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Research article

Coupling ecological and social network models to assess "transmission" and "contagion" of an aquatic invasive species

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ABSTRACT

Network analysis is used to address diverse ecological, social, economic, and epidemiological questions, but few efforts have been made to combine these field-specific analyses into interdisciplinary approaches that effectively address how complex systems are interdependent and connected to one another. Identifying and understanding these cross-boundary connections improves natural resource management and promotes proactive, rather than reactive, decisions. This research had two main objectives; first, adapt the framework and approach of infectious disease network modeling so that it may be applied to the socio-ecological problem of spreading aquatic invasive species, and second, use this new coupled model to simulate the spread of the invasive Chinese mystery snail (*Bellamya chinensis*) in a reservoir network in Southeastern Nebraska, USA. The coupled model integrates an existing social network model of how anglers move on the landscape with new reservoir-specific ecological network models. This approach allowed us to identify 1) how angler movement among reservoirs aids in the spread of *B. chinensis*, 2) how *B. chinensis* alters energy flows within individual-reservoir food webs, and 3) a new method for assessing the spread of any number of non-native or invasive species within complex, social-ecological systems.

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1. Introduction

Ecologists and conservationists are challenged by the increasing, unintentional spread of species from one location to another. One method to quantify how a species interacts with and influences its environment is ecological network analysis (ENA). This method is particularly helpful for investigating potential effects before a species has been introduced, allowing managers to be proactive rather than reactive, and it acknowledges that ecosystems consist of complex networks of interactions and allows for a holistic examination of the system in question; we can use ENA to assess how energy flows throughout an entire food web are directly and indirectly affected (Fath et al., 2007). Ecosystem resilience can be assessed by adding or removing nodes and observing how the system reacts in a simulated future (Janssen et al., 2006), and the strong human component embedded in the problem of spreading aquatic invasive species naturally leads to a direct link with social network analysis.

Parallels exist between modeling the spread of invasive species and modeling the spread of infectious diseases (Byers, 2009; Floerl et al., 2009; Meentemeyer et al., 2011). Infectious diseases spread through networks via physical contact of individuals (Meyers et al., 2005). The transmissibility of a disease is the average probability of an infected person transmitting the disease to a susceptible person through physical contact (Meyers et al., 2005). Network analysis allows scientists to calculate how many secondary cases are likely to occur as a result of contact with the primary host (Meyers et al., 2005), as well as the average number of connections an infected host has (Hethcote, 2000). Using this same framework, we calculated the probability of a species (the freshwater, non-native Chinese mystery snail *Bellamya chinensis* [Reeve 1863]) from an

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"infected and contagious" primary host reservoir being "transmitted" (introduced) to a new reservoir as a result of human movement. Once *B. chinensis* "infected" a new lake, we then calculated how long it took for the population to become abundant enough so that the reservoir became "contagious" and was capable of acting as a source population. We also monitored how the introduction of *B. chinensis* affected biomass and energy flows among groups in the altered ecosystem.

Bellamya chinensis is native to Asia and was first recorded in North America in 1892 as an imported live food source (Wood, 1892). The species has since spread to numerous lakes and slow-moving rivers throughout the USA, as well as southern Canada (Olden et al., 2013).

This prosobranch, freshwater species is large, reaching shell lengths up to 70 mm, lives 4–5 years (Jokinen, 1982), has an annual fecundity of 30 juveniles/female (Stephen et al., 2013), and can reach high population densities (Chaine et al., 2012) that fluctuate with environmental conditions (Haak et al., 2013).

All Chinese mystery snails graze on algae and periphyton, but adults >43 mm are also capable of suspension feeding (Olden et al., 2013). When present alone, *B. chinensis* does not appear to reduce native snail abundance (Solomon et al., 2010); however, when present with the invasive rusty crayfish *Orconectes rusticus* [Girard 1852], native snail biomass decreases (Johnson et al., 2009).

1.1. Objectives

A geographically focused case study is used to demonstrate how social and ecological models can be used together to answer social-ecological questions. The objectives of this research study were twofold: 1) couple a social network depicting human movement among regional reservoirs with each reservoir's individual ecosystem network model to assess how perturbations influence biomass and energy flows throughout the entire network, and 2) assess the specific impacts the non-native *Bellamya chinensis* could have on the region and estimate its introduction probability to individual reservoirs based on human activity.

2. Materials and methods

2.1. Study area

The Salt Valley region of southeastern Nebraska, USA comprises 19 reservoirs (near the City of Lincoln (40.8258 N, 96.6852 W) (Fig. 1). Reservoirs range from 0.048 to 7.28 km^2 in surface area and have variable fish communities and stocking regimes. Each reservoir has different established aquatic invasive species (Table 1). Salt Creek runs through the Salt Valley region and empties into the Platte River near Ashland, Nebraska (41.0393 N, 96.3683 W) (Martin, 2013).

Five of the 19 Salt Valley reservoirs (Branched Oak, Pawnee, Wild Plum, Wagon Train, and Holmes) have established *B. chinensis* populations; however, no research has examined how the snails affect energy flows within these flood-control reservoirs. Despite some species causing extensive damage to their novel ecosystems, it is estimated that 90% of non-native species have minimal effects in their introduced ranges (Williamson, 1996). The current lack of information on *B. chinensis* prompted its use in this research, as state resource managers are interested in learning more about its potential impact on local ecosystems.

2.2. Social network development

The Nebraska Game and Parks Commission (NGPC) and Nebraska Cooperative Fish and Wildlife Research Unit (NCFWRU) conducted in-person and mail-return angler surveys during 2009–2012. Data on number of anglers, angling methods, species sought, use of other Salt Valley reservoirs and demographics were collected and compiled, providing raw data for the social component of the current research project (Martin, 2013). Experimental design, data collection and results are well-documented (Chizinski et al., 2014; Martin et al., 2014).

Data on reservoir substitutability and angler preferences on where and how to fish were obtained from the in-person angler interviews and analyzed using the iGraph package in R v3.1.1 (R Development Core Team, 2014). Anglers were asked to identify a specific water body they would go to if their current reservoir was closed. Directed connections between nodes (reservoirs) were normalized to correct for different survey sizes and then weighted to depict the number of anglers who moved between two particular nodes. This provided a social network of how often anglers moved between and among reservoirs in the region. Boat anglers were also asked where they last fished (with their boat), enabling us to create a network depicting where anglers were coming from, including reservoirs and lakes outside of the current study area, a critical piece of information when studying aquatic invasive species that may be passively transported by humans.

The commonly used centrality measures of betweenness, closeness, and degree were calculated for each node in the network (Table 2). Betweenness is a measure of how a node lies on paths linking other reservoirs, closeness is the shortest path between two reservoirs, and degree is the total number of other nodes an individual node is connected to (Daly and Haahr, 2007). Additionally, connectance index, transfer efficiency, system omnivory index, and Finn's Cycling Index values were also calculated (described in Christensen et al., 2005).

2.3. Ecological network development

If a snail is successfully transported from an infected reservoir to a susceptible reservoir, then what will happen to the newly infected ecosystem? Answering this question required developing ecosystem network models for each of the 19 study reservoirs. Using the dominant fish community as the basis for each network (Table 1), we were able to identify and compartmentalize species or functional groups critical to the trophic web of each reservoir.

Models were developed using the software Ecopath with Ecosim v6.4.2 (EwE) (Polovina, 1984; Christensen and Pauly, 1995). The first step was creating a static mass-balanced model of each reservoir in Ecopath, based on the ecosystem's current community composition, using previously identified inputs (Allen, 1971; Walters et al., 1997). These values, combined with the fishing pressure on species within each reservoir (from the NGPC and NCFWRU project), were used to develop a mass-balanced model based on Equation (1).

$$B_i \times (P/B)_i \times EE_i = Y_i + \sum_{j=1}^{n} B_j \times (Q/B)_j \times DC_{ji} \quad (1)$$

where: B_i is the biomass of group i; $(P/B)_i$ is the production/biomass ratio of group i; EE_i is ecotrophic efficiency of group i; Y_i is the yield of group i, i.e., ($Y_i = F_i \times B_i$), where F_i is mortality due to fishing; B_j is the biomass of consumers or predators; $(Q/B)_j$ is food consumption per unit of biomass of predator j; and DC_{ji} is the proportion of prey i in the diet of predator j. Details on the development of this equation can be found in Christensen and Pauly (1992a, b).

Input data were collected from empirical studies on specific reservoirs when available; however, because much of this information has never been measured for these reservoirs, reported

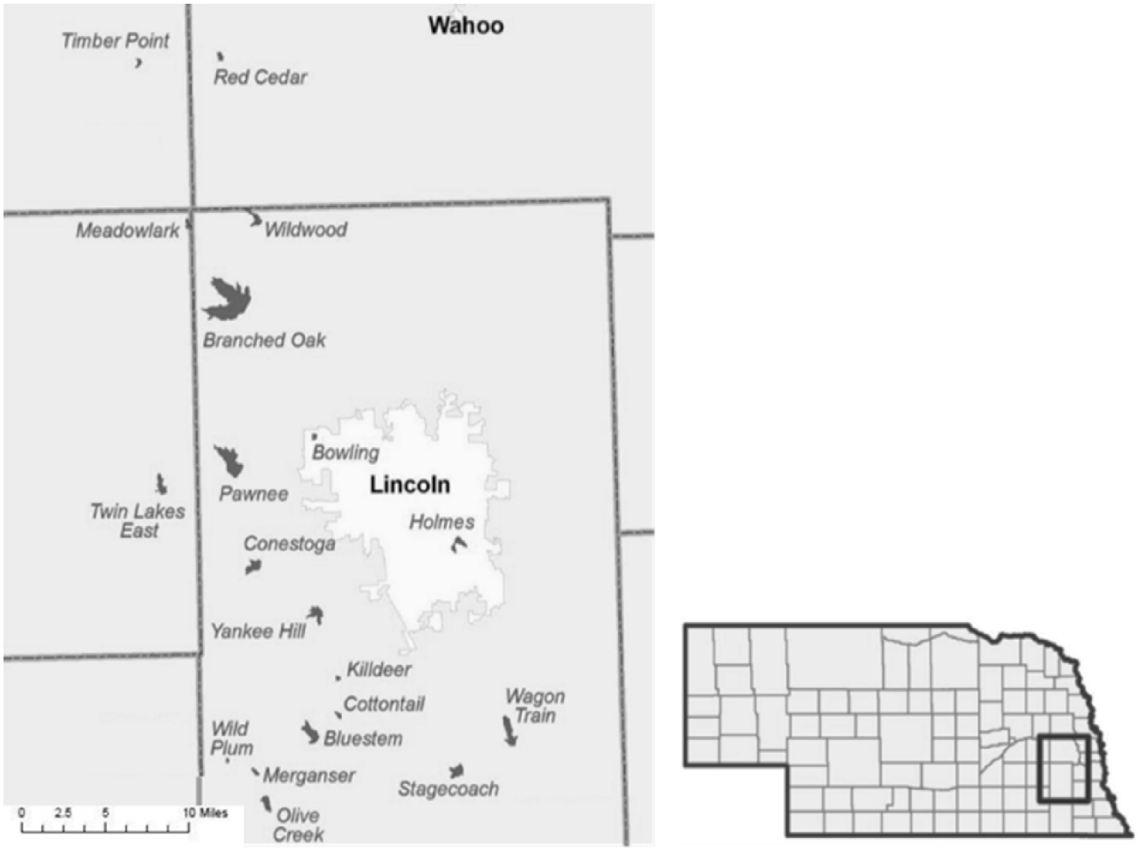

Fig. 1. Reservoir locations in the Salt Valley region of southeastern Nebraska.

Table 1
Name, area, fish community, and established aquatic invasive species of each Salt Valley reservoir. Fish with (*) are species stocked at least once since January 2010.

Reservoir (year of last renovation)	Area (km^2)	Dominant fish community	Established aquatic non-native species
Bluestem	1.32	*Lepomis macrochirus*, *Micropterus salmoides*, *Sander vitreus*, *Pomoxis spp.*, *Pylodictis olivaris*, *Ictalurus punctatus*, *Cyprinus carpio carpio*	
Bowling (2007)	0.05	*L. macrochirus*, *M. salmoides**, *I. punctatus* *, *Oncorhynchus mykiss**	
Branched Oak	7.28	*L. macrochirus*, *M. salmoides**, *S. vitreus**, *Pomoxis spp.*, *P. olivaris*, *I. punctatus**, *Ictalurus furcatus*, *C. carpio carpio*, *Morone chrysops x Morone saxatilis**, *Morone americana*	*Corbicula fluminea*, *Bellamya chinensis*, *M. americana*
Conestoga	0.93	*L. macrochirus*, *M. salmoides*, *S. vitreus**, *Pomoxis spp.*, *P. olivaris*, *I. punctatus*, *C. carpio carpio*, *M. chrysops x M. saxatilis*, *Aplodinotus grunniens*	
Cottontail (2006)	0.12	*L. macrochirus*, *M. salmoides**, *I. punctatus**, *Lepomis cyanellus*	
East/West Twin	1.09	*L. macrochirus*, *M. salmoides*, *S. vitreus**, *Esox masquinongy*, *Pomoxis spp.*, *I. punctatus**, *Ameiurus spp.*, *C. carpio carpio*	
Holmes (2004)	0.40	*L. macrochirus*, *M. salmoides*, *S. vitreus**, *I. punctatus**, *O. mykiss**	*B. chinensis*
Killdeer	0.08	*L. macrochirus*, *M. salmoides**, *Pomoxis spp.*, *I. punctatus**, *Ameiurus spp.*	
Meadowlark (2007)	0.22	*L. macrochirus*, *M. salmoides*, *Pomoxis spp.*, *I. punctatus**	
Merganser	0.17	*L. macrochirus*, *M. salmoides*, *I. punctatus**, *Ameiurus spp.*	
Olive Creek	0.71	*L. macrochirus*, *M. salmoides*, *I. punctatus**	
Pawnee	3.00	*L. macrochirus*, *M. salmoides**, *Sander canadensis*, *S. vitreus**, *Morone chrysops*, *Pomoxis spp.*, *P. olivaris*, *I. punctatus*, *C. carpio carpio*, *A. grunniens*, *M. americana*	*B. chinensis*, *M. americana*
Red Cedar	0.20	*L. macrochirus*, *M. salmoides*, *Pomoxis spp.*, *P. olivaris*, *I. punctatus*	
Stagecoach	0.79	*L. macrochirus*, *M. salmoides*, *S. vitreus**, *Pomoxis spp.*, *I. punctatus*, *C. carpio carpio*, *M. chrysops x M. saxatilis**	
Timber Point (2005)	0.11	*L. macrochirus*, *M. salmoides*, *E. masquinongy**, *Pomoxis spp.*, *I. punctatus**	
Wagon Train	1.27	*L. macrochirus*, *Lepomis microlophus*, *M. salmoides*, *S. vitreus**, *E. masquinongy**, *I. punctatus**	*B. chinensis*
Wild Plum	0.06	*L. macrochirus*, *M. salmoides*, *I. punctatus*	*B. chinensis*
Wildwood (2003)	0.42	*L. macrochirus*, *M. salmoides*, *S. vitreus**, *I. punctatus**	
Yankee Hill (2007)	0.84	*L. macrochirus*, *M. salmoides*, *S. vitreus**, *I. punctatus**	

Table 2
Betweenness, closeness, and degree values for each reservoir in the reservoir substitutability network and boater movement network.

Reservoir	Betweenness		Closeness		Degree	
	Reservoir suitability	Boater movement	Reservoir suitability	Boater movement	Reservoir suitability	Boater movement
Bluestem	37	0	0.83	0.02	19	15
Bowling	0	0	0.00	0.00	6	4
Branched Oak	8	36	0.72	0.04	25	26
Conestoga	23	20	0.89	0.03	22	21
Cottontail	15	8	0.60	0.03	19	13
East West Twin	0	0	0.00	0.00	11	8
Holmes	14	5	0.61	0.03	23	20
Killdeer	63	0	0.96	0.01	13	4
Meadowlark	21	0	0.63	0.03	15	12
Merganser	13	0	0.74	0.01	12	7
Olive Creek	21	46	0.64	0.03	27	26
Pawnee	20	17	0.48	0.04	21	19
Red Cedar	3	0	0.68	0.00	7	2
Stagecoach	3	18	0.55	0.04	23	25
Timber Point	36	29	0.68	0.03	12	18
Wagon Train	16	25	0.68	0.04	28	30
Wild Plum	93	0	0.98	0.02	15	9
Wildwood	42	28	0.79	0.04	31	27
Yankee Hill	14	28	0.59	0.04	25	25

values were collected from the literature, using values from similar aquatic ecosystems when possible (i.e., reservoirs or small lakes in the Midwestern USA). After inputs were entered, models did not always mass-balance immediately. To manually balance each model, the diet composition matrix was adjusted (never exceeding ±10% of the initial value). If necessary, small adjustments were made to input variables for which we had the least confidence (also never exceeding ±10% of the initial value) until balanced models were achieved for each reservoir.

Once mass-balanced models were developed, Ecosim was used to create dynamic models by re-expressing Equation (1) as a set of differential equations as illustrated by Equation (2).

$$\frac{dB_i}{dt} = f(B) - M_0 B_i - F_i B_i - \sum_{j=1}^{n} c_{ij}(B_i,\ B_j) \tag{2}$$

where: $f(B)$ is a function of B_i if i is a primary producer or

$f(B) = g_i \sum_{j=1}^{n} c_{ji} \times (B_i,\ B_j)$ if i is a consumer (Walters et al., 1997).

Ecosim reflects prey vulnerability when developing dynamic models, and adjusting vulnerability estimates dictates whether the model is donor-controlled or "joint limited." In donor-controlled models, consumer abundance is ignored when calculating flow from source (i) to receiver (j), and in joint-limited models, flows are adjusted based on prey and predator biomasses (Walters et al., 1997). Low vulnerability values create donor-controlled models, whereas high vulnerability values create joint-limited or "top-down" models with trophic cascades (Carpenter and Kitchell, 1993). In the current research, we discuss results based on donor-controlled models only.

Dynamic models were developed under two scenarios: 1) *Bellamya chinensis* were introduced at a density of 0.0003 t km^{-2} and projected without biomass forcing or 2) *Bellamya chinensis* were introduced at a density of 0.0003 t km^{-2} and a biomass forcing function was loaded to simulate effects resulting from snail biomasses determined by logistic growth (de Vladar, 2006) from the introduced density up to the carrying capacity. Carrying capacity was calculated for each reservoir (described in Langseth et al., 2012), using a conservative value of 10% (3.838 t km^{-2}) of the empirically calculated post-drought biomass of the *B. chinensis* population in Wild Plum of 38.58 t km^{-2} (Haak et al., 2013).

2.4. Coupling social and ecological network models

Within the framework for infectious disease modeling, we linked individual ecological reservoir models through the existing social network. We calculated the probability of *B. chinensis* from an "infected and contagious" primary host reservoir being "transmitted" (introduced) to a new "susceptible" reservoir as a result of human movement. Once *B. chinensis* "infected" a new lake, we then calculated how long it took for the population to become abundant enough so that the reservoir became "contagious" and was capable of acting as a source population. Once population size reached 10% of the estimated carrying capacity, it became a source population and the reservoir was categorized as "contagious" (Fogarty et al., 2011). Finally, we combined this information to project an invasion timeline within this group of reservoirs while also evaluating how a system's structure (biomass values) and function (energy flows) were affected by the introduction of *B. chinensis*. Mass-balanced models were extracted at 10, 15, and 20 years after the simulated invasion. Variations in how a system responded to the disturbance of an added species in the network enabled us to estimate how resilient an individual reservoir is to stressors on the system.

We estimated that the maximum percentage of live snails that could successfully be introduced to a new lake via hitchhiking on macrophytes attached to boat trailers as 0.12% (i.e., infection rate) (Johnson et al., 2001). This value gives us the propagule frequency but not the propagule size (Wittmann et al., 2014); propagule size is difficult to estimate. *Bellamya chinensis* females give live birth, and they may be carrying a number of viable juveniles at any given time (Jokinen, 1982; Stephen et al., 2013). Thus, we assume the introduction of a single individual is adequate to establish a new population. Finally, we assumed angler movement, fishing pressure, and fish stocking were all constant over time.

3. Results

3.1. Social network analysis

Of the 4601 anglers interviewed, 3746 (81%) stated they would move to another reservoir within the Salt Valley region (Fig. 2a).

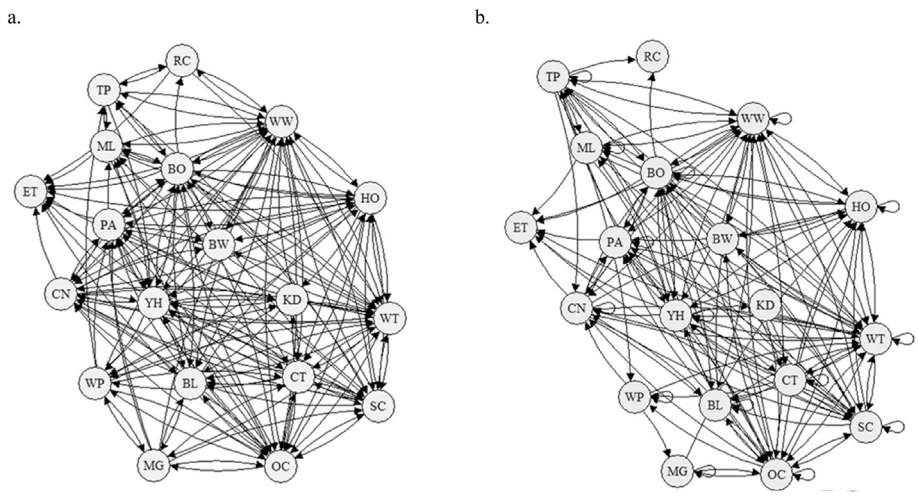

Fig. 2. a. Reservoir substitutability of anglers and b. movement of anglers using boats in Salt Valley, Nebraska. Nodes represent individual reservoirs and weighted, directed edges depict the human movement between reservoirs. Reservoir codes: Bluestem (BL), Branched Oak (BO), Bowling (BW), Conestoga (CN), Cottontail (CT), East & West Twin (ET), Holmes (HO), Killdeer (KD), Meadowlark (ML), Merganser (MG), Olive Creek (OC), Pawnee (PA), Red Cedar (RC), Stagecoach (SC), Timber Point (TP), Wagon Train (WT), Wild Plum (WP), Wildwood (WW), Yankee Hill (YH).

Betweenness values for East and West Twin Lake and Bowling Lake are zero because no in-person interviews were collected from these two reservoirs. Additionally, though there are only 19 reservoirs, the highest possible degree is 38 due to the directed nature of the network. Boat anglers were asked an additional question about which water body they last fished with their boat; 2582 responses were recorded. Of these, 1908 (74%) had last fished at a Salt Valley reservoir (Fig. 2b).

3.2. Ecological network analysis

When no biomass forcing function was used, *B. chinensis* populations stayed equal to their initial density or even decreased. There were no significant differences among comparable flow values at model years 0, 10, 15, or 20 (ANOVA, $P > 0.5$). When forcing biomass using a logistic growth model, mean flow values for consumption ($P = 0.0009$), exports ($P = 0.001$), respiration ($P = 0.00003$), production ($P = 0.0001$), flows to detritus ($P = 0.002$), and total system throughput ($P = 0.0002$) at simulation-year 20 were significantly greater than those of simulation year 0 (ANOVA followed by Tukey HSD, $P<(0.01$ for each)). Despite having significantly higher flows at simulation-year 20, there were no significant changes in network metrics of connectance index, transfer efficiency, or system omnivory index, even with biomass forcing (ANOVA, $P > 0.05$), though total system biomass (excluding detritus) significantly increased at year 20 (ANOVA, $P = 0.006$). In general, mid-trophic level fishes, such as *Pomoxis spp.*[Lesueur 1829, crappie], *Ictalurus punctatus* [Rafinesque 1818, channel catfish], and *Pylodictis olivaris* [Rafinesque 1818, flathead catfish] were negatively affected by the introduction of *B. chinensis* and showed reduced biomass values (Table 3). Piscivorous fish and terrestrial predators increased in biomass after an introduction, as did zooplankton and autotrophs.

3.3. Coupled social and ecological network models

Using the infection rate of 0.12% (Johnson et al., 2001), the lag time was calculated for each reservoir, and a map of projected invasion over the next 25 years was developed. Through this method, primary host reservoirs critical to the spread of *B. chinensis* were identified. Wagon Train, Branched Oak and Pawnee reservoirs are the top three reservoirs in which managers should prevent the snail from being transported out. Wildwood and Stagecoach are the two most important reservoirs in which managers should prevent the snail from being introduced. Wildwood and Stagecoach act as secondary hubs and aid the snail's spread to peripheral, less-visited reservoirs in the network (Fig. 3). At the end of the 25-year simulation, seven additional reservoirs were infected and contagious, and an additional three were infected.

Table 3
After the simulated introduction, a group's biomass within a lake increased, decreased, or had no change (column values are number of reservoirs that displayed each category).

Species/functional group	Increase	Decrease	No change
Ameiurus spp.	1	2	0
Aplodinotus grunniens	0	1	0
Autotrophs	12	0	2
Benthic macroinvertebrates	2	4	8
Cyprinus carpio carpio	2	0	2
Detritus	8	0	6
Esox masquinongy	2	0	0
Ictalurus punctatus	5	7	0
Lepomis macrochirus	4	3	7
Lepomis microlophus	0	1	0
Micropterus salmoides	12	2	0
Morone chrysops	0	0	1
Morone chrysops x Morone saxatilis	1	0	0
Oncorhynchus mykiss	0	0	1
Pomoxis spp.	3	7	1
Predatory birds	9	0	5
Pylodictus olivaris	1	2	0
Sander vitreus	4	2	0
Zooplankton	12	0	2

4. Discussion

Using ENA models to analyze the effects of invasive species is still a relatively new idea under development (Pinnegar et al., 2014). Miehls et al. (2009a, b) used ENA to compare ecosystems before and after a zebra mussel invasion, but because they had time series data spanning from pre-to post-invasion, they developed two static, mass-balanced models in Ecopath and compared the outputs. In contrast, Langseth et al. (2012) used EwE to develop

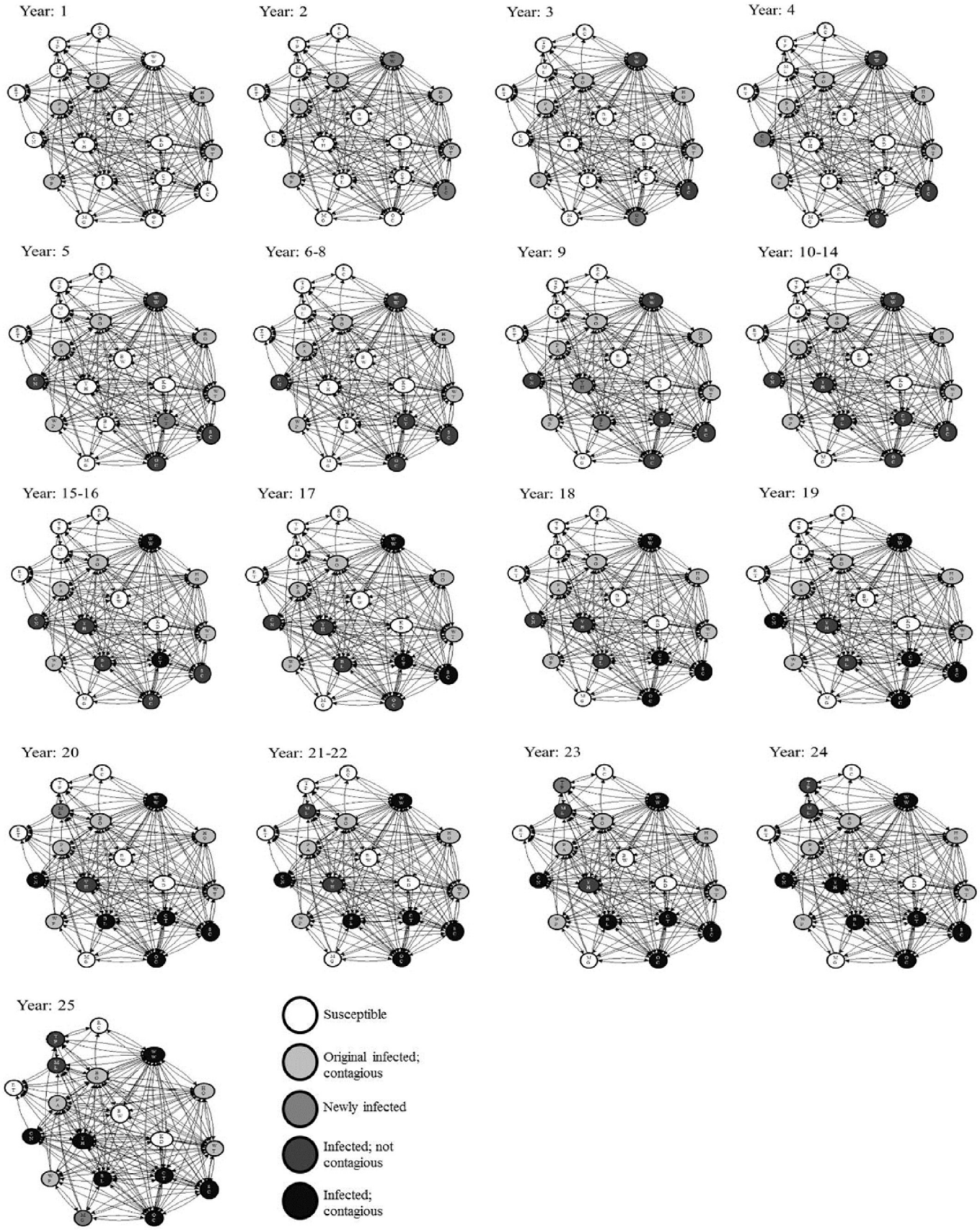

Fig. 3. Simulated invasion of *Bellamya chinensis* in the Salt Valley, Nebraska reservoirs. Consecutive years when no changes take place are grouped together.

models that mirror species invasions in Great Lakes Michigan and Huron. They too had time-series data from pre- and post-invasions; however, they tested four different methods to determine which introduction method is best when employing Ecosim to model a species' introduction to a new ecosystem. Based on the quality of the data available to us, we followed their recommendation to use biomass forcing to assess hypothetical impacts of an invasive species introduction (Langseth et al., 2012). This group also tried introducing the invasive species at a low biomass, but found they had to control the species' dynamics with an artificial fishery, which may also explain why we did not see major changes to the system when we introduced *B. chinensis* at low biomasses without the use of biomass forcing.

Though the mean flow values of total system consumption, exports, respiration, production, flows to detritus, and total system throughput were significantly higher in simulation year 20, none of the connectivity metrics commonly used to compare ecosystems were significantly different. Additionally, certain fish species were more susceptible to population declines after the introduction of the snail, though not all fish within a calculated trophic level were negatively affected. It appears *B. chinensis* causes changes to the distribution of the community's biomass, but overall function remains relatively constant despite these changes.

Previous applications of epidemiological models to ecological research have been discussed in the literature. Mack et al. (2000) discussed the theoretical similarities between epidemiological models and invasive species models. Floerl et al. (2009) modeled the spread of a hypothetical invader by hull fouling on recreational yachts in New Zealand; though this study was based on a social network of boat movement, it did not incorporate ecological networks into the analysis. Meentemeyer et al. (2011) used spatio-temporal, stochastic epidemiological modeling and geographical modeling to predict the invasion of a forest pathogen. Ferrari et al., 2014 also used epidemiology network theory to develop dynamic network models to simulate the spread of a terrestrial forest pathogen, though the pathogens in each of these examples spread independently and did not require a human network component for analyzing changes in distributions. To our knowledge, the present study is the first to apply the epidemiological model framework to an analysis including coupled social and ecological network models.

4.1. Network development

Ecopath with Ecosim has been consistently updated over the past 25–30 years and used in >150 peer-reviewed publications (Christensen and Walters, 2004); however, as with any model, some limitations exist. Ecopath provides a static "snapshot" of a mass-balanced system; it does not necessarily represent equilibrium conditions. Ideally, long-term time series data are used to fit parameters, but such data did not exist in our case. Our models represent starting points based on best current information and can be adjusted as additional empirical data become available. In fact, these models can be used to identify where the largest gaps in critical data exist. For example, there were few published reports or available data with macroinvertebrate abundance or biomass. Thus, we selected macroinvertebrates most commonly reported in the limited fish-diet data that exist and used biomass estimates from similar Midwestern reservoirs with published data. As a result, the macroinvertebrate species or functional groups included are taxonomically broad and biased toward species that are consumed by fish species receiving study and analysis. Future research would benefit from individual lake assessments, but this would increase the amount of data necessary for this approach to work.

Diet composition matrices are extremely important inputs for the development of Ecopath models, yet these proportions are estimates based on the species and functional groups included in the model. Including age stanzas to account for ontological diet changes would be beneficial but could not be included due to the uncertainty of the input data. This is another example of an existing information gap where future research could be focused to improve the current model.

In Ecosim, the vulnerability values are critical to how the model is structured. Lower vulnerability values simulate a network based on bottom-up control, and higher vulnerability values simulate a network based on top-down control (Christensen and Pauly, 1998; Ahrens et al., 2012). The vulnerability values used in the present study were estimated by the software and provide results of a donor-controlled model. Converting the Ecopath models to dynamic models in Ecosim is also complicated by temporal variation. Most likely, actual values of input parameters change over the course of a year, especially in temperate climates, but for simplicity a single value is entered for a period of one year.

The developers of EwE have actively identified strengths and weaknesses of the software as it continues to be developed (Walters et al., 1997; Pauly et al., 2000; Christensen and Walters, 2004), and reviews on the strengths and weaknesses of EwE, as well as comparisons with other ecological network models, have been published by other groups. The major strength of ecosystem network modeling, in general, is the ability to look at the system as a whole rather than limiting investigation to single-species effects; however, some caveats have been provided. When using EwE, accepting the default values provided by the software should be discretionary, and users should not use the software as a "black-box" modeling tool, especially when confidence in the data is limited (Plaganyi and Butterworth, 2004). Link et al. (2008) compared Ecopath with another software, EcoNetwrk, and found the results to be similar despite the differences underlying the models. Fath et al., 2013 compared Ecopath with the software NEA (Fath and Borrett, 2006) and found discrepancies in results between the two models, particularly with the calculated Finn's Cycling Index. In the current study, we heeded these warnings as much as possible (for example, by not including Finn's Cycling Index in the analyses).

The 25-year simulations that did not force *B. chinensis* biomass resulted in the snail either staying at a very low biomass or disappearing all together. One possibility is that we did not include all of the vital compartments specific to the functioning of that reservoir in the analysis. Nutrient concentrations and the microbial community were both excluded due to extremely low confidence in available data. Little (if any) data exist on macroinvertebrate biomass, and we could not conduct individual lake surveys for each species. This affects our ecological models because we had less confidence in biomass estimates for the lower trophic levels. However, it may also be that the reservoirs had enough functional redundancy allowing changes to ecosystem structure without changing ecosystem function.

4.2. Coupled social and ecological network models

To couple the social and ecological models, a number of assumptions were required. First, we assumed the transmission rate of 0.12% from Johnson et al. (2001) applied to *B. chinensis* movement on macrophytes attached to boat trailers. Aquatic invasive species are commonly moved by commercial and recreational boating (Schneider et al., 1998; Muirhead and Macisaac 2005). This estimate is conservative because it does not take into account other means of introduction, such as movement on wildlife or fishing gear, and it does not include intentional aquarium dumping (Padilla and Williams, 2004) or "merit releases" by people who wish to

establish a harvestable population as a food source (Vidthayanon, 2005).

Using this transmission rate, it is assumed snails will be introduced at boat landings, and subsequent populations will be found around these points in a reservoir (Rothlisberger et al., 2010). Once a lake is infected, there is a lag time before the population density is large enough to begin acting as a contagious source population.

Admittedly, this coupled approach is difficult to implement due to the data-intensive nature of the method. Collecting long-term data available on the movement of humans within a region and on the biotic community composition is a difficult task, particularly in an era of budget cuts and limited resources. In the present study, the survey data used to develop the social networks and the data on fishing pressure were collected over a four-year period as part of a PhD thesis (Martin, 2013), and not all lakes were included in each aspect of data collection, providing some limitations in the analysis. Stocking records were collected from the NGPC online database. Input data for the ecological networks were collected from empirical research on specific reservoirs, when possible, but many of the inputs were collected from research on other Midwestern USA reservoirs reported in the literature. Site-specific input data for each reservoir simply do not exist, but we tried to include values from as ecologically similar systems as possible. The resulting models are believed to be as accurate as possible with the constraints of current data availability.

4.3. Conclusions and management implications

We demonstrated that network coupling is possible and allows for the assessment of ecological resilience at a regional scale, as recommended by Pope et al. (2014). Our coupled social and ecological network approach enabled us to rank reservoirs in order of prioritization, both in terms of where invasive species management should focus on preventing individuals from leaving and where management should focus on preventing individuals from being introduced.

Based on simulations, three of the reservoirs that currently have *B. chinensis* populations and high levels of boating traffic, Wagon Train, Branched Oak, and Pawnee, are the most important source populations; preventing outgoing snails from these reservoirs will greatly limit, or at least slow, the spread of *B. chinensis* in the region. In contrast, despite having the largest population of *B. chinensis*, Wild Plum's population is of little importance in the spreading of snails through the network. If *B. chinensis* spreads in the manner suggested by simulations, then two reservoirs, Wildwood and Stagecoach, are the two invasion hubs, connecting peripheral, less-visited reservoirs to the infected and contagious reservoirs. This is indicated by their high betweenness and degree values, both for reservoir substitutability and boater movement. Additionally, these two reservoirs have high fishing pressure and close proximity to source populations. In the current model, anglers from Branched Oak infect Wildwood and anglers from Wagon Train infect Stagecoach, both in simulation year two. This is a tangible output agencies can use to ensure their efforts are as effective as possible.

This framework was implemented using *B. chinensis* as a study species, but it has the potential to be applied to other aquatic invasive species that spread via anthropogenic movement. It also helps managers identify how humans may be affecting the landscape by creating a visual representation of connection patterns that may not otherwise be apparent. Finally, this approach may be useful in determining regional effects of intentional (e.g., stocking) and unintentional (e.g., invasive species, natural disasters) disturbances.

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Appendix A. Supplementary data

Supplementary data related to this article can be found at http://dx.doi.org/10.1016/j.jenvman.2016.12.012.

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