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Across-ecoregion analysis suggests a hierarchy of ecological filters that regulate recruitment of a globally invasive fish

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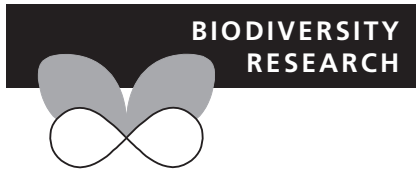
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Across-ecoregion analysis suggests a hierarchy of ecological filters that regulate recruitment of a globally invasive fish

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ABSTRACT

Aim Even successful invaders are abundant only in a fraction of locales they inhabit. One of the main challenges in invasion ecology is explaining processes that drive these patterns. We investigated recruitment of a globally invasive fish, common carp (*Cyprinus carpio*), across three ecoregions to determine the role of environmental characteristics, predatory communities and propagule pressure on the invasion process at coarse and fine spatial scales.

Location Lakes across Northern Forest, Temperate Forest and Great Plains ecoregions of North America.

Methods We used data from 567 lakes to model presence or absence of carp recruitment using environmental conditions (lake clarity, area, maximum depth), native predatory fishes (micropredators, mesopredators, large predators) and propagule pressure (abundance of adult carp). We formed a set of alternative models and evaluated their support using an information theoretic approach. Once most supported models were identified, we used classification tree to determine how variables included in these models interacted to affect carp recruitment. Finally, we conducted a field experiment to test the predictions of the classification tree analysis.

Results Carp recruitment was strongly regulated by processes associated with water clarity, which appeared to function as a broad-scale ecological filter. Carp were unlikely to recruit in clear, oligotrophic lakes (Secchi depth > 2 m) despite the presence of adults in many such systems. Recruitment was more likely to occur in regions with turbid lakes, but abundant micropredators could inhibit it there.

Main conclusions Carp recruitment and invasions across large geographic areas are attributable to a two-layer ecological filter with lake clarity/productivity acting as a coarse-scale filter and micropredators acting as a fine-scale filter. This two-layer filter might explain the complex patterns of carp invasions among and within different ecoregions. Ecological filters may also explain the success of other aquatic invaders that show similarly patchy spatial distribution patterns.

Keywords

Biological invasions, biotic resistance, *Cyprinus carpio*, ecological filters, propagule pressure.

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INTRODUCTION

A major challenge in invasion ecology is explaining the patchy nature of an invader's success across large geographic areas. Even the most successful invaders are abundant in

only a small fraction of locales they inhabit (Hansen *et al.*, 2013), suggesting the complex nature of processes that regulate invasion success. Ecological filters that operate at progressively finer scales have been used to explain the abundance and spatial composition of native species (Tonn, 1990;

Poff, 1997; Myers & Harms, 2009) and may also be useful in explaining the success of non-native species. In theory, coarse-scale filters related to fundamental environmental compatibility may make invasions possible across broad areas, whereas fine-scale filters such as predation or competition regulate invasions at specific locales (Crowl *et al.*, 2008). This approach has been adopted to explain the success of some terrestrial invaders (Funk *et al.*, 2008) and may also be useful in freshwater ecosystems where habitat patches are well defined and invasion rates high and spatially variable (Moyle & Marchetti, 2006).

Although fish invasions proceed rapidly in some ecoregions, they stall in others for reasons that are largely unknown (Kulhanek *et al.*, 2011a; Hansen *et al.*, 2013). Finding common traits of invasive fish or common features of invulnerable ecosystems to explain these patterns has proven challenging (Garcia-Berthou, 2007). The drivers of fish invasions may be more effectively identified by analysing an invader's success across large and diverse geographic areas. Such analyses are more likely to elucidate the coarse- and fine-scale ecological filters that regulate invader's success. However, fish invasions have usually been investigated within relatively small areas (but see Moyle & Light, 1996; Moyle & Marchetti, 2006; Kulhanek *et al.*, 2011b), and no studies have addressed the recruitment of invasive fish, which arguably is the most important phase of the invasion process (Miller *et al.*, 2014), across large and diverse geographic regions.

The common carp (*Cyprinus carpio*, hereafter termed 'carp') is one of the world's most invasive fish (Sorensen & Bajer, 2011). Carp were introduced throughout North America more than 100 years ago, providing ample time to establish self-sustaining populations over most of the continent. The carp is a good model for analysing processes that regulate the recruitment of invasive fish at regional and local scales because of its long history of establishment and broad geographic distribution. The life history of the common carp typifies that of many large and highly fecund fishes, some of which are also highly invasive (Chick & Pegg, 2001). Carp spawn in shallows areas where they broadcast small adhesive eggs over aquatic vegetation (Balon, 2004). Eggs hatch in a few days and develop into larvae that initially forage on zooplankton before switching to benthos (Dabrowski & Rusiecki, 1983; Weber & Brown, 2013b). Carp employ no parental care. The critical developmental period appears to last 3–4 months, after which time juvenile carp outgrow most predators and can utilize a broad range of food resources. In Australian floodplains, carp recruitment (i.e. the survival of the first few critical months of life) has been suggested to be limited by the availability of spawning habitat and larval food abundance (Wu *et al.*, 2013). Studies in lakes of the upper Mississippi River Basin in North America suggest that recruitment is sporadic and often controlled by micropredators (small sunfishes; *Lepomis* spp.) that consume carp eggs and larvae (Bajer *et al.*, 2012), while surveys of prairie lakes of South Dakota show consistent recruitment influenced

mainly by the abundance of adults and weather conditions (Phelps *et al.*, 2008; Weber & Brown, 2013a). We hypothesize that these apparently conflicting findings are attributable to regional differences in environmental conditions, predatory communities and propagule pressure that may support a common hierarchical pattern if analysed from a broad geographic perspective.

To investigate the possible hierarchy of ecological filters that regulate common carp recruitment at regional and local scales, we analysed the results of fisheries surveys across three neighbouring ecoregions in temperate North America that exhibit a wide range of environmental conditions, native predatory communities and adult carp abundance. We focused on environmental conditions related to ecosystem productivity and habitat conditions that may affect larval survival through food resources and vulnerability to predators. We split native predators into functional groups representing micropredators, mesopredators and large predators that may control different developmental stages of carp. Adult carp abundance was used to index propagule pressure (eggs). We then used model selection analysis followed by classification tree analysis to determine the main drivers of carp recruitment and the hierarchical nature of interactions among them. One of the main predictions from our analysis was tested using a field experiment. Our results suggest that the recruitment of common carp across broad and fine spatial scales can be largely explained by two ecological filters.

METHODS

Study region

Our study region encompassed a large area within the Mississippi River drainage across Minnesota, South Dakota and Nebraska, USA, and included three major ecoregions: Great Plains, Temperate Forest and Northern Forest (Fig. 1; Omerik, 2004). This region is characterized by a wide range of topography and soils ranging from forests and sandy soils in central and northern Minnesota to productive prairie ecosystems in southern Minnesota, Nebraska and South Dakota. More than 15,000 lakes and marshes over 4 ha in size occur in Minnesota (Minnesota Conservation Department, 1968). Nearly one million potholes, lakes, reservoirs and marshes occur in South Dakota, most of which are shallow, small and ephemeral, but at least 50,000 are larger than 1 ha (http://ofmpub.epa.gov/waters10/attains_state.control?p_state=SD). Lentic water bodies of Nebraska are dominated by much less numerous lakes and reservoirs (< 500 in total), many of which are larger than 1000 ha. (<http://outdoornebraska.ne.gov/fishing/programs/lakemapping/lakemapping.asp>). Lakes and reservoirs across the three ecoregions have a strong water clarity and productivity gradient. Northern Forest lakes are dominated by relatively deeper and clearer oligotrophic and mesotrophic systems. Temperate Forest lakes include mostly mesotrophic and eutrophic lakes, while Great Plains

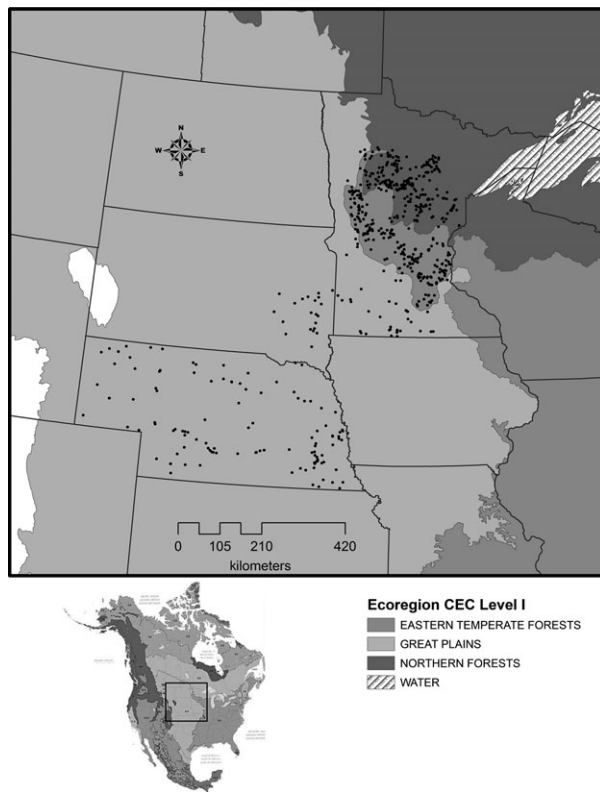


Figure 1 Study lakes (dots) within the three ecoregions.

lakes are dominated by shallow and turbid hypereutrophic prairie lakes (Heiskary & Wilson, 2008; see Appendix S1 in Supporting Information; Figs. S1, S2). Although more than 100 fish species occur within this region, native communities in lakes and reservoirs are dominated by bluegills (*Lepomis macrochirus*) that are micropredators of carp eggs and larvae (Bajer *et al.*, 2012; Silbernagel & Sorensen, 2013); white crappies (*Pomoxis annularis*), black crappies (*P. nigromaculatus*) and yellow perch (*Perca flavescens*) that are mesopredators and might potentially forage on carp larvae and fry; black bullheads (*Ameiurus melas*), yellow bullheads (*A. natalis*) and brown bullheads (*A. nebulosus*) that are benthic mesopredators; and walleye (*Sander vitreus*), northern pike (*Esox lucius*) and largemouth bass (*Micropterus salmoides*) that are top predators that might forage on larger juvenile carp (Weber & Brown, 2012). In terms of numbers, these ten species collectively comprised 80% of all fish present in fisheries lake surveys throughout the region (see below).

Carp recruitment and native fish catch rates across ecoregions

To investigate trends in carp recruitment, we analysed fish surveys conducted in 567 lakes across the three ecoregions during 1994–2011 (Table 1). These surveys were conducted by state agencies as part of routine surveys of recreational fisheries. These surveys include both gillnets and trapnets (Appendix S1). A catch per unit of effort (CPUE) was calculated for each species and net, and a mean CPUE was calculated for each species captured and each sampling gear. Because these surveys target recreational fisheries, they do not represent a random sample of lakes within the study region. Nevertheless, due to their extensive use over many years, these surveys have been shown to be important in elucidating invasion patterns (Kulhaneck *et al.*, 2011a,b). With these data, we quantified relative abundance (mean CPUE) of age-0 carp (carp < 150 mm) as an index of recruitment (Phelps *et al.*, 2008; Bajer *et al.*, 2012; Weber & Brown, 2013a), relative abundance of adult carp (carp > 300 mm) as an index of propagule pressure and relative abundance of the dominant species of native predators: bluegill, crappies (white and black combined), bullheads (black, yellow and brown combined), yellow perch, walleye and northern pike. Largemouth bass was not used in analyses because night-time electrofishing surveys are needed to accurately assess its abundance, which we lacked for most lakes. Separate CPUE estimates were derived for each year that a lake was sampled. We used gillnets to estimate the CPUEs of yellow perch, northern pike, walleye and adult carp and trapnets to estimate the CPUEs of bluegills, crappies, bullheads and age-0 carp.

Lake environmental conditions

For each lake sampled in the fish survey, we gathered existing data on summertime Secchi depth (m), maximum depth (m) and surface area (ha) (Minnesota Pollution Control Agency; South Dakota Games, Fish and Parks; Nebraska Department of Environmental Quality). We used Secchi depth to represent lake productivity and clarity because it has been shown to correlate with phosphorus concentrations, plankton biomass and fish production within the study region (Canfield Jr & Bachmann, 1981; Downing *et al.*, 1990); we were unable to use phosphorus to represent lake productivity because it was lacking for most lakes, but we verified that Secchi and total phosphorus concentrations

Table 1 Number of lakes sampled, number of observations (combinations of lakes and years), and number of instances when carp recruitment occurred (at least one age-0 carp captured in trapnets during a particular survey) in each of the three ecoregions. Also shown are median values of maximum depth (m), Secchi depth (m) and lake area (ha) in each ecoregion.

Ecoregion	Lakes	Total observations	Recruitment present	Max depth	Secchi depth	Lake Area
Great Plains	341	985	92	8.4	1.6	231.2
Temperate Forest	134	273	5	9.6	1.8	73.3
Northern Forest	92	187	1	12.6	3.0	155.6

were correlated using a subset of data for which both parameters were measured (\log_{10} Secchi = 1.26–0.62 \log_{10} total phosphorus; $\rho = -0.78$; $r^2 = 0.61$; $P < 0.001$). Maximum depth and lake area provided important information about lake morphology (e.g. shallower and larger lakes may provide more refuge areas for small carp). We used annual mean Secchi depth whenever available (39 lakes), but in most cases, only mean values over the entire sampling period (1994–2011) were available for each lake. We assumed that Secchi depth remained relatively constant in individual lakes over time. This assumption was corroborated by the data from the 39 lakes in which the range of recorded Secchi depths across different years exceeded 1 m in only four cases and in most cases was less than 0.5 m. Maximum depth and surface area were also assumed to be constant for each lake.

Analysis of carp recruitment across ecoregions

We examined patterns in carp recruitment across the three ecoregions using scatter plots and assessed correlations among predictor variables using Spearman's correlation coefficients. Initial assessments indicated that age-0 carp were captured in a relatively small number of lakes, suggesting that carp recruitment occurs infrequently (Figs S3, S4). Thus, we used logistic regression to predict the occurrence of carp recruitment as a binomial variable. We hypothesized that carp are more likely to recruit in lakes that have lower Secchi depths due to higher productivity, more abundant planktonic food resources for their larvae and/or lower visibility to sight predators. Similarly, we also hypothesized that lakes with lower maximum depths and larger areas include larger littoral areas where juvenile carp are more likely to find shelter from predators. Higher propagule pressure was expected to increase the probability of the occurrence of recruitment. Micropredators (bluegills), mesopredators (crappies, bullheads and yellow perch) and large predators (northern pike and walleye) were expected to decrease the probability of carp recruitment.

We developed a set of hypotheses to explain recruitment using different plausible combinations of environmental conditions, propagule pressure and various forms of predation as suggested by the literature. For example, we included Secchi depth, maximum depth, lake area and bluegill CPUE to test whether recruitment was attributable to environmental conditions and abundance of micropredators. Similarly, we included adult carp CPUE, northern pike CPUE and walleye CPUE to evaluate whether recruitment was attributable to propagule pressure and large predators. In all, 26 competing hypotheses (models) were developed using different combinations of predictor variables that were deemed biologically relevant (Table 2). In addition, each model also included ecoregion as a fixed effect and lake as a random effect because lakes were sampled more than once. Due to large number of zeros, all numerical predictor variables were evaluated for overdispersion and $\log_e(x + 1)$ -transformed if necessary to ensure that dispersion parameters were 1 ± 0.25 for each variable.

Support for each of the 26 models was evaluated using log likelihood values, Akaike's information criterion (AIC) scores and Akaike's weights (Burnham & Anderson, 2002). To rank models, we used 'AICcmodavg' package (Mazerolle, 2013) in R (R Development Core Team, 2013). To assess the overall model fit, we analysed the deviance of the best model as compared to that of the null (intercept) model and conducted concordance analysis to determine the accuracy with which the best model predicted the presence and absence of carp recruitment. To conduct the concordance analysis, we adjusted the intercept of the model using correction procedure for rare events data (King & Zeng, 2001). In this approach, the intercept β_0 is adjusted as follows: $\beta_0 - \ln \left[\frac{(1-\tau)}{\tau} \left(\frac{\bar{y}}{1-\bar{y}} \right) \right]$; where $\tau = 0.28$ is a fraction of events in population (the rate with which recruitment would occur in a random sample of lakes), which we estimated using data reported in Bajer *et al.* (2012) and Weber & Brown (2013a), and $\bar{y} = 0.068$ is fraction of events in sample (lake surveys used in this study). In the case of this study, the fraction of events (recruitment occurrence) was lower than expected because fisheries surveys often focus on lakes with abundant sport fish populations and rarely include seasonally unstable marshes where carp are more likely to recruit (Bajer *et al.*, 2012). While the intercept needed to be adjusted, undersampling of carp recruitment events does not change the coefficients or biological significance of predictor variables used in the model (King & Zeng, 2001).

To visualize how variables included in the best models ($\Delta AIC < 2$) regulate carp recruitment, we developed scatter plots and conducted a classification tree analysis using these variables. Classification tree analysis was especially helpful in visualizing the hierarchical nature of processes that control carp recruitment (ecological filters) by suggesting natural splits in the data that explain the presence or absence of carp recruitment (De'Ath, 2002). The classification tree was developed using 'rpart' package (Therneau *et al.*, 2014) in R. Once the tree was 'grown', it was 'pruned' to a size that minimizes the cross-validation error to avoid overfitting (De'Ath, 2002).

Field experiment

We conducted a field experiment to test the hypothesis identified by our ecoregion analysis that while carp recruitment is likely to occur in turbid and productive lakes, it can be overridden by micropredators. We constructed experimental arenas (20 m in diameter impermeable enclosures; Fig. S8) in two productive lakes in southern Minnesota: Lake Casey (mean summer Secchi depth = 0.19 m) and Lake Staring (mean summer Secchi depth = 0.49 m). Four enclosures were built in each lake in early spring and cleared of native fish. Two enclosures in each lake were stocked with approximately 150 bluegills (70 mm to 180 mm) to achieve a biomass of approximately 150 kg ha⁻¹ (Bajer *et al.*, 2012). One week later, the enclosures were stocked with the same number of carp eggs each; the number of eggs per enclosure varied between 120,000 and 240,000 between years. The eggs

Table 2 Results of model selection analysis. Environmental variables included Secchi depth (m), maximum depth (m) and lake area (ha); adult carp CPUE was used as a proxy for propagule pressure; bluegill CPUE was used as proxy for micropredators; mesopredators were represented by crappie spp. CPUE, yellow perch CPUE and bullhead spp. CPUE; large predators were represented by northern pike CPUE and walleye CPUE. ‘Environmental’ indicates that all three environmental variables were included in the model; ‘All predators’ indicates that all species of micro-, meso- and large predators were included in the model. In addition, all models included fixed ecoregion effect and a random lake effect.

Model	<i>K</i>	AICc	Δ_i	w_i	$w_i +$	log (<i>L</i>)
Environmental, propagule, micropredators	9	709.35	0.00	0.42	0.42	−345.61
Environmental, propagule	8	709.91	0.56	0.31	0.73	−346.91
Environmental	7	711.26	1.91	0.16	0.89	−348.59
Environmental, propagule, mesopredators	12	713.55	4.20	0.05	0.94	−344.67
Environmental, propagule, large predators	10	713.92	4.56	0.04	0.98	−346.88
Global	14	717.61	8.25	0.01	0.99	−344.66
Secchi, depth, micropredators, propagule	8	718.61	9.26	0.00	0.99	−351.26
Environmental, all predators	13	719.01	9.66	0.00	1.00	−346.38
Secchi, depth, micropredators	7	719.91	10.61	0.00	1.00	−352.94
Secchi, depth	6	723.04	13.68	0.00	1.00	−355.49
Secchi, propagule, micropredators	7	726.63	17.28	0.00	1.00	−356.28
Secchi, depth, all predators	12	727.59	18.24	0.00	1.00	−351.69
Secchi, micropredators	6	728.75	19.40	0.00	1.00	−358.35
Depth, area	6	731.37	22.02	0.00	1.00	−359.66
Secchi	5	733.39	24.03	0.00	1.00	−361.67
Depth, micropredators	6	738.83	29.48	0.00	1.00	−363.39
Depth	5	742.08	32.72	0.00	1.00	−366.02
Propagule, micropredators	6	794.44	85.09	0.00	1.00	−391.19
Propagule, all predators	11	795.36	86.01	0.00	1.00	−386.59
Propagule, mesopredators	9	795.84	86.49	0.00	1.00	−388.86
Propagule, large predators	7	799.65	90.30	0.00	1.00	−392.79
Propagule	5	801.23	91.88	0.00	1.00	−395.60
All predators	10	804.52	95.17	0.00	1.00	−392.19
Micropredators	5	804.75	95.40	0.00	1.00	−397.35
Mesopredators	8	806.48	97.13	0.00	1.00	−359.19
Large predators	6	807.45	98.10	0.00	1.00	−397.70

were collected with vegetation from a carp-spawning area. The experiment was conducted in only one of the two lakes in a given year: four enclosures (2 bluegills and 2 controls) were used in Casey in 2011; four enclosures (2 bluegills and 2 controls) were used in Lake Staring in 2012, 2013 and 2014. For details see Appendix S1.

We conducted five backpack electrofishing surveys (a single pass through entire enclosure) to estimate the recruitment of carp in each enclosure starting in late June and continuing through July at weekly intervals (carp captured during these surveys were released back into the enclosures). We counted all carp to calculate CPUE values, which were then averaged among the five surveys to represent mean annual CPUE for each enclosure. Mean annual CPUEs for each enclosure were averaged among the two replicates resulting in one CPUE estimate for bluegill enclosures and one for control enclosures for each year, or four such values in total for each treatment (one for each year) for the entire experiment. We then used a t-test to determine whether the mean common carp CPUE was different in control ($N = 4$) versus bluegill ($N = 4$) enclosures.

RESULTS

Ecoregion analysis

A total of 567 lakes sampled between 1994 and 2011 were used in this analysis resulting in 1445 observations (combinations of lakes and years). Age-0 common carp were captured (i.e. recruitment occurred) in 98 cases (6.8%; Table 1). The majority of recruitment events occurred in the Great Plains ecoregion ($N = 92$), followed by the Temperate Forest ecoregion ($N = 5$), and only one was noted in the Northern Forest ecoregion (Table 1; Figs. S3, S4). Carp recruitment occurred primarily in lakes that had low Secchi depths, were shallow and had low catch rates of native fish (Figs. S3, S4). Adult carp were captured in 463 instances (403 in Great Plains ecoregion, 57 in Temperate Forest ecoregion and 3 in Northern Forest ecoregion).

Environmental conditions varied considerably among individual lakes within each ecoregion (Table 1; Figs. S1, S2). Median values suggested that lakes of the Great Plains ecoregion tended to be larger, shallower and had lower Secchi

depths than lakes of the Temperate Forest or Northern Forest ecoregions (Table 1; Figs. S1, S2). Great Plains lakes also tended to have higher catch rates of adult carp (Fig. S1). Catch rates of native predators varied by more than an order of magnitude within each ecoregion, especially in Great Plains lakes (Fig. S2). Median CPUEs suggested that Great Plains lakes tended to have lower bluegill and northern pike CPUE and higher yellow perch and walleye CPUE than lakes of the Temperate and Northern Forest ecoregions (Fig. S2). A correlation matrix indicated that Secchi depth was positively correlated with maximum depth ($\rho = 0.70$) and northern pike CPUE ($\rho = 0.55$) and negatively correlated with adult carp CPUE ($\rho = -0.54$). Lake area was positively correlated with walleye CPUE ($\rho = 0.53$). Other correlation coefficients did not exceed $\rho = 0.5$ (Fig. S5).

Model selection analysis indicated that carp recruitment was influenced mainly by processes associated with lake productivity and morphology, propagule pressure and the abundance of micropredators while the abundance of mesopredators and large predators was less important (Table 2). The most supported model included the three environmental variables (i.e. Secchi depth, maximum depth and lake area), adult carp CPUE and bluegill CPUE (Table 2). The second most supported model included the combination of the three environmental variables and adult carp CPUE, while the third best model included just the three environmental variables (Table 2). All three of these models were similarly supported by the data ($\Delta AIC < 2$). Other models were less supported by the data ($\Delta AIC > 2$; Table 2). Because the three best models all included the

three environmental variables (Secchi depth, maximum depth and lake area), these variables appeared to be the main drivers of carp recruitment. Null deviance suggested that the most supported model was significantly better than the intercept-only model ($\chi^2 = 333.1$, d.f. = 7, $P < 0.001$). Concordance analysis indicated that the most supported model correctly predicted 62 of the 98 (62%) positive recruitment events and correctly predicted 1228 of the 1347 (91%) of negative events using recruitment occurrence probability of 0.5 as a cut-off.

Scatter plots developed for variables included in the three best models showed that recruitment occurred primarily in the Great Plains lakes with Secchi depth < 1 m, which also tended to be relatively shallow (Fig. 2). In these systems, recruitment occurred over a wide range of lake sizes, adult carp CPUEs and bluegill CPUEs, although recruitment was especially common in lakes with bluegill CPUE values below 10 (Fig. 2). With only one exception, no recruitment occurred in lakes in which Secchi depths exceeded 2 m, regardless of their depth, size, adult carp CPUE or bluegill CPUE (Fig. 2; Fig. S6).

The most parsimonious classification tree included two data splits. It suggested that carp recruitment was most likely to occur in systems where summer Secchi depths declined below 0.29 m, and less likely to occur in lakes in which Secchi depths exceeded 0.29 m (Fig. 3). Further, within the first group of lakes (Secchi < 0.29 m), recruitment was more likely to occur in systems in which bluegill CPUEs values were below 1.6 and less likely to occur in systems in which bluegill CPUE exceeded 1.6 (Fig. 3). At the first split, the

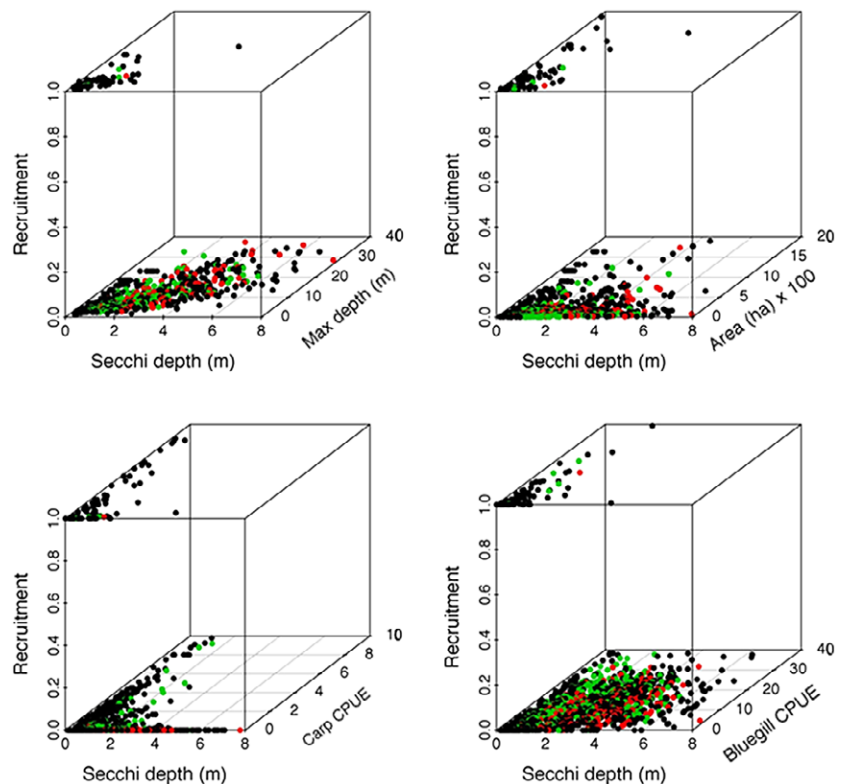


Figure 2 Relationships between common carp recruitment, Secchi depth (m), maximum depth (m), area (ha), adult carp CPUE and bluegill CPUE. Black circles indicate lakes of the Great Plains ecoregion, green circles indicate lakes of the Temperate Forest ecoregion, and red circles indicate lakes of the Northern Forest ecoregion. Rare events (maximum depth > 40 m, area > 2000 ha, adult carp CPUE > 10 , bluegill CPUE > 50), which comprised less than 1% of the data, are not plotted for clarity.

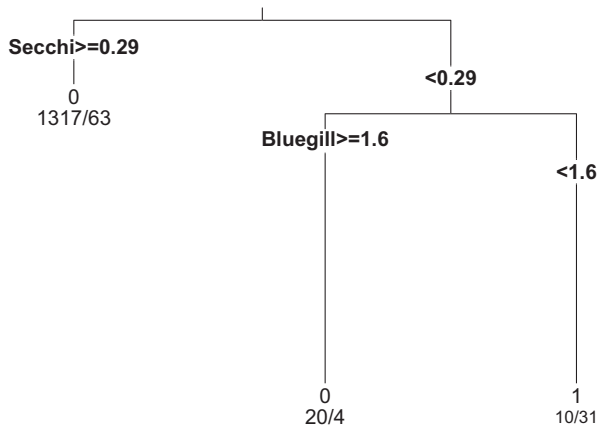


Figure 3 ‘Pruned’ classification tree showing hierarchical effect of Secchi depth (m) and bluegill CPUE on the occurrence of common carp recruitment. Nodes that split to the left show that recruitment was unlikely to occur, while nodes that split to the right show that recruitment was likely to occur. Numbers show sample size (no recruitment/recruitment) at each node.

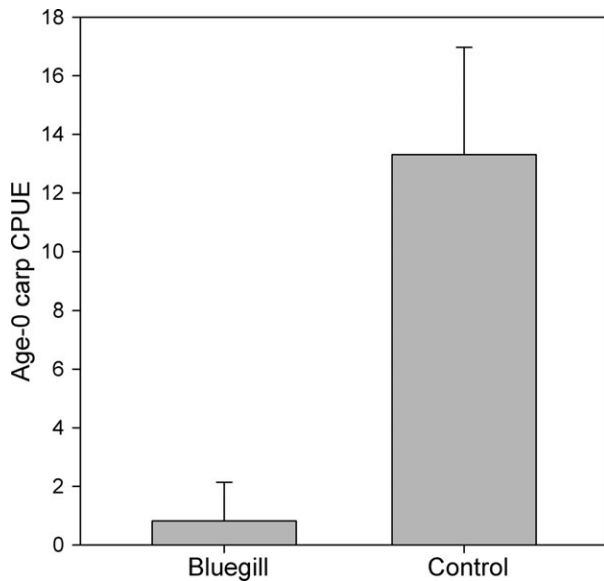


Figure 4 Mean electrofishing catch per unit of effort (CPUE) of age-0 common carp in experimental enclosures stocked with bluegills or in controls that had no native fish (both treatments were initially stocked with the same number of carp eggs); $N = 4$ per treatment.

classification tree correctly classified 95% of negative recruitment events (1317 of 1380) and 54% of positive events (35 of 65). At the second split, the classification tree correctly classified 83% of negative events (20 of 24) and 76% of positive events (31 of 41; Fig. 3)

Experiment

In 2011 and 2013, experimental enclosures were overtopped by water following torrential rains after only two

electrofishing surveys were collected. These two surveys were used to estimate age-0 carp CPUE in each of the enclosures. In addition, two enclosures (one control and one treatment) were damaged in 2013 before any data were collected (these enclosures were not used in the analysis). In 2012 and 2014, the experiment ran a full course. Both in 2011 and 2013, no carp were captured in the enclosures stocked with bluegills (CPUE = 0), while on average, approximately 15 carp were captured per survey in the control enclosures. In 2012, the mean electrofishing catch rate of age-0 carp in bluegill enclosures was 2.78, while it was 14.8 in the control enclosures. In 2014, these values were 0.5 in bluegill enclosures and 7.9 in control enclosures. When averaged across all 4 years, the mean catch rate of carp in bluegill enclosures was significantly lower (mean = 0.82; SD = 1.32; $N = 4$) compared to control enclosures (mean = 13.31; SD = 3.66; $N = 4$; $t = 6.41$, d.f. = 3.77, $P = 0.004$; Fig. 4).

DISCUSSION

This study suggests that the recruitment of a globally invasive fish, the common carp, across large geographic areas is attributable to a hierarchy of at least two ecological filters. We propose that processes related to lake productivity and water transparency act as a broad-scale filter that makes recruitment likely to occur within regions with productive, turbid lakes but unlikely to occur in non-productive regions with clear lakes (regardless of other conditions such as predator abundance or propagule pressure). The occurrence of carp recruitment within productive lakes is further regulated by the abundance of micropredators, which act as a local (i.e. lake level) ecological filter. Ecological filters have been previously suggested to play an important role in fish invasions (Crowl *et al.*, 2008). For example, Tucker *et al.* (2010) demonstrated that ultraviolet radiation curbs the invasion of clear-water lakes by the bluegill, whereas Kelly (2014) suggested that environmental thermal extremes facilitate ectotherm invasions. Invasive fish themselves have been suggested to act as an ecological filter, limiting native diversity in Iberian reservoirs (Clavero & Hermoso, 2011). This study advances our understanding of ecological invasion filters by identifying two important filters that explain a large amount of variation in invader’s recruitment across several ecoregions.

The most novel of our findings is that carp recruitment appears to be regulated by processes associated with water clarity. Several hypotheses might explain this relationship. Secchi depth often reflects both water transparency and productivity (Canfield & Bachmann, 1981), and we suspect that both of these properties have several important effects on carp recruitment. First, carp larvae are small (~5 mm in length) and forage on smaller zooplankton organisms for the first few days after hatching (Dabrowski *et al.*, 1983; Khadka & Rao, 1986; Opuszynski & Shireman, 1994). The abundance of zooplankton is often lower in clear oligotrophic lakes (McCauley & Kalff, 1981; Pace, 1986), so larval carp may

experience slower growth rates in such systems. Smaller body size is likely to increase the vulnerability of larval carp to sight predators in these clear-water systems, especially given the lack of parental care in this species. Larval carp may also experience higher mortality rates in oligotrophic lakes due to nutritional deficiencies, although dietary requirements of larval carp have not been sufficiently described in natural lakes to address this possibility.

This study raises the question of possible interactions between lake trophic status and the carp's ability to facilitate its own invasions through niche construction mechanisms. The common carp is known to increase water turbidity and nutrient concentrations due to its benthic feeding habits (Schrage & Downing, 2004; Weber & Brown, 2009). Accordingly, one might hypothesize that the survival of carp eggs and larvae is enhanced in systems modified by the foraging activity of adults. However, several pieces of evidence suggest that carp invasions are regulated primarily by regional differences in water productivity rather than niche construction abilities. First, current maps of carp biomass (Kulhanek *et al.*, 2011a) closely reflect pre-settlement phosphorus concentrations that were at least twice as high in the Great Plains lakes than in the Northern Forest lakes (Ramstack *et al.*, 2004). These differences persist to the present day. Further, palaeolimnological data suggest that many lakes of the Great Plains ecoregion had poor water clarity even before carp introduction creating receptive conditions for carp invasion (Ramstack *et al.*, 2004; Heiskary & Wilson, 2008). Similar conditions are not thought to have occurred in lakes of the Northern Forest ecoregion (Ramstack *et al.*, 2004; Heiskary & Wilson, 2008). Finally, carp recruitment is usually highest when the density of adults is low; thus, niche construction effects are negligible (Bajer *et al.*, 2009; Weber & Brown, 2013a). Although the carp can modify habitats it invades and might in some circumstances promote its own success, its invasions seem to follow pre-existing patterns in nutrient concentration. Thus, pre-invasion productivity conditions could be used to predict which habitats are likely to be invaded by this species.

This study advances our understanding of micropredation (predation on eggs, larvae and early juveniles) in controlling aquatic invasions. Our analysis suggests that within productive ecoregions, carp recruitment can be suppressed by a high abundance of bluegills. Bluegills are effective predators of carp eggs and larvae (Bajer *et al.*, 2012; Silbernagel & Sorensen, 2013) and are abundant throughout much of the eastern United States (Becker, 1983; Rahel, 1984; Bachmann *et al.*, 1996). They are abundant across a broad range of lake trophic levels, including hypereutrophic systems (Bachmann *et al.*, 1996; Fig. S7), suggesting potentially wide-ranging effects. However, in northern regions, such as our study area, bluegill populations often decline in individual lakes as a result of winter hypoxia (Rahel, 1984; Bajer *et al.*, 2012) that occurs with varying severity among lakes and years. Due to this patchy nature of abundance, we propose that bluegills function as a local (lake level) filter of carp recruitment, with hypoxia-prone systems comprising carp nurseries within larger systems of productive lakes

(Bajer & Sorensen, 2010). Whereas bluegills are important in curbing aquatic invasions in lakes of the American Midwest (Hein *et al.*, 2007), other micropredators may increase biotic resistance elsewhere. For example, eastern mosquitofish (*Gambusia holbrooki*) has been shown to curb the success of small-bodied invasive fish in Florida (Thompson *et al.*, 2012). Whether micropredators play an especially important role in controlling aquatic invasions warrants further attention, but this hypothesis is supported by the fact that they tend to be more abundant than larger predators and target the earliest life stages of the invader.

Propagule pressure has been suggested to play a key role in biological invasions of both plants and animals (Holle & Simberloff, 2005; Simberloff, 2009). Because propagule pressure is able to overwhelm biotic resistance in some communities (Holle & Simberloff, 2005; Hollebone & Hay, 2007), it is prudent to restrict the number or size or propagules to reduce invasion risk (Ricciardi, 2006). Our results indicate that carp recruited only in a small number of instances (6.8% of all lake-year combinations) even though adults were captured in nearly half the lakes (Figs. S3, S6). The rarity of carp recruitment, despite the presence of adults, suggests that propagule pressure might be important only if other, more fundamental conditions such as high lake productivity and low abundance of micropredators are met (Bajer & Sorensen, 2010). In productive systems with few micropredators, even low propagule pressure may cause carp invasions (Weber & Brown, 2013a). On the other hand, we hypothesize that propagule pressure alone is unlikely to result in carp invasions in systems that have abundant micropredators and/or low productivity.

Our analysis suggests that meso- and large predators play a less important role in controlling carp recruitment than micropredators. Evidence from prairie pothole lakes supports this conclusion by showing that communities dominated by large predators, such as walleye, but which have few bluegills, have low ability to control carp recruitment (Weber & Brown, 2013a). Largemouth bass, a top predator in many lakes of the region, was not included in our analyses due to limited night-time electrofishing data. However, a post hoc analysis using gillnet catch rates as a proxy suggested that the addition of largemouth bass to our best model did not improve model performance (AICc increased by 1.8 and log likelihood remained the same). Meso- and large predators may have an important additive effect on carp recruitment by controlling larger individuals that escape micropredators. However, behavioural interactions among predators and intraguild predation could reduce biotic resistance in ways that are not intuitive. Studies of biocontrol suggest that adding a top predator may suppress small predators (Müller & Brodeur, 2002; Vance-Chalcraft *et al.*, 2007) and that functional traits of predators are often more important than the diversity of predatory community (Straub *et al.*, 2008). We propose experimental tests to document differences in the ability of native micro-, meso- and large predators to locate and consume carp eggs, larvae and juveniles (Weber & Brown, 2012; Silbernagel & Sorensen, 2013). We suggest that differ-

ent combinations of predators should be tested for biotic resistance over a gradient of lake productivities using realistic field settings.

Although it is an apparent enigma that adult carp are often found in many lakes in the absence of young, this species' life history may offer explanations. First, in ecologically stable systems with abundant micropredator populations, carp populations can be sustained by extremely low recruitment rates that are unlikely to be detected using routine sampling. Such populations are rarely invasive and are characterized by few carp whose life span can exceed several decades. Second, in chains of productive lakes that include both ecologically stable basins of high biotic resistance and lakes that are ecologically unstable (e.g. winterkill-prone) and lack micropredators, age-0 carp are typically captured only in the unstable basins, while adults occur/move throughout (Bajer & Sorensen, 2010). Finally, in productive systems in which biotic resistance is generally weak due to frequent hypoxia, such as some of the prairie lakes in which bluegill populations are chronically low, recruitment can be pervasive with adults and recruits routinely captured in most lakes (Weber & Brown, 2013a). Given these nuances of carp population dynamics, we suggest that future surveys of carp recruitment across landscapes target a representative diversity of water bodies, including shallow marshes and wetlands that have rarely been included in standardized fish surveys.

Across a wide range of taxa, invasive species are abundant in less than ten per cent of sites to which they are introduced (Hansen *et al.*, 2013). Analyses that span broad geographic areas and incorporate both abiotic and biotic processes (cross-site heterogeneity is unlikely to be driven solely by abiotic processes) are needed to understand these patterns. Recruitment, which often is the driver of invasive species abundance (Miller *et al.*, 2014), should be the main focus of such analyses. Despite their potential to identify clear drivers of biological invasions, analyses of invasive species recruitment across ecoregions have been conducted with surprising rarity in favour of geographically confined studies. For example, we are not aware of any of such analyses for invasive fish. For the common carp, which is one of better studied species, and whose recruitment has been investigated within several locations in North America and Australia (King *et al.*, 2003; Phelps *et al.*, 2008; Bajer & Sorensen, 2010; Bajer *et al.*, 2012; Silbernagel & Sorensen, 2013; Weber & Brown, 2013a), ours is the first study to investigate this phenomenon across several ecoregions. Our approach identified a hierarchy of ecological filters that control carp recruitment at broad and fine spatial scales that had not been detectable by previous, more localized studies. While our interpretation of observed patterns needs to be tested, our analysis may be useful in explaining common carp invasions in many regions of the world given their productivity and micropredator communities. More broadly, our approach shows that by using a wide ecological lens that covers regions in which invaders are successful as well as those where they are not, one might substantially advance understanding of biological invasions.

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SUPPORTING INFORMATION

Additional Supporting Information may be found in the online version of this article:

Appendix S1 Detailed description of lake surveys, detailed description of field experiment, Figures S1–S8.

Figure S1 Environmental conditions and adult carp relative catch rates across the Great Plains (GP), Northern Forest (NF) and Temperate Forest (TF) ecoregions.

Figure S2 Relative catch rates of native predatory fishes across the Great Plains (GP), Northern Forest (NF) and Temperate Forest (TF) ecoregions.

Figure S3 Scatterplots of common carp recruitment (presence or absence) versus Secchi depth, lake area, lake maximum depth and adult carp catch rate in lakes of the Great Plains (GP), Northern Forest (NF) and Temperate Forest (TF) ecoregions.

Figure S4 Scatterplots of common carp recruitment (presence or absence) versus catch per effort (CPUE) of the dominant native predators: bluegill, crappies, bullheads, yellow perch, northern pike, and walleye in lakes of the Great Plains (GP), Northern Forest (NF) and Temperate Forest (TF) ecoregions.

Figure S5 Spearman’s correlation matrix among the predictor variables.

Figure S6 Relationships between common carp recruitment (presence/absence), Secchi depth (m) and adult carp CPUE (Carp) in lakes of the Great Plains (black), Northern Forest (red) and Temperate Forest (green) ecoregions.

Figure S7 Relationship between bluegill catch per effort (CPUE) and Secchi depth in lakes of the Great Plains (GP), Northern Forest (NF) and Temperate Forest (TF) ecoregions.

Figure S8 Experimental enclosures.

BIOSKETCH

Przemyslaw G. Bajer is a Research Assistant Professor at the University of Minnesota. He is interested in processes that facilitate fish invasions, especially recruitment, micropredation and environmental instability. He is also interested in developing integrated pest management strategies for invasive fish by exploiting weaknesses in their behaviour, life history and population dynamics.

Author contributions: P.G.B. conceived the idea; T.K.C., C.J.C. and M.J.W. provided lake data for Minnesota, Nebraska and South Dakota, respectively. J.D.L., P.G.B. and P.W.S. designed and conducted the field experiment; P.G.B., C.J.C., T.K.C. and M.J.W. conducted the analyses; P.G.B. led the writing of the manuscript, which included contributions from all authors.

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