuals per ha. Because abundance parameters of interest for a FIW are the boundaries and midpoint for each node, the mean, low, and high abundance values from monitoring were used as node inputs. These data provided inputs for four of the five essential components for modeling community interactions (nodes, linkages, linkage signs, and abundances).

As in most systems, explicit measures of interaction strengths were unavailable. Hence, initial estimates of qualitative interaction strengths were based on published literature when available and natural history understandings as necessary. This was done using a variety of sources. For example, diet information was used to initialize food web interactions for black bears based on local research (Greer, 1987) informed by DNA-based dietary analysis of bear scats from the ranch (P. Ramsey et al., unpublished data). Competitive interactions among native and exotic plant functional groups and precipitation input effects were initialized from local field experiments (Pearson et al., 2017). Intraguild predation and related nonlethal trait-mediated effects of mountain lions on coyotes (*Canis latrans*) were initialized based on telemetry and remote camera studies (Prugh & Sivy, 2020). These initial parameter inputs allowed the model to run. However, the initial equilibrated model did not reflect long-term mean abundances for many nodes. Hence, based on the assumptions that web topology was valid (i.e., black bears consume grasses, berries, etc., which negatively affected these nodes) and average long-term abundance values reflect expected node means for the system at equilibrium, it was determined that some initial interaction coefficients fell outside their norms. Accordingly, the model was manually “tuned” by iteratively modifying interaction strengths until it equilibrated such that each node fell within 5% (usually $\leq 2\%$) of its mean. This approach overcomes the problem of estimating individual interaction strengths using knowledge of the other four elements of the community matrix to solve for the final unknown variable, community interaction strengths, akin to an algebra equation. The underlying assumption is that the long-term averages reflect the underlying community dynamics.

The fuzzification process allows for the seamless integration and standardization of these divergent data into a FIW that qualitatively predicts the effects of perturbing any one node in the system on all other nodes. For example, applying the MPG Ranch user interface, we created

an experiment that maximized hunting pressure from an average of 52 to 120 kills per year of elk/deer (*Cervus canadensis*, *Odocoileus virginianus* and *O. hemionus*). This perturbation reduced the abundance of the elk/deer node sufficiently to see predicted increases in native grasses and forbs that translated to indirect increases in herbivorous small mammals and invertebrates and even slight increases in pollinators (note that these predicted changes are only considered significant if they generate fuzzy category shifts; see Appendix S2: Figure S1). Interestingly, suppression of elk/deer abundance indirectly reduced exotic grass and forb abundance via increased competition with native plants. This latter prediction is consistent with local studies of plant interactions (Pearson et al., 2017). However this is the first depiction of these outcomes arising as indirect effects permeating across a whole community driven by hunting pressure. Mountain lion abundance was also predicted to decline in response to the suppression of elk/deer, their primary food resource, and indirectly reduce mesocarnivore abundance because mountain lion provisioning of ungulate carcasses to mesocarnivores is depressed, consistent with predicted indirect effects (Allen et al., 2015). Based on published literature, model predictions from the MPG Grasslands matrix are consistent with expected interactions for this system. While this is not surprising for the direct interactions, which were explicitly parameterized as described above, it is notable that indirect effects are not explicitly modeled but arise as a function of system dynamics (Baker et al., 2016). This case study illustrates how FIWs can be constructed to model complex ecological systems while incorporating a full range of ecological interaction types and overcoming the barriers to estimating interaction strengths to generate realistic predictions of community perturbation outcomes.

FUTURE DIRECTIONS

Recent calls have been made for the field of ecology to move beyond trophically and taxonomically restricted studies of basic ecological interactions like competition and facilitation to address the milieu within which these interactions take place and advance understanding of ecological systems (García-Callejas et al., 2018; Seibold et al., 2018). FIWs provide a practical tool to simultaneously incorporate multiple trophic levels and interaction types into ecological studies to integrate theoretical and empirical ecology better (sensu Ives & Carpenter, 2007). FIWs can be applied to implement studies of specific ecological questions about the importance of competition, predation, facilitation, and so forth, in

structuring local communities and exploring the effects of anthropogenic perturbations on whole ecosystems for addressing global change. While we have focused on prediction, we note that FIWs also provide the means for heuristically exploring conceptualizations of how the component parts of ecological systems interact to drive the patterns expressed in nature (see Roberts, 1986). Importantly, the practicality of FIWs can accelerate the development of empirically parameterized community interaction webs, thereby generating a database of empirical case studies. Building such a database would enhance the integration of empirical and theoretical studies of ecological networks (Ives & Carpenter, 2007).

Advancing ecology requires integrating theoretical and empirical approaches (Grainger et al., 2022). While theoretical ecologists have extensively explored critical questions about the relationships between network complexity and structure (e.g., connectance, nestedness, interaction strengths, and modularity) and stability (e.g., May, 1972; McCann et al., 1998; Stouffer & Bascompte, 2011), the extent to which these findings reflect real system dynamics remains unclear (Downing et al., 2020; Ives & Carpenter, 2007). This situation exists in part because the development of empirical data sources has not kept pace with modeling efforts (Ives & Carpenter, 2007) and empirical data collection has been strongly biased toward bipartite networks (e.g., pollinator networks), food webs, and smaller, more easily manipulated species (e.g., de Ruiter et al., 1995; Domínguez-García & Kéfi, 2021; Landi et al., 2018). FIWs provide a means for addressing several critical hurdles to developing empirical models of complex, multitrophic, multi-interaction-type networks (e.g., Bartomeus et al., 2021; Fontaine et al., 2011; Kéfi et al., 2015; Pocock et al., 2012) that could help to generate large databases of realistic empirical case studies for better integrating theoretical and empirical ecology.

Like all modeling approaches, FIWs have limitations that prevent them from being a simple panacea for ecological modeling. For example, they do not address temporal dynamics like how long or what path a system might take in response to perturbations to reach an equilibrium state. Other weaknesses include sensitivity to model parameterization (necessitating uncertainty analyses) (Baker et al., 2018); difficulty in incorporating time-varying interaction strengths, which can significantly impact community dynamics (Ushio et al., 2018); and the phenomenological nature of these models, which necessitates further research into robustly incorporating expert opinion into analyses (Ramsey & Veltman, 2005). It is also difficult to model trait-mediated interactions with FIWs, but it is possible (see Dambacher & Ramos-Jiliberto, 2007). Finally, FIWs are community specific, that is, they are built to the specifications of a particular system or case study. While

this is a strength for evaluating real systems where context dependence is determinant (Ramsey & Veltman, 2005), it limits the ability to draw generalizations regarding how key network attributes linked to connectance and structure relate to stability, a major focus of theoretical network modeling approaches (McCann et al., 1998). Importantly, other approaches like Bayesian modeling techniques (Ramsey et al., 2012) and structural equation modeling (Grace, 2006) could potentially be integrated with the approaches we propose here for addressing model structure uncertainty and estimating community interaction coefficients to model ecological systems. Finally, traditional quantitative modeling has contributed extensively to ecological understanding and will continue to do so (Godoy et al., 2018; Kleinhesselink et al., 2022; Novak et al., 2016). Hence, we do not propose FIWs as the sole solution to ecological modeling. However, the simplicity of this approach introduces a certain elegance and practicality to ecological modeling that can accompany other methods to greatly advance the field of ecology.

CONCLUSIONS

Historical limitations of quantitative models, the challenges of addressing model structure uncertainty, and the difficulty of estimating interaction strengths across whole communities have long hindered ecological modeling and hence a greater understanding of ecological systems. The approaches proposed here hold the potential to overcome these hurdles to facilitate the modeling of complex, ecologically relevant systems that extend far beyond simple food webs. FIWs provide a means for: (1) fully integrating a variety of data from highly quantitative to purely qualitative; (2) utilizing data from a variety of field sampling approaches for diverse taxa to approximate species abundance; (3) estimating interaction strengths for complex real-world communities; and (4) incorporating a full range of interaction types (e.g., predation, competition, facilitation). Finally, FIWs can incorporate not only species but also processes such as logging or climate change, enabling the integration of anthropogenic actions into ecological systems, an essential requirement for contemporary ecology. As more FIWs are built within and among systems, this will generate empirically based databases to better inform theoretical modeling approaches, while reciprocally providing a means for formally testing model-based theory in fuzzy model systems.

AUTHOR CONTRIBUTIONS

Dean E. Pearson and T. J. Clark-Wolf jointly developed the ideas and contributed equally to the writing. Dean E. Pearson initiated the draft manuscript.

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CONFLICT OF INTEREST STATEMENT

The authors declare no conflicts of interest.

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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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