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

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19   Abstract

20   Network analysis is used to address diverse ecological, social, economic, and

21   epidemiological questions, but few efforts have been made to combine these field-specific

22   analyses into interdisciplinary approaches that effectively address how complex systems are

23   interdependent and connected to one another. Identifying and understanding these cross-

24   boundary connections improves natural resource management and promotes proactive, rather

25   than reactive, decisions. This research had two main objectives; first, adapt the framework and

26   approach of infectious disease network modeling so that it may be applied to the socio-ecological

27   problem of spreading aquatic invasive species, and second, use this new coupled model to

28   simulate the spread of the invasive Chinese mystery snail (*Bellamya chinensis*) in a reservoir

29   network in Southeastern Nebraska, USA. The coupled model integrates an existing social

30   network model of how anglers move on the landscape with new reservoir-specific ecological

31   network models. This approach allowed us to identify 1) how angler movement among reservoirs

32   aids in the spread of *B. chinensis*, 2) how *B. chinensis* alters energy flows within individual-

33   reservoir food webs, and 3) a new method for assessing the spread of any number of non-native

34   or invasive species within complex, social-ecological systems.

35   Keywords: *Bellamya chinensis*, Chinese mystery snail, ecological network analysis,

36   epidemiological network analysis, social network analysis, Ecopath with Ecosim, aquatic

37   invasive species

38   Introduction

39   Ecologists and conservationists are challenged by the increasing, unintentional spread of

40   species from one location to another. One method to quantify how a species interacts with and

41   influences its environment is ecological network analysis (ENA). This method is particularly

42   helpful for investigating potential effects before a species has been introduced, allowing

43   managers to be proactive rather than reactive, and it acknowledges that ecosystems consist of

44   complex networks of interactions and allows for a holistic examination of the system in question;

45   we can use ENA to assess how energy flows throughout an entire food web are directly and

46   indirectly affected (Fath *et al.* 2007). Ecosystem resilience can be assessed by adding or

47   removing nodes and observing how the system reacts in a simulated future (Janssen *et al.* 2006),

48   and the strong human component embedded in the problem of spreading aquatic invasive species

49   naturally leads to a direct link with social network analysis.

50   Parallels exist between modeling the spread of invasive species and modeling the spread

51   of infectious diseases (Byers 2009; Floerl *et al.* 2009; Meentemeyer *et al.* 2011). Infectious

52   diseases spread through networks via physical contact of individuals (Meyers *et al.* 2005). The

53   transmissibility of a disease is the average probability of an infected person transmitting the

54   disease to a susceptible person through physical contact (Meyers *et al.* 2005). Network analysis

55   allows scientists to calculate how many secondary cases are likely to occur as a result of contact

56   with the primary host (Meyers *et al.* 2005), as well as the average number of connections an

57   infected host has (Hethcote 2000). Using this same framework, we calculated the probability of a

58   species (the freshwater, non-native Chinese mystery snail *Bellamya chinensis* [Reeve 1863])

59   from an "infected and contagious" primary host reservoir being "transmitted" (introduced) to a

60   new reservoir as a result of human movement. Once *B. chinensis* "infected" a new lake, we then

61 calculated how long it took for the population to become abundant enough so that the reservoir

62 became "contagious" and was capable of acting as a source population. We also monitored how

63 the introduction of *B. chinensis* affected biomass and energy flows among groups in the altered

64 ecosystem.

65 *Bellamya chinensis* is native to Asia and was first recorded in North America in 1892 as

66 an imported live food source (Wood 1892). The species has since spread to numerous lakes and

67 slow-moving rivers throughout the USA, as well as southern Canada (Olden *et al.* 2013).

68 This prosobranch, freshwater species is large, reaching shell lengths up to 70 mm, lives 4-5 years

69 (Jokinen 1982), has an annual fecundity of 30 juveniles/female (Stephen *et al*. 2013), and can

70 reach high population densities (Chaine *et al*. 2012) that fluctuate with environmental conditions

71 (Haak *et al*. 2013).

72 All Chinese mystery snails graze on algae and periphyton, but adults > 43 mm are also

73 capable of suspension feeding (Olden *et al*. 2013). When present alone, *B. chinensis* does not

74 appear to reduce native snail abundance (Solomon *et al.* 2010); however, when present with the

75 invasive rusty crayfish *Orconectes rusticus* [Girard 1852], native snail biomass decreases

76 (Johnson *et al.* 2009).

77 *Objectives*

78 A geographically focused case study is used to demonstrate how social and ecological

79 models can be used together to answer social-ecological questions. The objectives of this

80 research study were twofold: 1) couple a social network depicting human movement among

81 regional reservoirs with each reservoir's individual ecosystem network model to assess how

82 perturbations influence biomass and energy flows throughout the entire network, and 2) assess

83   the specific impacts the non-native *Bellamya chinensis* could have on the region and estimate its

84   introduction probability to individual reservoirs based on human activity.

85   Materials and methods

86   *Study area*

87   The Salt Valley region of southeastern Nebraska, USA comprises 19 reservoirs (near the

88   City of Lincoln (40.8258 N, 96.6852 W) (Fig. 1). Reservoirs range from 0.048 to 7.28 km^2 in

89   surface area and have variable fish communities and stocking regimes. Each reservoir has

90   different established aquatic invasive species (Table 1). Salt Creek runs through the Salt Valley

91   region and empties into the Platte River near Ashland, Nebraska (41.0393 N, 96.3683 W)

92   (Martin 2013).
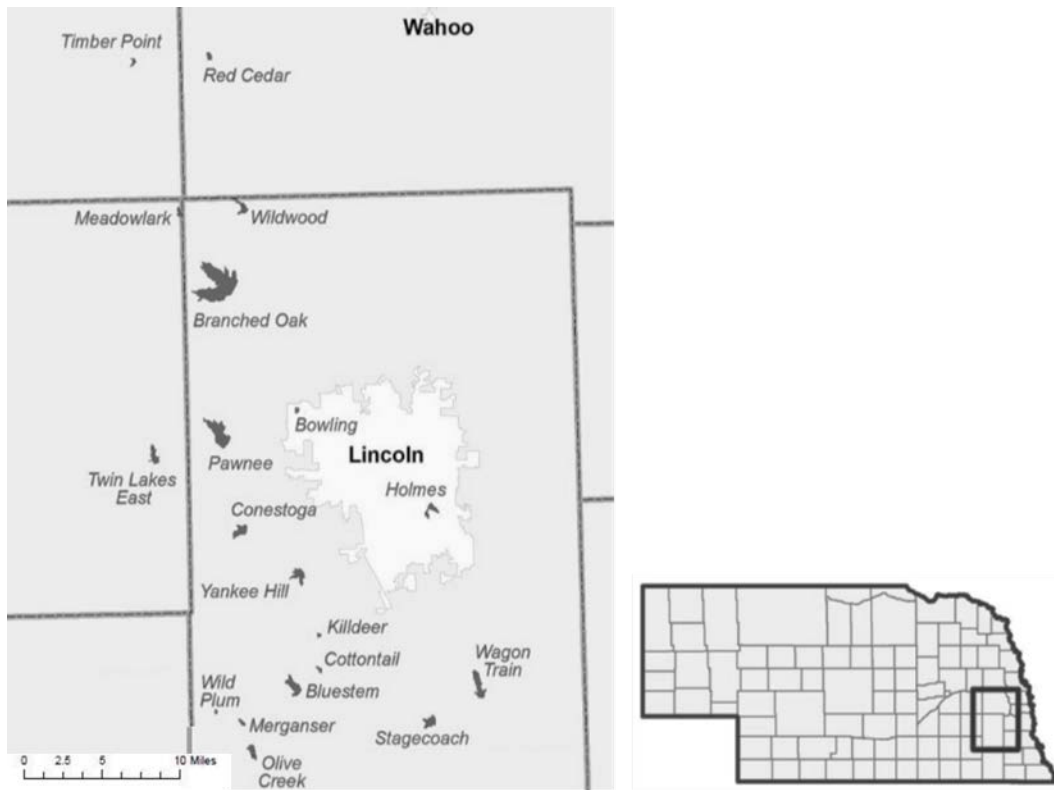
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94   Figure 1. Reservoir locations in the Salt Valley region of southeastern Nebraska.

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

98

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**	

99   Five of the 19 Salt Valley reservoirs (Branched Oak, Pawnee, Wild Plum, Wagon Train,

100   and Holmes) have established *B. chinensis* populations; however, no research has examined how

101   the snails affect energy flows within these flood-control reservoirs. Despite some species causing

102   extensive damage to their novel ecosystems, it is estimated that 90% of non-native species have

103   minimal effects in their introduced ranges (Williamson 1996). The current lack of information on

104   *B. chinensis* prompted its use in this research, as state resource managers are interested in

105   learning more about its potential impact on local ecosystems.

106   *Social network development*

107   The Nebraska Game and Parks Commission (NGPC) and Nebraska Cooperative Fish and

108   Wildlife Research Unit (NCFWRU) conducted in-person and mail-return angler surveys during

109   2009 – 2012. Data on number of anglers, angling methods, species sought, use of other Salt

110   Valley reservoirs and demographics were collected and compiled, providing raw data for the

111   social component of the current research project (Martin 2013). Experimental design, data

112   collection and results are well-documented (Chizinski *et al.* 2014; Martin *et al.* 2014).

113   Data on reservoir substitutability and angler preferences on where and how to fish were

114   obtained from the in-person angler interviews and analyzed using the iGraph package in R v3.1.1

115   (R Development Core Team 2014). Anglers were asked to identify a specific water body they

116   would go to if their current reservoir was closed. Directed connections between nodes

117   (reservoirs) were normalized to correct for different survey sizes and then weighted to depict the

118   number of anglers who moved between two particular nodes. This provided a social network of

119   how often anglers moved between and among reservoirs in the region. Boat anglers were also

120   asked where they last fished (with their boat), enabling us to create a network depicting where

121   anglers were coming from, including reservoirs and lakes outside of the current study area, a

122   critical piece of information when studying aquatic invasive species that may be passively

123   transported by humans.

124   The commonly used centrality measures of betweenness, closeness, and degree were

125   calculated for each node in the network (Table 2). Betweenness is a measure of how a node lies

126   on paths linking other reservoirs, closeness is the shortest path between two reservoirs, and

127   degree is the total number of other nodes an individual node is connected to (Daly & Haahr

128   2007). Additionally, connectance index, transfer efficiency, system omnivory index, and Finn's

129   Cycling Index values were also calculated (described in Christensen, Walters & Pauly 2005).

130   *Ecological network development*

131   If a snail is successfully transported from an infected reservoir to a susceptible reservoir,

132   then what will happen to the newly infected ecosystem? Answering this question required

133   developing ecosystem network models for each of the 19 study reservoirs. Using the dominant

134   fish community as the basis for each network (Table 1), we were able to identify and

135   compartmentalize species or functional groups critical to the trophic web of each reservoir.

136   Models were developed using the software Ecopath with Ecosim v6.4.2 (EwE) (Polovina

137   1984; Christensen & Pauly 1995). The first step was creating a static mass-balanced model of

138   each reservoir in Ecopath, based on the ecosystem's current community composition, using

139   previously identified inputs (Allen 1971; Walters, Christensen & Pauly 1997). These values,

140   combined with the fishing pressure on species within each reservoir (from the NGPC and

141   NCFWRU project), were used to develop a mass-balanced model based on Equation 1.

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

143   where: B_i is the biomass of group i; $(P/B)_i$ is the production/biomass ratio of group i; EE_i is

144   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

145   mortality due to fishing; B_j is the biomass of consumers or predators; $(Q/B)_j$ is food consumption

146   per unit of biomass of predator j; and DC_{ji} is the proportion of prey i in the diet of predator j.

147   Details on the development of this equation can be found in Christensen & Pauly (1992a, b).

148   Input data were collected from empirical studies on specific reservoirs when available;

149   however, because much of this information has never been measured for these reservoirs,

150   reported values were collected from the literature, using values from similar aquatic ecosystems

151   when possible (i.e., reservoirs or small lakes in the Midwestern USA). After inputs were entered,

152   models did not always mass-balance immediately. To manually balance each model, the diet

153   composition matrix was adjusted (never exceeding ±10% of the initial value). If necessary, small

154   adjustments were made to input variables for which we had the least confidence (also never

155   exceeding ±10% of the initial value) until balanced models were achieved for each reservoir.

156   Once mass-balanced models were developed, Ecosim was used to create dynamic models

157   by re-expressing Equation 1 as a set of differential equations as illustrated by Equation 2.

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

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

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

161   Ecosim reflects prey vulnerability when developing dynamic models, and adjusting

162   vulnerability estimates dictates whether the model is donor-controlled or "joint limited." In

163   donor-controlled models, consumer abundance is ignored when calculating flow from source (i)

164   to receiver (j), and in joint-limited models, flows are adjusted based on prey and predator

165   biomasses (Walters *et al.* 1997). Low vulnerability values create donor-controlled models,

166   whereas high vulnerability values create joint-limited or "top-down" models with trophic

167   cascades (Carpenter & Kitchell 1993). In the current research, we discuss results based on donor-

168   controlled models only.

169   Dynamic models were developed under two scenarios: 1) *Bellamya chinensis* were

170   introduced at a density of 0.0003 t km^{-2} and projected without biomass forcing or 2) *Bellamya*

171   *chinensis* were introduced at a density of 0.0003 t km^{-2} and a biomass forcing function was

172   loaded to simulate effects resulting from snail biomasses determined by logistic growth (de

173   Vladar 2006) from the introduced density up to the carrying capacity. Carrying capacity was

174   calculated for each reservoir (described in Langseth *et al.* 2012), using a conservative value of

175   10% (3.838 t km^{-2}) of the empirically calculated post-drought biomass of the *B. chinensis*

176   population in Wild Plum of 38.58 t km^{-2} (Haak *et al.* 2013).

177   *Coupling social and ecological network models*

178   Within the framework for infectious disease modeling, we linked individual ecological

179   reservoir models through the existing social network. We calculated the probability of *B.*

180   *chinensis* from an "infected and contagious" primary host reservoir being "transmitted"

181   (introduced) to a new "susceptible" reservoir as a result of human movement. Once *B. chinensis*

182   "infected" a new lake, we then calculated how long it took for the population to become

183   abundant enough so that the reservoir became "contagious" and was capable of acting as a

184   source population. Once population size reached 10% of the estimated carrying capacity, it

185   became a source population and the reservoir was categorized as "contagious" (Fogarty, Cote &

186   Sih 2011). Finally, we combined this information to project an invasion timeline within this

187   group of reservoirs while also evaluating how a system's structure (biomass values) and function

188   (energy flows) were affected by the introduction of *B. chinensis*. Mass-balanced models were

189   extracted at 10, 15, and 20 years after the simulated invasion. Variations in how a system

190   responded to the disturbance of an added species in the network enabled us to estimate how

191   resilient an individual reservoir is to stressors on the system.

192   We estimated that the maximum percentage of live snails that could successfully be

193   introduced to a new lake via hitchhiking on macrophytes attached to boat trailers as 0.12% (i.e.,

194   infection rate) (Johnson, Ricciardi & Carlton 2001). This value gives us the propagule frequency

195   but not the propagule size (Wittmann *et al.* 2014); propagule size is difficult to estimate.

196   *Bellamya chinensis* females give live birth, and they may be carrying a number of viable

197   juveniles at any given time (Jokinen 1982; Stephen *et al.* 2013). Thus, we assume the

198   introduction of a single individual is adequate to establish a new population. Finally, we assumed

199   angler movement, fishing pressure, and fish stocking were all constant over time.

200   Results

201   *Social network analysis*

202   Of the 4601 anglers interviewed, 3746 (81%) stated they would move to another reservoir

203   within the Salt Valley region (Fig. 2a). Betweenness values for East and West Twin Lake and

204   Bowling Lake are zero because no in-person interviews were collected from these two reservoirs.

205   Additionally, though there are only 19 reservoirs, the highest possible degree is 38 due to the

206   directed nature of the network. Boat anglers were asked an additional question about which

207   water body they last fished with their boat; 2582 responses were recorded. Of these, 1908 (74%)

208   had last fished at a Salt Valley reservoir (Fig. 2b).

209

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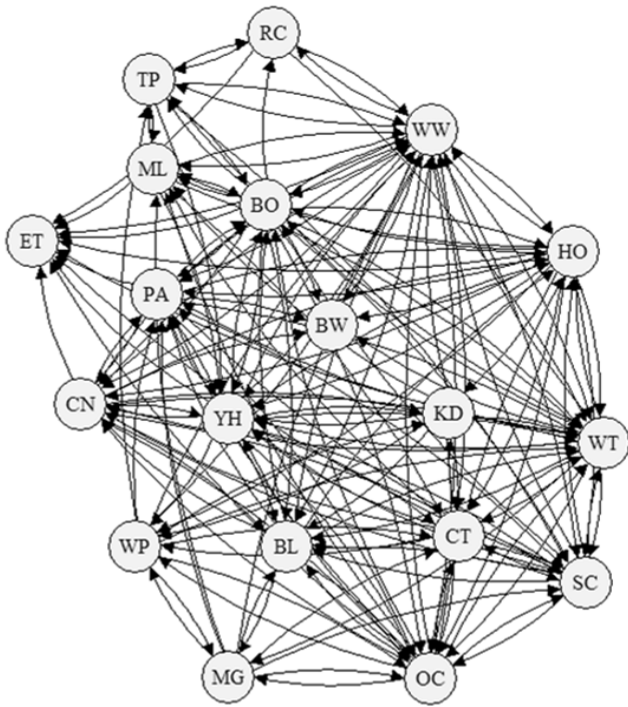
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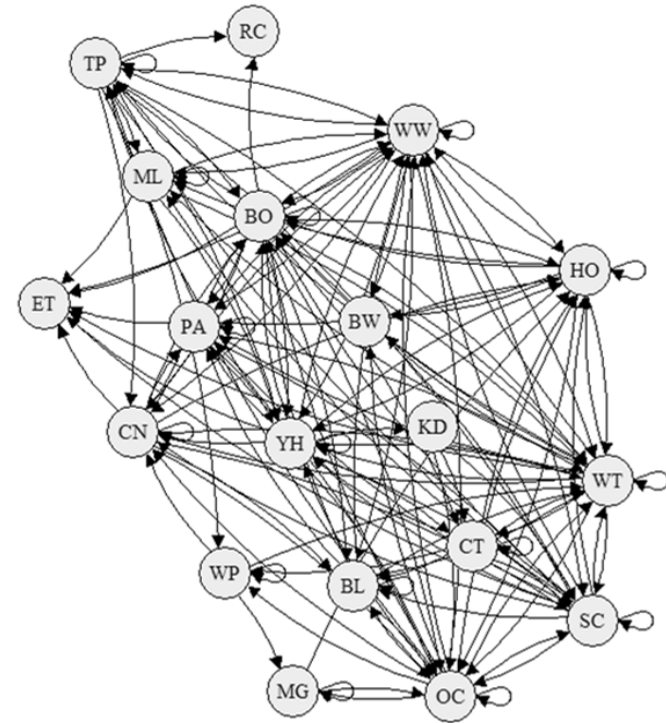
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213   Figure 2. a. Reservoir substitutability of anglers and b. movement of anglers using boats in Salt Valley, Nebraska. Nodes represent
214   individual reservoirs and weighted, directed edges depict the human movement between reservoirs. Reservoir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

218 Table 2. Betweenness, closeness, and degree values for each reservoir in the reservoir
219 substitutability network and boater movement network.
220

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

221

222 *Ecological network analysis*

223 When no biomass forcing function was used, *B. chinensis* populations stayed equal to

224 their initial density or even decreased. There were no significant differences among comparable

225 flow values at model years 0, 10, 15, or 20 (ANOVA, *P*>0.5). When forcing biomass using a

226 logistic growth model, mean flow values for consumption (*P*=0.0009), exports (*P*=0.001),

227 respiration (*P*=0.00003), production (*P*=0.0001), flows to detritus (*P*=0.002), and total system

228 throughput (*P*=0.0002) at simulation-year 20 were significantly greater than those of simulation

229 year 0 (ANOVA followed by Tukey HSD, *P*<(0.01 for each)). Despite having significantly

230   higher flows at simulation-year 20, there were no significant changes in network metrics of

231   connectance index, transfer efficiency, or system omnivory index, even with biomass forcing

232   (ANOVA, $P>0.05$), though total system biomass (excluding detritus) significantly increased at

233   year 20 (ANOVA, $P=0.006$). In general, mid-trophic level fishes, such as *Pomoxis spp.*[Lesueur

234   1829, crappie], *Ictalurus punctatus* [Rafinesque 1818, channel catfish], and *Pylodictis olivaris*

235   [Rafinesque 1818, flathead catfish] were negatively affected by the introduction of *B. chinensis*

236   and showed reduced biomass values (Table 3). Piscivorous fish and terrestrial predators

237   increased in biomass after an introduction, as did zooplankton and autotrophs.

238   Table 3. After the simulated introduction, a group's biomass within a lake increased, decreased,
239   or had no change (column values are number of reservoirs that displayed each category).
240

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

241

242

243   *Coupled social and ecological network models*

244   Using the infection rate of 0.12% (Johnson *et al.* 2001), the lag time was calculated for

245   each reservoir, and a map of projected invasion over the next 25 years was developed. Through

246   this method, primary host reservoirs critical to the spread of *B. chinensis* were identified. Wagon

247   Train, Branched Oak and Pawnee reservoirs are the top three reservoirs in which managers

248   should prevent the snail from being transported out. Wildwood and Stagecoach are the two most

249   important reservoirs in which managers should prevent the snail from being introduced.

250   Wildwood and Stagecoach act as secondary hubs and aid the snail's spread to peripheral, less-

251   visited reservoirs in the network (Fig. 3). At the end of the 25-year simulation, seven additional

252   reservoirs were infected and contagious, and an additional three were infected.
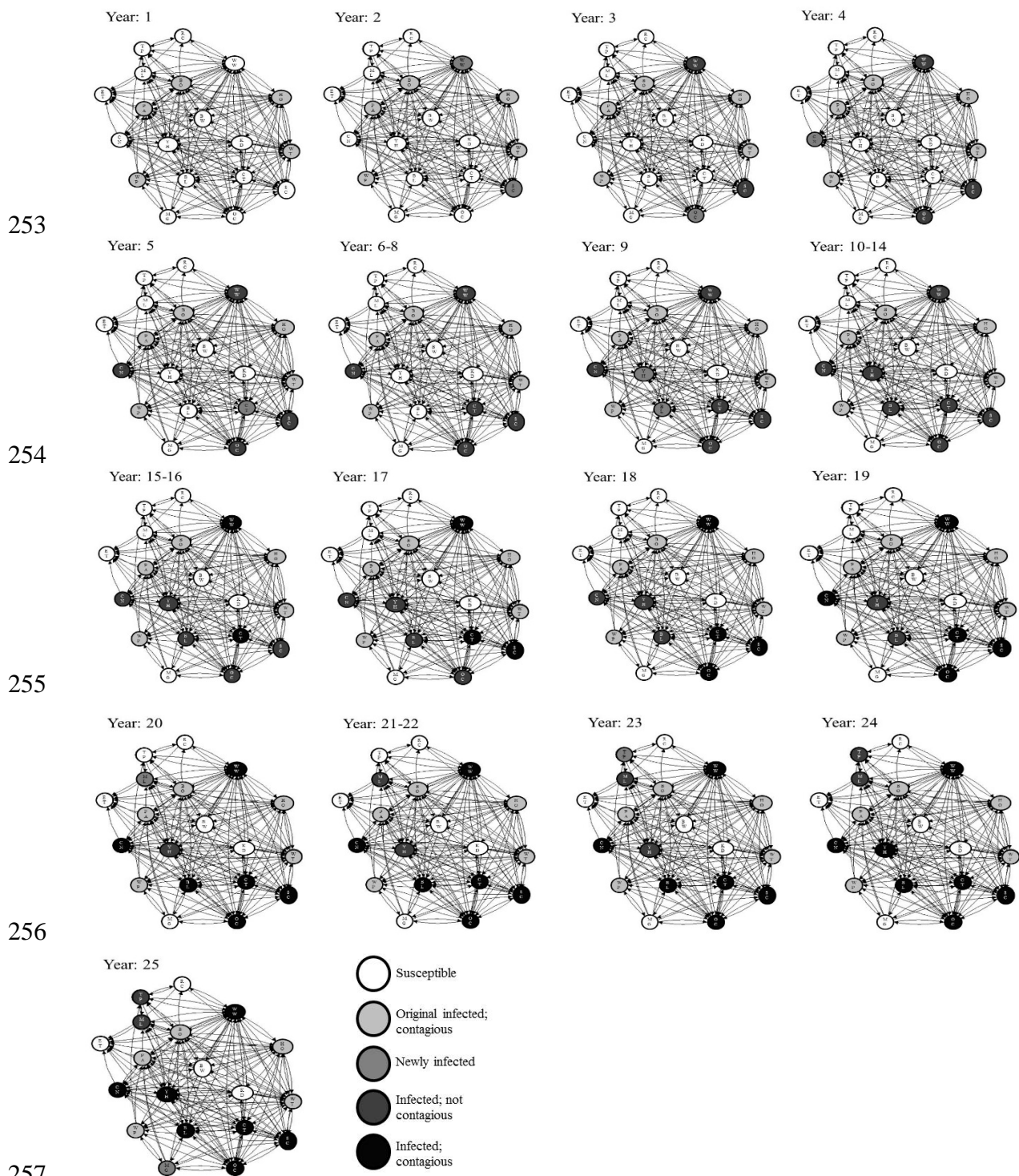
Figure 3. Simulated invasion of *Bellamya chinensis* in the Salt Valley, Nebraska reservoirs. Consecutive years when no changes take place are grouped together.

264   Discussion

265   Using ENA models to analyze the effects of invasive species is still a relatively new idea

266   under development (Pinnegar, Tomczak & Link 2014). Miehls *et al.* (2009a, b) used ENA to

267   compare ecosystems before and after a zebra mussel invasion, but because they had time series

268   data spanning from pre- to post-invasion, they developed two static, mass-balanced models in

269   Ecopath and compared the outputs. In contrast, Langseth, Rogers & Zhang (2012) used EwE to

270   develop models that mirror species invasions in Great Lakes Michigan and Huron. They too had

271   time-series data from pre- and post-invasions; however, they tested four different methods to

272   determine which introduction method is best when employing Ecosim to model a species'

273   introduction to a new ecosystem. Based on the quality of the data available to us, we followed

274   their recommendation to use biomass forcing to assess hypothetical impacts of an invasive

275   species introduction (Langseth *et al.* 2012). This group also tried introducing the invasive species

276   at a low biomass, but found they had to control the species' dynamics with an artificial fishery,

277   which may also explain why we did not see major changes to the system when we introduced *B.*

278   *chinensis* at low biomasses without the use of biomass forcing.

279   Though the mean flow values of total system consumption, exports, respiration,

280   production, flows to detritus, and total system throughput were significantly higher in simulation

281   year 20, none of the connectivity metrics commonly used to compare ecosystems were

282   significantly different. Additionally, certain fish species were more susceptible to population

283   declines after the introduction of the snail, though not all fish within a calculated trophic level

284   were negatively affected. It appears *B. chinensis* causes changes to the distribution of the

285   community's biomass, but overall function remains relatively constant despite these changes.

286   Previous applications of epidemiological models to ecological research have been

287   discussed in the literature. Mack *et al.* (2000) discussed the theoretical similarities between

288   epidemiological models and invasive species models. Floerl *et al.* (2009) modeled the spread of a

289   hypothetical invader by hull fouling on recreational yachts in New Zealand; though this study

290   was based on a social network of boat movement, it did not incorporate ecological networks into

291   the analysis. Meentemeyer *et al.* (2011) used spatio-temporal, stochastic epidemiological

292   modeling and geographical modeling to predict the invasion of a forest pathogen. Ferrari,

293   Preisser & Fitzpatrick (2014) also used epidemiology network theory to develop dynamic

294   network models to simulate the spread of a terrestrial forest pathogen, though the pathogens in

295   each of these examples spread independently and did not require a human network component

296   for analyzing changes in distributions. To our knowledge, the present study is the first to apply

297   the epidemiological model framework to an analysis including coupled social and ecological

298   network models.

299   *Network development*

300   Ecopath with Ecosim has been consistently updated over the past 25 – 30 years and used

301   in >150 peer-reviewed publications (Christensen & Walters 2004); however, as with any model,

302   some limitations exist. Ecopath provides a static "snapshot" of a mass-balanced system; it does

303   not necessarily represent equilibrium conditions. Ideally, long-term time series data are used to

304   fit parameters, but such data did not exist in our case. Our models represent starting points based

305   on best current information and can be adjusted as additional empirical data become available. In

306   fact, these models can be used to identify where the largest gaps in critical data exist. For

307   example, there were few published reports or available data with macroinvertebrate abundance

308   or biomass. Thus, we selected macroinvertebrates most commonly reported in the limited fish-

309   diet data that exist and used biomass estimates from similar Midwestern reservoirs with

310   published data. As a result, the macroinvertebrate species or functional groups included are

311   taxonomically broad and biased toward species that are consumed by fish species receiving study

312   and analysis. Future research would benefit from individual lake assessments, but this would

313   increase the amount of data necessary for this approach to work.

314   Diet composition matrices are extremely important inputs for the development of

315   Ecopath models, yet these proportions are estimates based on the species and functional groups

316   included in the model. Including age stanzas to account for ontological diet changes would be

317   beneficial but could not be included due to the uncertainty of the input data. This is another

318   example of an existing information gap where future research could be focused to improve the

319   current model.

320   In Ecosim, the vulnerability values are critical to how the model is structured. Lower

321   vulnerability values simulate a network based on bottom-up control, and higher vulnerability

322   values simulate a network based on top-down control (Christensen & Pauly 1998; Ahrens,

323   Walters & Christensen 2012). The vulnerability values used in the present study were estimated

324   by the software and provide results of a donor-controlled model. Converting the Ecopath models

325   to dynamic models in Ecosim is also complicated by temporal variation. Most likely, actual

326   values of input parameters change over the course of a year, especially in temperate climates, but

327   for simplicity a single value is entered for a period of one year.

328   The developers of EwE have actively identified strengths and weaknesses of the software

329   as it continues to be developed (Walters *et al.* 1997; Pauly *et al.* 2000; Christensen & Walters

330   2004), and reviews on the strengths and weaknesses of EwE, as well as comparisons with other

331   ecological network models, have been published by other groups. The major strength of

332   ecosystem network modeling, in general, is the ability to look at the system as a whole rather

333   than limiting investigation to single-species effects; however, some caveats have been provided.

334   When using EwE, accepting the default values provided by the software should be discretionary,

335   and users should not use the software as a "black-box" modeling tool, especially when

336   confidence in the data is limited (Plaganyi & Butterworth 2004). Link *et al.* (2008) compared

337   Ecopath with another software, EcoNetwrk, and found the results to be similar despite the

338   differences underlying the models. Fath, Scharler & Baird (2013) compared Ecopath with the

339   software NEA (Fath & Borrett 2006) and found discrepancies in results between the two models,

340   particularly with the calculated Finn's Cycling Index. In the current study, we heeded these

341   warnings as much as possible (for example, by not including Finn's Cycling Index in the

342   analyses).

343   The 25-year simulations that did not force *B. chinensis* biomass resulted in the snail

344   either staying at a very low biomass or disappearing all together. One possibility is that we did

345   not include all of the vital compartments specific to the functioning of that reservoir in the

346   analysis. Nutrient concentrations and the microbial community were both excluded due to

347   extremely low confidence in available data. Little (if any) data exist on macroinvertebrate

348   biomass, and we could not conduct individual lake surveys for each species. This affects our

349   ecological models because we had less confidence in biomass estimates for the lower trophic

350   levels. However, it may also be that the reservoirs had enough functional redundancy allowing

351   changes to ecosystem structure without changing ecosystem function.

352   *Coupled social and ecological network models*

353   To couple the social and ecological models, a number of assumptions were required.

354   First, we assumed the transmission rate of 0.12% from Johnson, Ricciardi & Carlton (2001)

355   applied to *B. chinensis* movement on macrophytes attached to boat trailers. Aquatic invasive

356   species are commonly moved by commercial and recreational boating (Schneider, Ellis &

357   Cummings 1998; Muirhead & Macissac 2005). This estimate is conservative because it does not

358   take into account other means of introduction, such as movement on wildlife or fishing gear, and

359   it does not include intentional aquarium dumping (Padilla & Williams 2004) or "merit releases"

360   by people who wish to establish a harvestable population as a food source (Vidthayanon 2005).

361   Using this transmission rate, it is assumed snails will be introduced at boat landings, and

362   subsequent populations will be found around these points in a reservoir (Rothlisberger *et al.*

363   2010). Once a lake is infected, there is a lag time before the population density is large enough to

364   begin acting as a contagious source population.

365   Admittedly, this coupled approach is difficult to implement due to the data-intensive

366   nature of the method. Collecting long-term data available on the movement of humans within a

367   region and on the biotic community composition is a difficult task, particularly in an era of

368   budget cuts and limited resources. In the present study, the survey data used to develop the social

369   networks and the data on fishing pressure were collected over a four-year period as part of a PhD

370   thesis (Martin 2013), and not all lakes were included in each aspect of data collection, providing

371   some limitations in the analysis. Stocking records were collected from the NGPC online

372   database. Input data for the ecological networks were collected from empirical research on

373   specific reservoirs, when possible, but many of the inputs were collected from research on other

374   Midwestern USA reservoirs reported in the literature. Site-specific input data for each reservoir

375   simply do not exist, but we tried to include values from as ecologically similar systems as

376   possible. The resulting models are believed to be as accurate as possible with the constraints of

377   current data availability.

378   *Conclusions and management implications*

379   We demonstrated that network coupling is possible and allows for the assessment of

380   ecological resilience at a regional scale, as recommended by Pope, Allen & Angeler (2014). Our

381   coupled social and ecological network approach enabled us to rank reservoirs in order of

382   prioritization, both in terms of where invasive species management should focus on preventing

383   individuals from leaving and where management should focus on preventing individuals from

384   being introduced.

385   Based on simulations, three of the reservoirs that currently have *B. chinensis* populations

386   and high levels of boating traffic, Wagon Train, Branched Oak, and Pawnee, are the most

387   important source populations; preventing outgoing snails from these reservoirs will greatly limit,

388   or at least slow, the spread of *B. chinensis* in the region. In contrast, despite having the largest

389   population of *B. chinensis*, Wild Plum's population is of little importance in the spreading of

390   snails through the network. If *B. chinensis* spreads in the manner suggested by simulations, then

391   two reservoirs, Wildwood and Stagecoach, are the two invasion hubs, connecting peripheral,

392   less-visited reservoirs to the infected and contagious reservoirs. This is indicated by their high

393   betweenness and degree values, both for reservoir substitutability and boater movement.

394   Additionally, these two reservoirs have high fishing pressure and close proximity to source

395   populations. In the current model, anglers from Branched Oak infect Wildwood and anglers from

396   Wagon Train infect Stagecoach, both in simulation year two. This is a tangible output agencies

397   can use to ensure their efforts are as effective as possible.

398   This framework was implemented using *B. chinensis* as a study species, but it has the

399   potential to be applied to other aquatic invasive species that spread via anthropogenic movement.

400   It also helps managers identify how humans may be affecting the landscape by creating a visual

401   representation of connection patterns that may not otherwise be apparent. Finally, this approach

402   may be useful in determining regional effects of intentional (e.g., stocking) and unintentional

403   (e.g., invasive species, natural disasters) disturbances.

404

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