

Whole-lake invasive crayfish removal and qualitative modeling reveal habitat-specific food web topology

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Abstract. Patterning of the presence/absence of food web linkages (hereafter topology) is a fundamental characteristic of ecosystems that can influence species responses to perturbations. However, the insight from food web topology into dynamic effects of perturbations on species is potentially hindered because most described topologies represent data integrated across spatial and temporal scales. We conducted a 10-year, whole-lake experiment in which we removed invasive rusty crayfish (*Orconectes rusticus*) from a 64-ha north-temperate lake and monitored responses of multiple trophic levels. We compared species responses observed in two sub-habitats to the responses predicted from all topologies of an integrated, literature-informed base food web model of 32 potential links. Out of 4.3 billion possible topologies, only 308,833 (0.0072%) predicted responses that qualitatively matched observed species responses in cobble habitat, and only 12,673 (0.0003%) matched observed responses in sand habitat. Furthermore, when constrained to predictions that both matched observed responses and were highly reliable (i.e., predictions were robust to link strength values), only 5040 (0.0001%) and 140 (0.000003%) topologies were identified for cobble and sand habitats, respectively. A small number of linkages were nearly always present in these valid, reliable networks in sand, while a greater variety of possible network configurations were possible in cobble. Direct links involving invasive rusty crayfish were more important in cobble, while indirect effects involving *Lepomis* spp. were more important in sand. Importantly, the importance of individual species linkages differed dramatically among cobble and sand sub-habitats within a single lake, even though species composition was identical. Although the true topology of food webs is difficult to determine, constraining topologies to include spatial resolution that matches observed experimental outcomes may reduce possibilities to a small number of plausible alternatives.

Key words: food web; indirect effects; invasive species; qualitative modeling; rusty crayfish; topology.

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INTRODUCTION

Predicting and understanding ecosystem responses to perturbations and anthropogenic drivers such as invasive species, harvest, and climate change is a central goal of ecology. Single-species responses to perturbation are well-documented (e.g., Peterson and Vieglais 2001, Pacifici et al. 2015). Yet all species are embedded in

ecosystems and are inextricably linked to other species via food webs. Food webs can be remarkably complex, consisting of multiple direct and indirect pathways through which changes in one species affect other species (Montoya et al. 2006, Bascompte 2009). The details of how species are linked may determine species responses to perturbations (McCann 2012). Moreover, perturbations themselves can re-arrange the food web

structure and interaction strengths (van der Putten et al. 2004, Tylianakis et al. 2008).

Though the importance of food webs for our understanding dynamic interactions is widely recognized (Schmitz 2010, McCann 2012), in most situations, we know remarkably little about how food webs of natural ecosystems are “wired”—that is, the arrangement of the presence/absence of links among components (i.e., the topology) of the food web. One traditional approach to constructing topological food webs has been to include all connections that are supported by natural history observations, and to then identify common topological or structural properties among food webs (Cohen 1978, Cohen et al. 1990). A separate field of food web research has focused on identifying dynamically important linkages, as revealed by adding and removing species in an experimental setting (Paine 1966, Carpenter et al. 1985). There has been surprisingly little convergence between studies that emphasize topological food web properties and those that focus on dynamic linkages (e.g., O’Gorman et al. 2010, Solomon et al. 2011). The need for new insights into how food webs and ecosystems respond to anthropogenic perturbations has never been greater, and topology could have important implications for ecosystem responses to environmental change (Tylianakis et al. 2008).

A common assumption of food web research is that variation in important links among species results solely from community attributes (i.e., species diversity and community composition). Yet food web topology can differ even when composed of similar or identical species (Křivan and Schmitz 2003, Montano-Moctezuma et al. 2008). One explanation is that abiotic conditions and habitat can mediate feeding interactions among locations within the same ecosystem (Menge and Sutherland 1987, Thompson and Townsend 2005), with important dynamic consequences (Danielson 1991, Oksanen et al. 1992). In this study, we use a whole-lake experimental removal of an invasive crayfish in combination with qualitative modeling (sensu Levins 1974, Dambacher et al. 2002) to (1) infer the underlying topology of the food web based on dynamic responses to a species removal and (2) determine whether topology varies in different habitats of the same ecosystem.

METHODS

Study system and experimental data

Invasive rusty crayfish were experimentally removed from Sparkling Lake, Wisconsin, USA (46.008°, −89.701°), a 64-ha mesotrophic seepage lake (<http://lter.limnology.wisc.edu>). Rusty crayfish invaded Sparkling Lake in the 1970s, and a whole-lake manipulation began in 2001 (Hein et al. 2007). Rusty crayfish were manually removed via trapping from 2001 to 2008, and fishing regulations were changed in 2001 to reduce angler harvest and increase predation on juvenile crayfish. Crayfish density, macrophyte percent cover, littoral benthic macroinvertebrate densities, fish population sizes, and fish diets were monitored through 2010 (Hansen et al. 2013a). Responses of these groups were separated into two major littoral habitat types: cobble (i.e., rocky) substrate, and sandy/silty substrate, which became dominated by macrophytes as crayfish removal progressed (hereafter sand habitat). Macrophytes were also present in cobble substrate, albeit at lower densities.

We grouped fishes, benthic macroinvertebrates, and macrophytes into 10 littoral “trophic species” (sensu Menge 1976) that are known to share common predators and prey (Table 1). Benthic macroinvertebrate orders (non-crayfish) included in this analysis comprised 91% of all sampled benthic invertebrates by number (Hansen 2012). We estimated the change in each trophic species in response to rusty crayfish removal as the mean response of each group from years of high rusty crayfish abundance (2002–2003; mean catch rates ≥ 1 crayfish per trap per day) to years of low crayfish abundance (2008–2010; mean catch rates < 1 crayfish per trap per day; Table 2). The abundance of each trophic species was modeled on the natural log scale as a function of rusty crayfish relative abundance (high or low), habitat (when applicable), and their interaction, and for some groups included random effects to account for non-independence among samples collected at the same sites or depth (Table 2; Hansen et al. 2013a). We calculated the difference between the maximum-likelihood estimate of abundance in years of low and high crayfish abundance, and classified species responses as increase, decrease, or no change. For benthic macroinvertebrates, differences of < 0.1 natural log units ($< 10\%$ change) were classified as no change. Qualitative responses in each habitat

Table 1. Trophic species included in the interaction web of the Sparkling Lake littoral community.

Group	Description (functional group)	Taxa
Bass	Littoral non-sunfish centrarchids (generalist predators)†‡	Smallmouth bass (<i>Micropterus dolomieu</i>), rock bass (<i>Ambloplites rupestris</i>)
<i>Lepomis</i>	Sunfishes (mainly invertivores)†‡	Bluegill sunfish (<i>L. macrochirus</i>), pumpkinseed sunfish (<i>L. gibbosus</i>)
Rusty crayfish	Invasive rusty crayfish (omnivores)§	Rusty crayfish (<i>Orconectes rusticus</i>)
Odonata	Dragonfly larvae (mainly predators)¶	Aeshnidae, Coenagrionidae, Corduliidae, Gomphidae, Libellulidae, Macromiidae
Ephemeroptera	Mayfly larvae (scrapers, collector-gatherers)¶	Baetidae, Caenidae, Ephemerellidae, Ephemeridae, Heptageniidae, Leptophlebiidae, Polymitarcyidae
Trichoptera	Caddisfly larvae (collector-gatherers, scrapers, shredders, herbivores)¶	Hydroptilidae, Leptoceridae, Limnephilidae, Phryganeidae, Polycentropodidae
Gastropoda	Snails (scrapers)††	Hydrobiidae, Lymnaeidae, Physidae, Planorbidae, Valvatidae
Diptera	Midge larvae (collector-gatherers, predators)¶	Ceratopogonidae, Chironomidae, Chaoboridae
Amphipoda	Amphipods (grazer, collector-gatherer)‡‡	<i>Hyalella azteca</i>
Macrophyte	Aquatic plants (primary producers)	All littoral vegetation. Dominated by <i>Chara</i> spp., <i>Eleocharis acicularis</i> , <i>Isoetes</i> spp., <i>Juncus pelocarpus</i> , <i>Najas flexilis</i> , <i>Potamogeton gramineus</i> , and <i>Vallisneria americana</i>

† Empirical diet data.

‡ Becker (1983).

§ Capelli (1980), Whitledge and Rabeni (1997), Roth et al. (2006).

¶ Merritt and Cummins (1996).

†† Thorp and Covich (2010).

‡‡ Strong (1972).

served as validation criteria to evaluate alternative food web topologies using qualitative modeling.

Qualitative modeling

We used a qualitative approach to describe species interactions (Levins 1974, Puccia and Levins

1985). Qualitative descriptions of link presence–absence within a network provide information about food webs when quantitative estimates of interaction strengths are not feasible to obtain. A network of n species can be represented as an n by n matrix (**A**), where a_{ij} is the element in the i th

Table 2. Methods of quantifying the response of each trophic species to rusty crayfish removal from Sparkling Lake.

Taxa	Response variable (lowest unit of observation)	Units†	Fixed effects	Random effects
Rusty crayfish	CPUE (site)	No.·trap ⁻¹ ·d ⁻¹	Yeargroup‡, Habitat, Yeargroup × Habitat	Transect§, Year
Bass	Mark–recapture population estimate (whole lake)	No.	Yeargroup	NA
<i>Lepomis</i>	Mark–recapture population estimate (whole lake)	No.	Yeargroup	NA
Macrophytes	Percent cover of all species (quadrat)	% cover (all spp.)	Yeargroup, Habitat, Yeargroup × Habitat	Transect, Year, Depth¶
Amphipoda	Density (quadrat)	No./m ²	Yeargroup, Habitat, Yeargroup × Habitat	Site††, Year
Diptera	Density (quadrat)	No./m ²	Yeargroup, Habitat, Yeargroup × Habitat	Site††, Year
Ephemeroptera	Density (quadrat)	No./m ²	Yeargroup, Habitat, Yeargroup × Habitat	Site††, Year
Gastropoda	Density (quadrat)	No./m ²	Yeargroup, Habitat, Yeargroup × Habitat	Site††, Year
Odonata	Density (quadrat)	No./m ²	Yeargroup, Habitat, Yeargroup × Habitat	Site††, Year
Trichoptera	Density (quadrat)	No./m ²	Yeargroup, Habitat, Yeargroup × Habitat	Site††, Year

† All modeled on natural log scale.

‡ High (2002–2003) or low (2008–2010) crayfish density.

§ One of 43 standardized trapping and monitoring locations.

¶ Categorical classification: 0–1 m, 1–2 m, 2–3 m, 3–4 m.

†† Depth-specific transect location (either 1, 3, or 5 m depth).

row and j th column representing the effect of a change in density of species j on species i and can be either positive (1), negative (-1), or zero (Levins 1974, Puccia and Levins 1985, Dambacher et al. 2002). Topological food webs can be represented by signed digraphs composed of positive (arrow point) and negative (open dot) interactions from one group to another (Fig. 1).

We used qualitative modeling to identify topologies consistent with observed changes in species abundance following a press perturbation (Montano-Moctezuma et al. 2007, Raymond et al. 2011). The effect of a press perturbation at equilibrium on each species is represented by the negative inverse of the community matrix ($-A^{-1}$), also known as the prediction matrix (Levins 1974, Bender et al. 1984). The prediction matrix represents the response of each species (rows) to changes in the abundance of each other species (columns). Thus, by generating prediction matrices for all possible topologies, predicted responses to a perturbation in one species can be compared to observed responses from the perturbation (Montano-Moctezuma et al. 2007).

We constructed a base topological food web (Fig. 1) composed of biologically plausible links between trophic species. The base topology only included links supported by diet data and published literature. All predator-prey interactions between bass and other animals were included with the exception of Gastropoda, which appeared in bass diets an order of magnitude less frequently than any other invertebrate prey (Hansen 2012). We included predator-prey interactions between *Lepomis* and all invertebrate species (including rusty crayfish; Becker 1983, Tetzlaff et al. 2010, Hansen 2012). Predator-prey interactions between rusty crayfish and all other invertebrates were included with the exception of Amphipoda, as crayfish generally consume less active invertebrate prey (Momot et al. 1978, Whitledge and Rabeni 1997). A negative interaction between rusty crayfish and macrophytes was included (Lodge and Lorman 1987, Lodge 1991, Olsen et al. 1991). We included positive (habitat-mediated) interactions between macrophytes and *Lepomis* (Mittelbach 1981, 1984, Crowder and Cooper 1982) and macrophytes and benthic macroinvertebrates (Rabe and Gibson 1984, Gregg and Rose 1985, Brown and Lodge 1993, Rennie and Jackson 2005), with the exception of Diptera that in this

system are primarily sediment dwellers (Merritt and Cummins 1996). Predatory interactions between Odonata and Diptera, Ephemeroptera, and Trichoptera prey were also included (Merritt and Cummins 1996). We included competitive interactions between Gastropoda, Ephemeroptera, and Trichoptera, the three orders containing some scraper taxa most likely to compete for periphyton resources (which are not included in the model; Table 1).

We assessed topology separately for cobble and sand habitat in Sparkling Lake. We used the same base topology for both habitat types, which included 32 links comprising both trophic (predator-prey) and non-trophic (competitive, habitat, destructive) relationships (Table 3, Fig. 1). A total of 2^{32} (approximately 4.3 billion) topological food webs representing all possible combinations of the 32 links were assembled. We specified whether each possible link in the base topology was positive or negative a priori. Due to the vast number of potential topologies in this study, we limited the number of potential configurations by constraining certain types of links when they were present. Predator-prey links were reciprocal; that is, when a predator-prey interaction was included, predators negatively affected prey and prey positively affected predators ($a_{ij} = -a_{ji}$). Competitive links were also reciprocal; when included, both species negatively influenced each other ($a_{ij} = a_{ji} = -1$). Habitat and destructive links were not reciprocal; habitat-providing species positively influenced the species for which it provided habitat ($a_{ij} = 1$; $a_{ji} = 0$), and destructive species negatively influenced the species it destroyed ($a_{ij} = -1$; $a_{ji} = 0$). Every simulated topological food web included negative self-dampening effects for each group (-1 elements on the diagonal axis of the community matrix; Raymond et al. 2011); these represent density-dependent population growth and dependence on elements not included in the model.

To assess the relative importance of each link, we followed the procedure outlined in Fig. 2, similar to that employed by Montano-Moctezuma et al. (2007). For each topology, we assessed the Lyapunov stability of the community matrix following Puccia and Levins (1985) and Dambacher et al. (2003), and unstable topologies were discarded. The negative inverse of the community matrix was calculated for stable topologies. Topologies for which the direction of the predicted

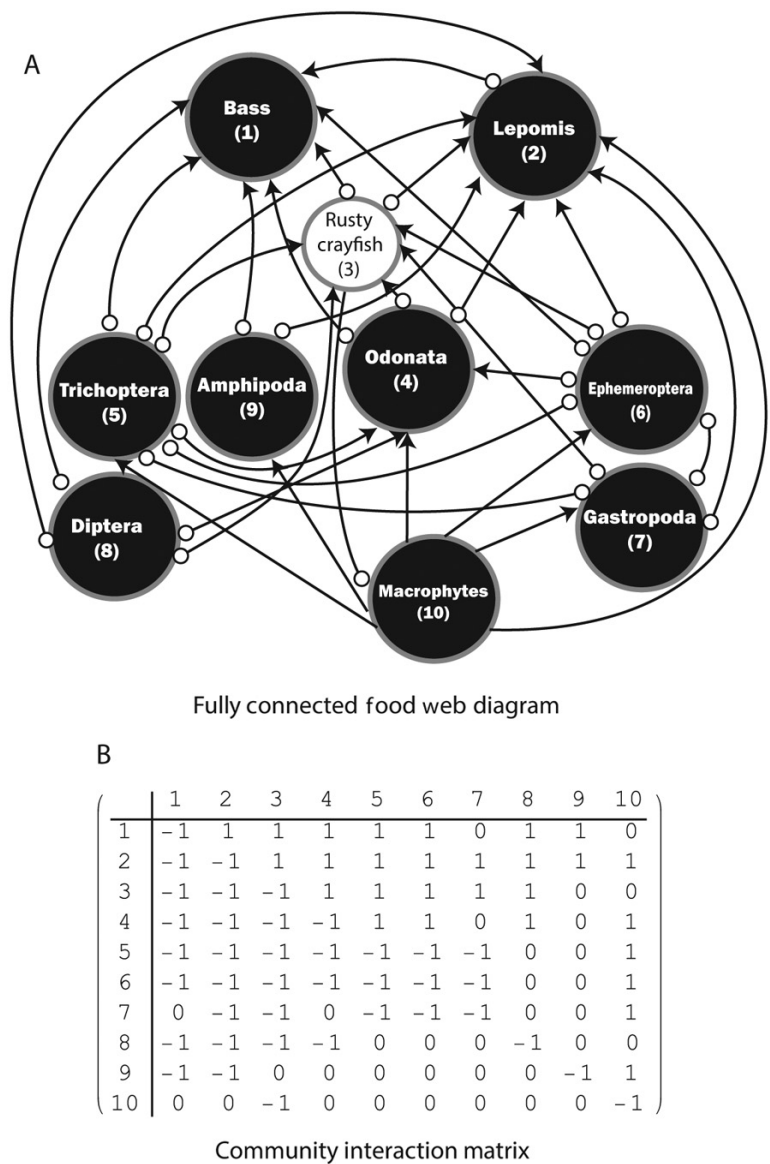


Fig. 1. Signed digraph (A) and qualitative community interaction matrix (B) representing the full topological model (all potential interactions included) in Sparkling Lake. Numbers in parentheses in the digraph are species identification codes used in the interaction matrix; the effect of species j on species i (a_{ij}) occurs in the i th row of the j th column. Interactions between community members are directional; in the signed digraph, interactions are negative (open circle), positive (arrow point), or no effect (no symbol or no line), corresponding to -1 , 1 , and 0 in the community interaction matrix, respectively. All topologies considered included a negative self-dampening effect for each group to represent density dependence (diagonal of the community matrix), not shown in the digraph for clarity of representation.

Table 3. The proportion of valid, stable, reliable topologies in which each potential interaction was present in qualitative models of the Sparkling Lake food web in cobble and sand habitats, as well as the difference in frequency of occurrence in the two habitats (positive values = more frequent in cobble; negative values = more frequent in sand).

Species 1	Species 2	Type	Frequency in final models (%)		Difference
			Cobble	Sand	
Bass	<i>Lepomis</i>	Predator-prey	0.2	0.14	0.06
Bass	Crayfish	Predator-prey	0.55	0.29	0.26
Bass	Odonate	Predator-prey	0.15	0.14	0.01
Bass	Ephemeroptera	Predator-prey	0.31	0.14	0.17
Bass	Trichoptera	Predator-prey	0.15	0.14	0.01
Bass	Diptera	Predator-prey	0.16	0.14	0.02
Bass	Amphipoda	Predator-prey	0.23	0.14	0.09
<i>Lepomis</i>	Crayfish	Predator-prey	0.1	0.16	-0.06
<i>Lepomis</i>	Gastropod	Predator-prey	0.35	0.63	-0.28
<i>Lepomis</i>	Ephemeroptera	Predator-prey	0.57	1	-0.43
<i>Lepomis</i>	Diptera	Predator-prey	0.1	1	-0.9
<i>Lepomis</i>	Trichoptera	Predator-prey	0.28	1	-0.72
<i>Lepomis</i>	Odonate	Predator-prey	0.27	0.53	-0.26
<i>Lepomis</i>	Amphipoda	Predator-prey	1	1	0
Odonate	Ephemeroptera	Predator-prey	0.49	0.24	0.25
Odonate	Diptera	Predator-prey	0.25	0	0.25
Odonate	Trichoptera	Predator-prey	0.18	0.24	-0.06
Crayfish	Gastropod	Predator-prey	0.68	0.64	0.04
Crayfish	Ephemeroptera	Predator-prey	0	0	0
Crayfish	Diptera	Predator-prey	0.16	0	0.16
Crayfish	Odonate	Predator-prey	0.47	0	0.47
Crayfish	Trichoptera	Predator-prey	0.57	0	0.57
Crayfish	Macrophyte	Destructive	1	1	0
Macrophyte	<i>Lepomis</i>	Habitat	0.43	0.82	-0.39
Macrophyte	Gastropod	Habitat	0.7	0.84	-0.14
Macrophyte	Ephemeroptera	Habitat	0	0	0
Macrophyte	Odonate	Habitat	0.54	0	0.54
Macrophyte	Trichoptera	Habitat	0.67	0	0.67
Macrophyte	Amphipoda	Habitat	0	0	0
Gastropod	Trichoptera	Competition	0	0	0
Gastropod	Ephemeroptera	Competition	0	0	0
Ephemeroptera	Trichoptera	Competition	0	0	0

Note: Interactions occurring in at least 50% of valid, stable, reliable models for both habitat types are shown in bold.

response of each trophic species to rusty crayfish removal matched observed responses in a given habitat were deemed plausible representations of the true topology (hereafter “valid topologies”) for that habitat. These valid topologies were further constrained to those for which all predicted responses were deemed reliable based on the weighted prediction matrix (Dambacher et al. 2002, 2003). Prediction weights measure the robustness of qualitative predictions; prediction weights >0.5 were considered reliable (Dambacher et al. 2002, 2003). Thus, our final set of topologies included only stable topologies for which the

predicted response of each trophic species to the removal of rusty crayfish matched the observed response (valid predictions) and was reliable (prediction weights >0.5; Fig. 2). The relative importance of each link was quantified as the percentage of stable, valid, reliable topologies (hereafter final topologies) containing that link for each habitat (Montano-Moctezuma et al. 2007). Because each link was included in 50% of the simulated set of topologies, links appearing in more than 50% of final topologies for a given habitat were considered most important. All analyses were conducted using custom-developed MATLAB code (version

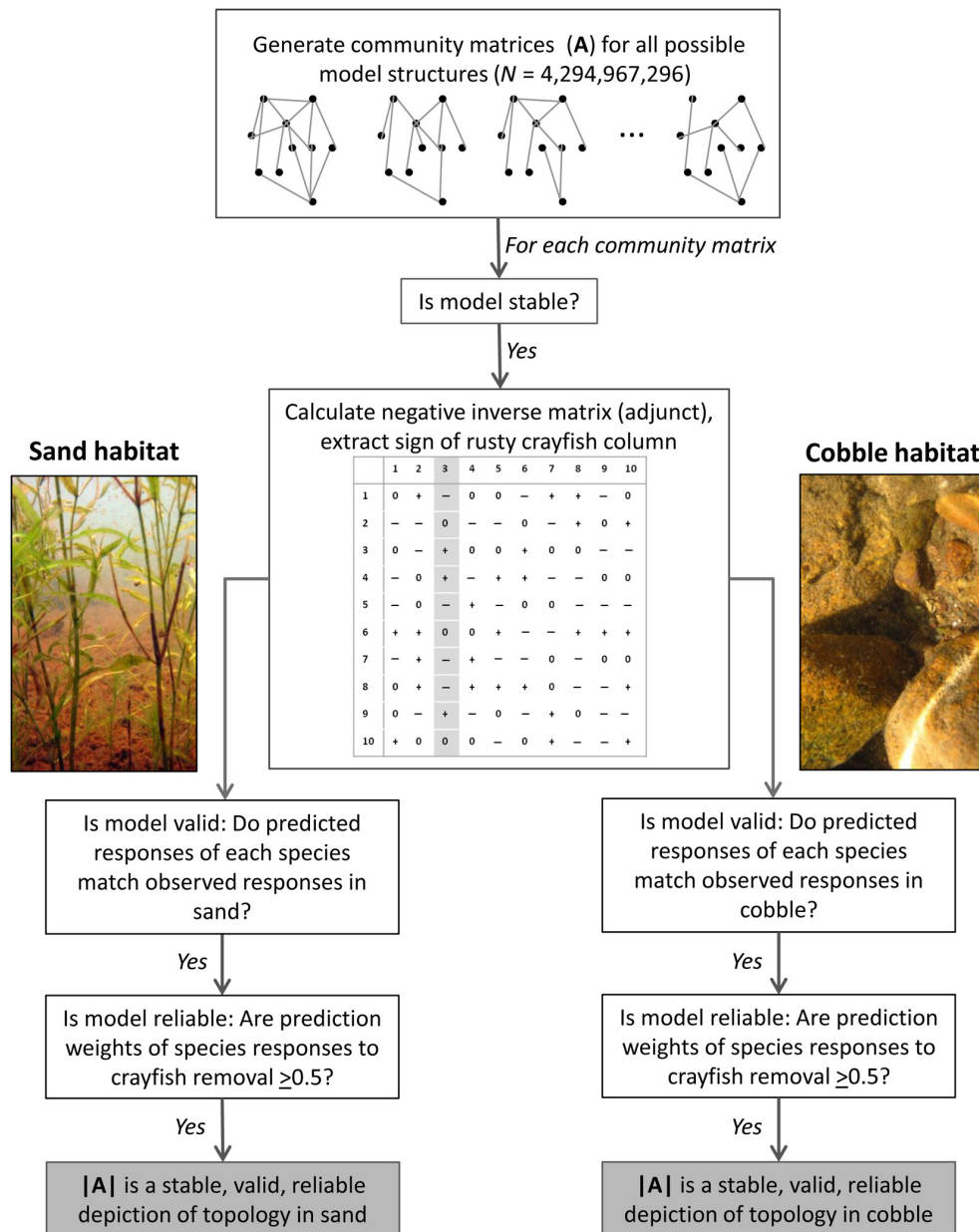


Fig. 2. Flow chart outlining qualitative simulation approach. All possible combinations of the 32 biologically plausible interactions were constructed as topological food webs, and unstable topologies were discarded. Stable topologies for which predicted responses of each species to the removal of rusty crayfish matched observed responses for a given habitat type in Sparkling Lake were retained as valid. These topologies were further filtered to only include those for which predicted responses were reliable, meaning their prediction weights were ≥ 0.5 . See text for further details.

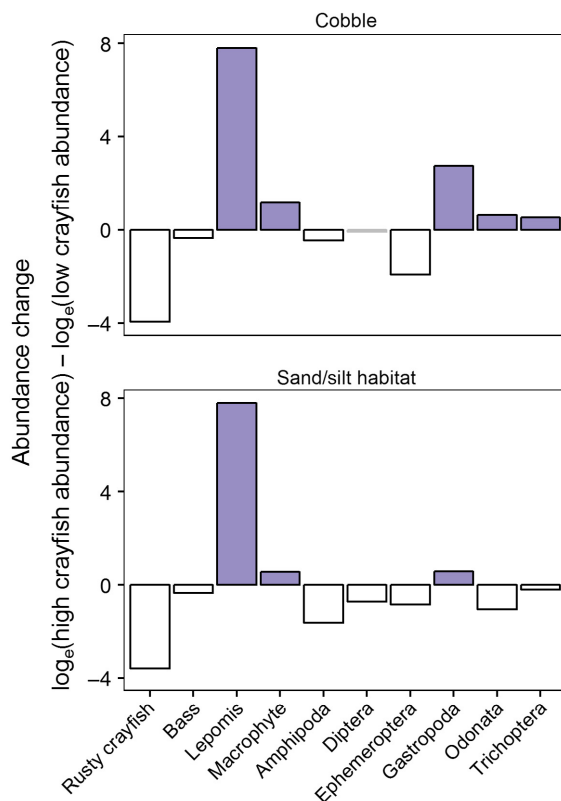


Fig. 3. Response of all trophic species to the experimental rusty crayfish removal (see Table 2 for information on how each group was measured), calculated as the modeled mean abundance in high crayfish years (2002–2003)—mean abundance in low crayfish years (2008–2010) on the natural log scale. Color of bars reflects the qualitative response of each group to the experimental removal of rusty crayfish used for validation of qualitative models: no fill = decrease, purple fill = increase, no fill with gray outline = no change (Diptera in cobble habitat only). Bass and *Lepomis* were measured on the whole-lake scale, and changes in the two habitats are identical. Other groups were measured separately in each habitat type.

2011b; The MathWorks, Inc., Natick, Massachusetts, USA) and distributed to a cluster of computers using HTCondor (Litzkow et al. 1988) to accelerate the analysis of the 4.3 billion models. All code is available upon request.

RESULTS

Rusty crayfish abundance declined by two orders of magnitude over the course of the

experimental removal. We observed substantial changes in the abundance of most trophic species, and some responses differed among habitats (Fig. 3; see also Hansen et al. 2013a). In both habitats, *Lepomis*, macrophytes, and Gastropoda increased in abundance.

Out of 4.3 billion possible topologies, 308,833 (0.0072%) were stable and valid for cobble habitat, and 12,673 (0.0003%) were stable and valid for sand habitat. No topologies were valid for both habitats, indicating that different topologies were required to describe food web responses to the manipulation in the two habitats. When further constrained to include only topologies for which the predicted responses were reliable (prediction weights >0.5), only 5040 (0.0001%) and 140 (0.000003%) topologies were identified for cobble and sand habitats, respectively.

The frequency of each link in final topologies differed among habitats (Table 3, Fig. 4). In cobble, nine links occurred in more than 50% of final topologies (Fig. 4A). Two links occurred in 100% of final topologies: rusty crayfish destruction of macrophytes, and *Lepomis* predation on Amphipoda. Rusty crayfish were also directly linked with all species to which potential linkages were possible in cobble habitat, with the exception of Trichoptera. Interactions with macrophytes were critical for explaining the response of Gastropoda, Odonata, Trichoptera, and *Lepomis* in cobble habitat.

In sand habitat, 10 links occurred in 50% or more of final topologies, and half of these interactions occurred in 100% of cases (Table 3, Fig. 4B). Of these five essential links, four were predator–prey interactions involving *Lepomis* and their prey. *Lepomis* linkages with all other species occurred some proportion of final topologies, and all but two of these interactions were present in greater than 50% of final topologies in sand habitat. Rusty crayfish destruction of macrophytes occurred in 100% of final topologies in sand habitat, and rusty crayfish predation on Gastropoda was also important, appearing in 64% of final topologies. Rusty crayfish did not interact directly with other invertebrates excepting Gastropoda in any final topologies in sand habitat.

Of the 32 potential links, five were present in >50% of final topologies for both habitats (Table 3, Fig. 4): *Lepomis* predation on Ephemeroptera, *Lepomis* predation on Amphipoda, rusty crayfish

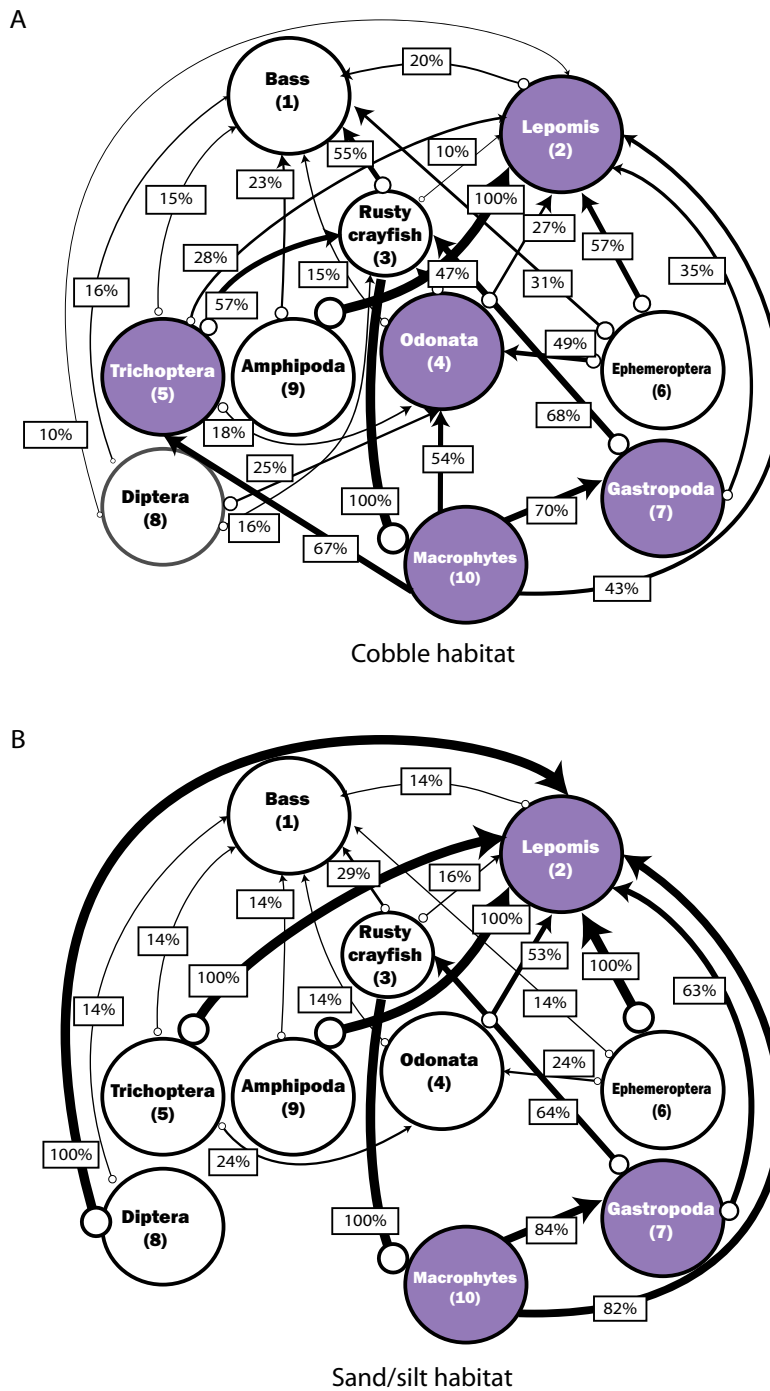


Fig. 4. Interactions occurring in valid, stable, reliable models in (A) cobble habitat; (B) macrophyte habitat. Interactions occurring in >50% of valid, stable, reliable models are highlighted in bold. Circle fill colors correspond to the observed directional response of each trophic species to experimental removal of rusty crayfish shown in Fig. 2; filled purple circles represent groups that increased in abundance; and open circles represent species that decreased in abundance, and open circles with gray outline represent species that did not change in abundance (Diptera in cobble habitat only). Species involved in interactions are connected by directed lines, where arrows point in the direction of a positive interaction, while circles point in the direction of a negative interaction.

predation on Gastropoda, rusty crayfish destruction of macrophytes, and provision of habitat for Gastropoda by macrophytes. All final topologies in both habitats contained rusty crayfish destruction of macrophytes and *Lepomis* predation on Amphipoda.

DISCUSSION

Perhaps the most basic question of food web ecology is “Which species interact?” A large and influential body of food web research has examined patterns of food web topology in catalogs of food webs (e.g., Cohen 1978, Dunne et al. 2002). While this body of literature has described many interesting empirical patterns, one shortcoming is that an understanding of food web topology has little applicability for our understanding of food web dynamics, such as predicting species responses to perturbations (Paine 1988). Here, we attempt to bridge this structure-dynamic gap by reverse engineering topology from dynamic community responses to a species removal. Specifically, we use a qualitative food web modeling approach (Levins 1974, Montano-Moctezuma et al. 2007) to identify specific topological food webs, drawn from a broad range of possible food webs, which predict responses consistent with observed responses to a whole-lake invasive species removal experiment. Only a small fraction of the >4 billion potential topologies predicted reliable responses consistent with the observed community responses. These topologies provided the basis for assessing which specific linkages were most important, thus providing unique insights into food web topology that were specifically informed by dynamic responses to a food web perturbation.

Habitat heterogeneity plays an important role in food webs by influencing species composition and interaction strengths (Oksanen et al. 1992, Thompson and Townsend 2005). We found that topology in littoral communities differed between cobble and sand habitats in Sparkling Lake, despite the fact that community composition was the same (Fig. 4). In cobble habitat, we observed more direct links between rusty crayfish and other species. Cobble offers some refuge from fish predation for both crayfish (Garvey et al. 1994) and non-crayfish invertebrates (Free et al. 2009). However, crayfish are effective

predators on other invertebrates in cobble (Momot et al. 1978), consistent with our findings. The direct effects of rusty crayfish were less frequent in sand habitat; here, direct interactions between *Lepomis* and invertebrate prey were common. *Lepomis* were linked directly to all species in sand habitat and mediated indirect effects of crayfish on macroinvertebrates through their connection to macrophytes. *Lepomis* use macrophyte habitat preferentially to avoid predation by piscivorous fish such as bass and forage on invertebrates (Mittelbach 1988). Furthermore, rusty crayfish impacts on north-temperate lake food webs are generally mediated through their direct effects on macrophytes and indirect effects on *Lepomis* (Roth et al. 2007, Hansen et al. 2013b).

Rusty crayfish can potentially interact (directly or indirectly) with every trophic species in both habitats, but the implications of these interactions in terms of species responses to perturbation depend critically on topology. For example, a direct predatory link between rusty crayfish and Trichoptera produces a positive response of Trichoptera to crayfish removal in cobble habitat, while indirect links mediated by macrophytes and *Lepomis* result in a negative response of Trichoptera to crayfish removal in sand habitat (Fig. 4). Such variability in topology could explain inconsistencies in the observed responses of macroinvertebrates to rusty crayfish invasion reported in other studies. In three previous whole-lake studies, the responses of five invertebrate orders to rusty crayfish invasion were reported in each, and none of these orders responded consistently across all three studies (Wilson et al. 2004, McCarthy et al. 2006, Nilsson et al. 2012). Indeed, consideration of the broader food web is necessary for understanding the effects of rusty crayfish invasions or removal (Hansen et al. 2013a). We argue that to explain or predict changes in species abundance resulting from perturbations such as species invasions, it is critical to consider more of the community than just the invader and its main prey. The dynamic consequences of invaders (or any other perturbation) will be highly uncertain when food web topology is unknown, and can vary in sign and magnitude based on different topologies. Further, the indirect effects of invaders may outweigh direct effects and reverse the sign of species responses (White et al. 2006, Brown et al. 2011). Variation in network structure among habitats with identical

species composition is an important factor to consider when assessing the dynamic impacts of invasion, or other environmental drivers of change in ecosystems (Poisot et al. 2012, 2015).

The dynamic changes observed in the littoral community of Sparkling Lake suggest that the actual topology of a given food web contains only a fraction of the possible linkages described in the literature. These findings caution that food webs constructed based on all plausible connections may be over-connected, with implications for individual species dynamic responses to whole food web stability (May 1973, Dunne et al. 2002). Few studies have examined food web structure change across environmental and habitat gradients, despite the importance of this variation for the conservation of biodiversity due to important connections between habitat and food web dynamics (Thompson and Townsend 2005, McCann 2007). We found no single topology that was consistent with the observed dynamic responses in both habitats (Fig. 4), suggesting that topology varies among habitats within a single lake, and that in some cases habitat itself may be an important interactor in determining community response. However, several links were present in more than 50% of valid, reliable topologies in both habitats. These core links are likely to be critical in determining the community response to perturbation and may be important in other locations (Lane 1986). Indeed, the effects of rusty crayfish on Gastropoda, macrophytes, and *Lepomis* are those most consistently reported across multiple studies (Olsen et al. 1991, Lodge et al. 1994, Wilson et al. 2004, Hansen et al. 2013a), and we found these interactions to be consistently important in explaining observed responses to rusty crayfish removal.

Identifying the role of food web linkages in the stability of ecosystems is a major research challenge for predicting species responses to perturbations such as species invasions or extinctions. Much research on this topic considers topology and stability at the whole food web level. However, we found that topological structure within a single lake differed at the habitat scale as cobble habitats had more realized links than sand/silt habitats despite being composed of the same species. Based on theory, we would then expect that food webs in the two habitats would differ in their stability (May 1973, Dunne et al. 2002). One way

to determine stability is to assess the ability of a system to resist change following a perturbation (i.e., resistance), where the smaller the change the more resistant the system is to perturbation (McCann 2012). In our experiment, the same species in different habitats differed in the magnitude and direction of their change in abundance following crayfish removal. Because our results show that topology and species abundance changes differ among habitats, we expect that the resilience and robustness at the whole system level is dependent on this habitat-level variation. How this habitat-scale variation in topology and species dynamics affects stability at the whole system level is an important question for future research.

Here, we demonstrate the use of dynamic responses to a press perturbation to infer the topology of a north-temperate lake food web. Food web topology is crucial in bounding expectations of community response to disturbance. Our work highlights the idea that use of perturbations can provide insights into direct link topology that will likely underpin better predictions of food web responses to anthropogenic disturbance, which may ultimately influence the provision of ecosystem services and maintenance of biodiversity (van der Putten et al. 2004, Tylianakis et al. 2008).

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