Biological invasion by a benthivorous fish reduced the cover and species richness of aquatic plants in most lakes of a large North American ecoregion

PRZEMYSLAW G. BAJER[1], MARCUS W. BECK[1]*, TIMOTHY K. CROSS[2], JUSTINE D. KOCH[1], WILLIAM M. BARTODZIEJ[3] and PETER W. SORENSEN[1]

[1]*Department of Fisheries, Wildlife and Conservation Biology, Minnesota Aquatic Invasive Species Research Center, University of Minnesota, 135 Skok Hall, 2003 Upper Buford Circle, St. Paul, MN 55108, USA*, [2]*Minnesota Department of Natural Resources, Fisheries Research, 20596 Hwy 7, Hutchinson, MN 55350, USA*, [3]*Ramsey Washington Metro Watershed District, 2665 Noel Drive, Little Canada, MN 55117, USA*

Abstract

Biological invasions are projected to be the main driver of biodiversity and ecosystem function loss in lakes in the 21st century. However, the extent of these future losses is difficult to quantify because most invasions are recent and confounded by other stressors. In this study, we quantified the outcome of a century-old invasion, the introduction of common carp to North America, to illustrate potential consequences of introducing non-native ecosystem engineers to lakes worldwide. We used the decline in aquatic plant richness and cover as an index of ecological impact across three ecoregions: Great Plains, Eastern Temperate Forests and Northern Forests. Using whole-lake manipulations, we demonstrated that both submersed plant cover and richness declined exponentially as carp biomass increased such that plant cover was reduced to <10% and species richness was halved in lakes in which carp biomass exceeded 190 kg ha^{-1}. Using catch rates amassed from 2000+ lakes, we showed that carp exceeded this biomass level in 70.6% of Great Plains lakes and 23.3% of Eastern Temperate Forests lakes, but 0% of Northern Forests lakes. Using model selection analysis, we showed that carp was a key driver of plant species richness along with Secchi depth, lake area and human development of lake watersheds. Model parameters showed that carp reduced species richness to a similar degree across lakes of various Secchi depths and surface areas. In regions dominated by carp (e.g., Great Plains), carp had a stronger impact on plant richness than human watershed development. Overall, our analysis shows that the introduction of common carp played a key role in driving a severe reduction in plant cover and richness in a majority of Great Plains lakes and a large portion of Eastern Temperate Forests lakes in North America.

Keywords: biodiversity, common carp, *Cyprinus carpio*, ecological impact, ecological threshold, ecosystem function, macrophytes, non-native

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Introduction

Biological invasions are projected to be a major driver of biodiversity and ecosystem function loss in freshwater lakes in the 21st century (Miller, 1989; Sala *et al.*, 2000; Gallardo *et al.*, 2016). However, although freshwater invaders have been shown to exert local impacts, it is less clear whether they could also be the dominant drivers of biodiversity and ecosystem function loss across broad geographic areas. This is likely attributable to at least three factors. First, most freshwater invasions are relatively recent and their impacts may not

yet be fully evident, as has been shown for marine invaders (Byers *et al.*, 2015). Second, of the thousands of introduced freshwater species, only a small percentage ever become damaging (Kolar & Lodge, 2002), and studies that do not focus on this small group of particularly damaging species, such as top predators or ecosystem engineers, might not clearly demonstrate invasion impacts (Gurevitch & Padilla, 2004). Finally, freshwater biological invasions often occur at times when lakes and rivers are impacted by other, potentially confounding stressors that can mask effects of invaders. For example, the extinction of several native fishes in Lake Victoria that was initially attributed to the introduction of Nile perch (*Lates niloticus*) was later drawn into question due to concurrent eutrophication and overexploitation (Verschuren *et al.*, 2002; Aloo, 2003). Teasing out the importance of biological invasions relative to other stressors is of paramount

Correspondence: Przemyslaw G. Bajer, tel. 612 625 6722, fax 612 625 5299, e-mail: bajer003@umn.edu
*Present address: Gulf Ecology Division, USEPA National Health and Environmental Effects Research Laboratory, 1 Sabine Island Drive, Gulf Breeze, FL 32561, USA

importance to ecologists, policymakers and managers alike. We hypothesize that the possibility that invasive species might be the leading drivers of large-scale biodiversity and ecosystem function loss in freshwater lakes might be most clearly demonstrated by analyses that quantify the outcomes of widespread invasions of ecologically important species such as ecosystem engineers in the context of other anthropogenic stressors. We present the first such analysis for one of the world's oldest invasive fish.

The common carp (*Cyprinus carpio*, or 'carp') is among the oldest and most widespread aquatic invaders. Native to eastern Europe and Asia, it was introduced to North America in the late 1800s, where it quickly became widespread (Sorensen & Bajer, 2011). In the more than 100 years since its introduction, the carp established itself in various regions and ecosystem types throughout North America. This species also dominates large areas of Australia, Africa, South America and western Europe (Beklioglu *et al.*, 2003; Vilizzi, 2012). The common carp exemplifies an ecosystem engineer (Matsuzaki *et al.*, 2009), and it is especially well known for increasing water turbidity and uprooting aquatic plants while searching for food in lake sediments, which can lead to a complete elimination of submersed plants (Haas *et al.*, 2007; Bajer *et al.*, 2009; Bajer & Sorensen, 2015). This does not only reduce plant biodiversity, but it can also have cascading effects on the abundance and diversity of waterfowl, insects and amphibians that plummet in lakes dominated by carp (Stewart & Downing, 2008; Bajer *et al.*, 2009; Kloskowski, 2011). Decline in plant diversity and cover also hinders fundamental ecosystem functions such as maintaining water clarity, reducing erosion or sequestering nutrients (Engelhardt & Ritchie, 2001; Haas *et al.*, 2007). The abundance of carp tends to be highest in hypereutrophic lakes in agricultural and urban areas (Kulhanek *et al.*, 2011a,b; Bajer *et al.*, 2015). Although site-specific studies have shown the effects of carp on aquatic ecosystems (Vilizzi *et al.*, 2015), it has not been demonstrated whether common carp can be prevalent and important enough to cause sweeping declines in diversity and ecosystem function across entire geographic regions.

In this study, we quantified the impacts of common carp on species richness and cover of submersed aquatic plants in lakes of three North American ecoregions in the context of anthropogenic stressors and natural variability in lake characteristics. We focused on aquatic plants because carp directly impacts plants and changes in plant cover and richness drive many important ecosystem processes. First, we conducted whole-lake manipulations to determine the causality of carp's impacts and the relationship between carp biomass and plant cover and species richness. While this relationship often resembles a gradual decline over moderate levels of carp biomass (Haas *et al.*, 2007; Bajer *et al.*, 2009), it is also useful (especially for management purposes) to define a threshold for carp biomass that can drive severe qualitative changes in lake ecology (Scheffer *et al.*, 2001). Using our whole-lake manipulations, we defined this biomass threshold as one that drove a decline in plant cover to 10%, at which point lakes often switch to turbid state (Wallsten & Forsgren, 1989) and lose their function as habitat for waterfowl (Bajer *et al.*, 2009). Then, we used mark–recapture analyses to determine what catch rates of common carp are indicative of lakes with such damaging carp biomass level. Subsequently, we examined patterns of carp catch rates and plant richness in over 2000 lakes to determine the percentage of lakes in which carp biomass exceeded the identified threshold in each ecoregion. Finally, for a group of several hundreds of lakes for which detailed data were available, we determined the relative role of carp in driving aquatic plant richness among other variables such as water clarity (proxy of trophic status), anthropogenic use of watersheds or lake morphology. Broadly speaking, we asked whether biological invasions by ecosystem engineers can be important, ecoregion-wide drivers of biodiversity and ecosystem function loss in freshwater lakes.

Materials and methods

Study region

Our study region encompassed a large area within the Mississippi River Drainage located within Minnesota (USA) that included three major ecoregions: Great Plains, Eastern Temperate Forests, and Northern Forests (Fig. 1; level 1 in Omernik, 2004). This region is characterized by a wide range of topography and soils ranging from sandy soils and coniferous forests in the Northern Forests to deciduous forests of the Eastern Temperate Forests, to productive prairie ecosystems of the Great Plains. More than 15 000 lakes and marshes over 4 ha in size occur in this area, which have a strong water clarity and productivity gradient: Northern Forests lakes are dominated by relatively deeper and clearer oligotrophic and mesotrophic systems; Eastern Temperate Forests include mostly mesotrophic and eutrophic lakes, whereas Great Plains are dominated by shallow and turbid hypereutrophic prairie lakes (Heiskary & Wilson, 2008). Aquatic plant communities vary across these ecoregions following gradients in alkalinity and productivity. Plant diversity is typically highest in moderately productive lakes in the Eastern Temperate Forests where communities are neither nutrient limited nor light limited (Radomski & Perleberg, 2012). Plants can be limited by high turbidity in Great Plains lakes, or by low nutrient concentrations in the Northern Forests lakes. Carp are common
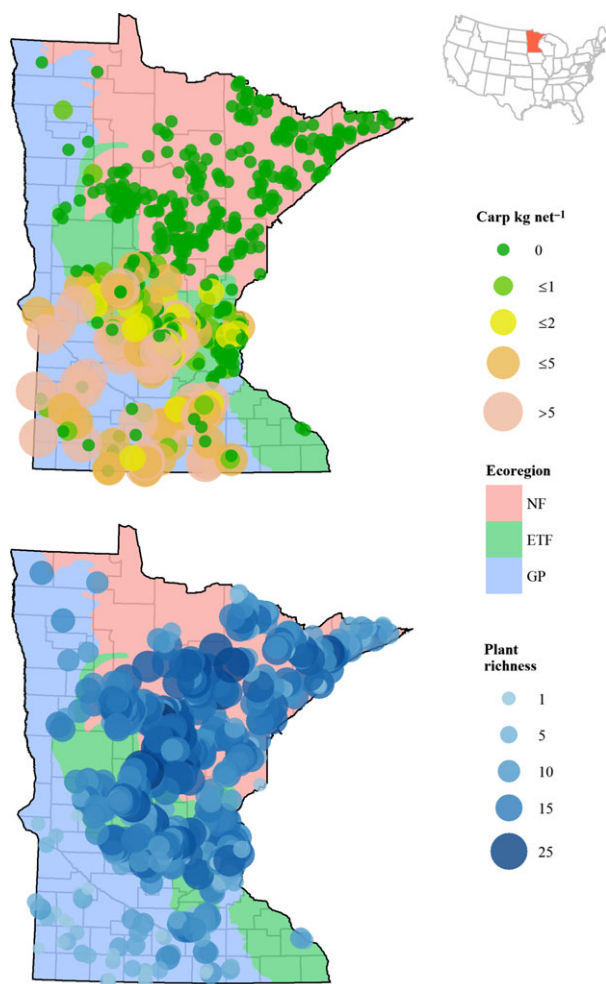
Fig. 1 Study region showing lakes across three temperate ecoregions (Great Plains, Eastern Temperate Forests, Northern Forests) with their common carp biomass (kg net^{-1}) and aquatic plant species richness.

throughout the region but are particularly abundant in the Great Plains and also Eastern Temperate Forests ecoregions (Kulhanek *et al.*, 2011a,b; Bajer *et al.*, 2015).

Whole-lake experiments to determine causality and severity of carp impacts on plants

We conducted whole-lake assessments of carp biomass in six lakes in south-central Minnesota located within the Eastern Temperate Forests ecoregion, followed by carp biomass reduction in four of those lakes. The lakes ranged in size from 5 to 150 ha and had maximum depths of 1 to 13 m (Table S1). Growing season (May–September, measured every 2 weeks in 2–3 locations in each lake) total phosphorus concentrations ranged from 20 to 220 μg L^{-1} while May–September Secchi depths ranged from 0.26 to 3.7 m (Table S2). Springtime (May and June) Secchi depths usually exceeded 1.5 m (Table S2); thus, we assumed that light was not limiting for the early

season plant growth up to a depth of approximately 2 m (our plant surveys were conducted in late spring up to a depth of 2 m). Two of the shallowest lakes remained well mixed throughout the year while others were dimictic or polymictic (Table S1). The bottom substrate in the lakes varied from sandy to soft, but it was not rigorously sampled.

Carp populations in these lakes were studied during 2006–2014, and mark–recapture estimates of abundance and biomass were available for all lakes, except for Lake Ann, in which carp population was estimated using boat electrofishing (Bajer & Sorensen, 2012) (Table S1). Once carp populations were estimated and surveys of plant cover and species richness conducted (see below), we reduced the number and biomass of carp in four lakes that initially had moderate to high carp biomass (Table S2) by targeting their winter aggregations with seine nets as described in Bajer *et al.* (2011). In one lake (Lake Casey), carp population was eliminated by reducing water level in the fall and freezing the lake to the bottom (Table S2). Reduction of biomass occurred over 1–4 years (Table S2) and was accompanied by surveys of aquatic plants.

Plant surveys were conducted in June and early July. Ten transects distributed approximately equidistant from each other were mapped in each lake using ArcGIS; the same transects were surveyed each year. These transects were perpendicular to shore and plants were sampled at locations where water depth reached 0.5, 1, 1.5 and 2 m along each transect. At each sampling location, visual estimates of percent plant cover (nearest 10%) and the presence of plant species were recorded within a 2 m × 2 m area using the front of the boat (2 m long) as a visual reference (Bajer & Sorensen, 2015). To validate the accuracy of our visual assessments and species identification, a sampling grapple was lowered to the bottom, twisted three times and pulled on the boat at every other transect. Collected plants were then drained of excess water and weighed (nearest 10 g). Results were averaged across transects to represent a mean percent plant cover in littoral zone (depth <2 m) of each lake. Total number of plant species (richness) found in each lake was also recorded; only submersed plants and macroalgae (*Chara* sp.) were included as they are directly impacted by carp.

To quantify the effects of carp biomass on plants in our whole-lake experiments, we first examined the relationship between carp biomass and plant cover and species richness across the six lakes by fitting simple linear models. We also examined changes in aquatic plant cover and species richness in response to carp removal. To explore possible confounding effects, we also fitted a multivariable linear model to assess additional effects of water clarity and TP on plant cover and richness. By examining the responses of aquatic plants to varying levels of carp biomass, we determined carp biomass that caused a reduction in plant cover to 10% (i.e., our threshold for severe ecological damage). Using a conservative threshold (e.g., one that caused a nearly complete elimination of plant cover in our whole-lake experiments), we assumed that all lakes in which carp biomass exceeded this threshold are significantly impacted by the carp regardless of other factors such as water clarity or lake morphology.

Developing biomass – catch rate relationship to obtain a low-effort index of carp biomass

Because all lakes described above (except Lake Casey) are routinely surveyed with standardized gillnets, we were able to develop a statistical relationship between mark–recapture estimates of carp biomass (kg ha^{-1}) and their catch rates in gillnets (kg net^{-1}). To increase our sample size, this data set was augmented by four additional lakes (Table S3) in which both mark–recapture and gillnet surveys were conducted (but no plant surveys were conducted). Using these data, we fitted a linear model to estimate gillnet catch rate that was representative of the threshold for severe ecological damage to aquatic plants (see above). We then determined the percentage of lakes across the three ecoregions in which gillnet catch rates exceeded this threshold.

Both mark–recapture and gillnet surveys were conducted in the same year in approximately half of the lakes (Table S3). In other lakes, mark–recapture analyses occurred within 1–4 years of gillnet surveys, which followed a pre-established 5-year cycle (conducted by the Minnesota Department of Natural Resources). This separation in time did not cause a statistical bias because all of those carp populations were stable over time, which we verified by conducting annual boat electrofishing and trapneting surveys to inform ongoing carp management schemes (Bajer & Sorensen, 2010, 2012, 2015; Bajer *et al.*, 2011, 2012).

Analysis of plant species richness and carp catch rates across ecoregions

If the common carp has an important effect on aquatic plants across large geographic areas, then one might hypothesize that (i) its catch rates will exceed levels associated with severe ecological damage in a large number of lakes, (ii) the distribution of plant cover and species richness across the landscape will show patterns opposite to the distribution of carp, and (iii) carp will rank as an important variable among other variables (water clarity, regional geology or human impact) known for regulating plant cover and richness.

To address these hypotheses, we used existing fish and plant surveys collected by Minnesota DNR in lakes across the three ecoregions following standardized procedures (http://files.dnr.state.mn.us/publications/fisheries/special_reports/147.pdf). Fish surveys were conducted in 2422 lakes during 1991–2014, with each lake typically being surveyed at least once every 5 years. These surveys employed standardized gillnets, which we used to calculate mean carp catch rate (kg net^{-1}) in each survey in each lake, as in Kulhanek *et al.* (2011a,b). The nets were set overnight and their number typically varied between five and 15 depending on lake area. Aquatic plants were surveyed in 717 lakes, not necessarily at the same time, or in the same lakes in which fish surveys were conducted. Plants were sampled using belt transects that were 6 m wide and extended to the outer depth limit of the plant edge. Transects extended to the center of the lake for locations with plant cover in the entire basin. Plant surveys were performed in July through mid-September. The number of transects ranged from 10 to 50 depending on lake surface area. In each transect, plant species were visually assessed and a double-sided sampling grapple was used whenever a more detailed identification of species was required. The number of plant species was recorded for each transect, and each species was characterized as rare, abundant or null in case of small number of species that were observed in the lake but were not found in the transects. We used these data to determine number of species present in each lake during each survey (species richness). We only included species of submersed plants and macroalgae (*Chara* sp.), because they are directly impacted by carp. Because plant cover was recorded only qualitatively, we were unable to use these data to analyze the effect of carp on plant cover; all further analyses of the ecoregion data focus on plant species richness.

Fish and plant data across the three ecoregions were used to conduct three analyses corresponding to our three hypotheses. First, we developed frequency histograms to determine the distribution of carp catch rates (lake-specific mean over the entire sampling period 1991–2014) across the three ecoregions to examine in how many lakes carp catch rates exceeded the threshold for severe ecological damage. We also developed histograms for plant species richness for lakes within each ecoregion to examine whether plant richness and carp catch rates showed generally opposite trends. Lastly, we conducted model selection analysis to examine the importance of carp in structuring plant species richness among other variables across the three ecoregions. To conduct the model selection analysis, we selected lakes in which carp biomass and plant species richness were surveyed in the same year; $n = 378$ lakes (193 Eastern Temperate Forests, 32 Great Plains, 153 Northern Forests). For each of these lakes, we gathered information on variables other than carp known to influence plant species richness, which included water clarity (lake-specific mean May–September Secchi depth during 1991–2014; m), lake area (ha), maximum depth (m), shoreline development index (SDI – a measure of shoreline irregularity), proportion of land developed by humans within the watershed (Phuman; a sum of land under human development or land used for agriculture), watershed area (ha) and ecoregion, which was used as a categorical variable. Using this data set, we first examined scatter plots and correlations among predictor variables and plant species richness (Fig. S2). Carp catch rates and Phuman were log10+1-transformed, while Secchi depth, maximum depth and lake area were log10-transformed to achieve linear relationships with species richness. Following the initial examination, we conducted model selection analyses using Akaike's information criterion (AIC). First, we identified the most parsimonious model (AIC value closest to zero) as well as competing models by examining relevant combinations of predictor variables and interaction terms. Models whose AIC scores were within two units were considered as having similar support (Burnham & Anderson, 2002). Then, we determined relative importance (sum of AIC weights) of predictor variables included in the most parsimonious model (Burnham & Anderson, 2002). Following the model selection analysis for all three ecoregions combined, we conducted similar analyses for each ecoregion separately to

assess the robustness of our predictor variables across and within ecoregions. All analyses were performed in R 2.15.1 (R Development Core Team, 2013). Candidate models were fitted using the 'LME4' package (Bates *et al.*, 2015). Variable importance was calculated using the 'importance' function of the 'MUMLN' package (Barton, 2015).

Results

Whole-lake manipulation experiments

Both plant cover and species richness were negatively influenced by carp biomass in our whole-lake experiments (Fig. 2). Overall (pre- and postremoval data combined), carp biomass explained 87% of variance in plant cover (plant cover = $10^{(2.08-0.0056 \cdot \text{carp biomass})}$,
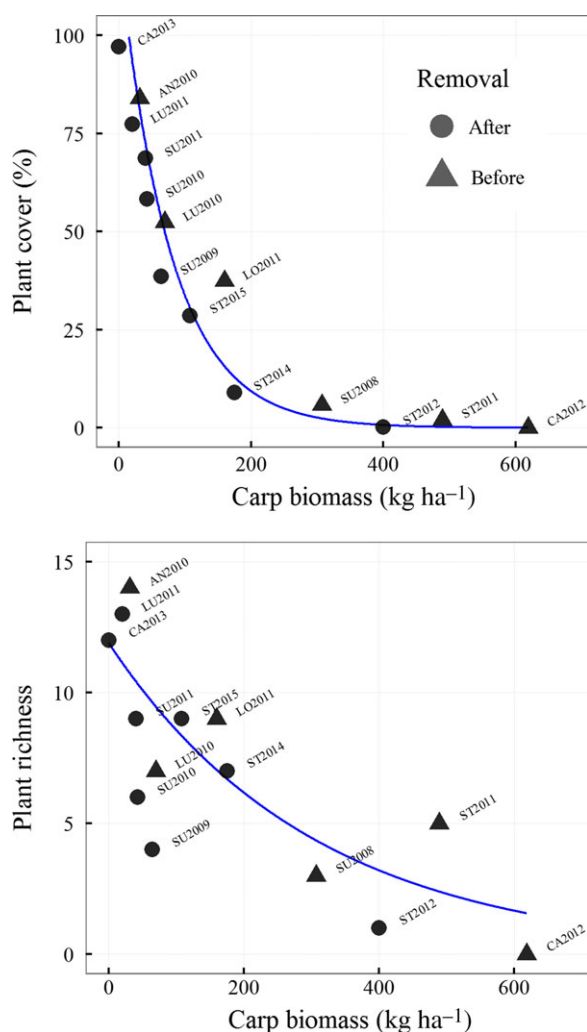
$P < 0.001$) and 68% of variance in plant species richness (plant species = 15.91–4.52 • log10 (carp biomass +1); $P < 0.001$) (Fig. 2). Carp removal from lakes Lucy, Susan, Staring and Casey was associated with consistent increases in both plant cover and species richness (Tables S2, S4; Fig. 2), suggesting a cause and effect relationship in all four of these lakes. Removal of carp was also associated with an increase in Secchi depth, especially in lakes in which carp biomass was initially high (>200 kg ha^{-1}; Table S2), which might have further accelerated the increase in plant cover and richness. However, linear model analysis suggested that once the effect of carp on plant cover or species richness was incorporated, the effect of Secchi depth was nonsignificant (Tables S5, S6; i.e., carp biomass drove both plants and Secchi). Observed relationships between carp biomass and plant cover and richness suggested that carp biomass of 190 kg ha^{-1} caused a decline of plant cover to 10% (Fig. 2). Thus, we concluded that this biomass level would likely cause a severe ecological impact in lakes in general.

Relationship between carp biomass and catch rate

Analysis of carp catch rates in gillnets (kg net^{-1}) in lakes in which mark–recapture biomass estimates were conducted (kg ha^{-1}) showed that gillnet catch rates were nil in lakes with carp biomass below 50 kg ha^{-1} and then increased linearly with an increase in carp biomass. A linear model fitted to the data (catch rate = −0.92 + 0.012 • biomass; $r^2 = 0.60$ $P < 0.001$; Fig. S1) suggested that gillnet catch rates equal to or higher than 1.4 kg net^{-1} are representative of lakes in which carp biomass equals or exceeds 190 kg ha^{-1} (the threshold for severe ecological damage defined above). Thus, we assumed that lakes with carp catch rates equal to or exceeding 1.4 kg net^{-1} are likely to be severely impacted by this species.

Carp catch rates and plant richness across three ecoregions

Frequency histograms of carp catch rates suggested that this species reached or exceeded the threshold for severe ecological damage (1.4 kg net^{-1}) in 70.6% Great Plains lakes, 23.3% Eastern Temperate Forests lakes and 0% Northern Forests lakes (Fig. 3). Carp catch rates exceeded 10 kg net^{-1}, over five times above the threshold, in 40% of Great Plains lakes and were generally skewed to the left (Fig. 3). Plant species richness in Great Plains lakes showed an opposing trend (skewed right) with many lakes having less than five species of aquatic plants (Fig. 3). Plant species richness in lakes of Northern Forests and Eastern

Fig. 2 Relationship between common carp biomass (kg ha^{-1}) and littoral zone (depth <2 m) plant cover (top) and species richness (bottom) in whole-lake manipulations. Triangles indicate values before carp removal, circles indicate values after carp removal. For details see Table S2.
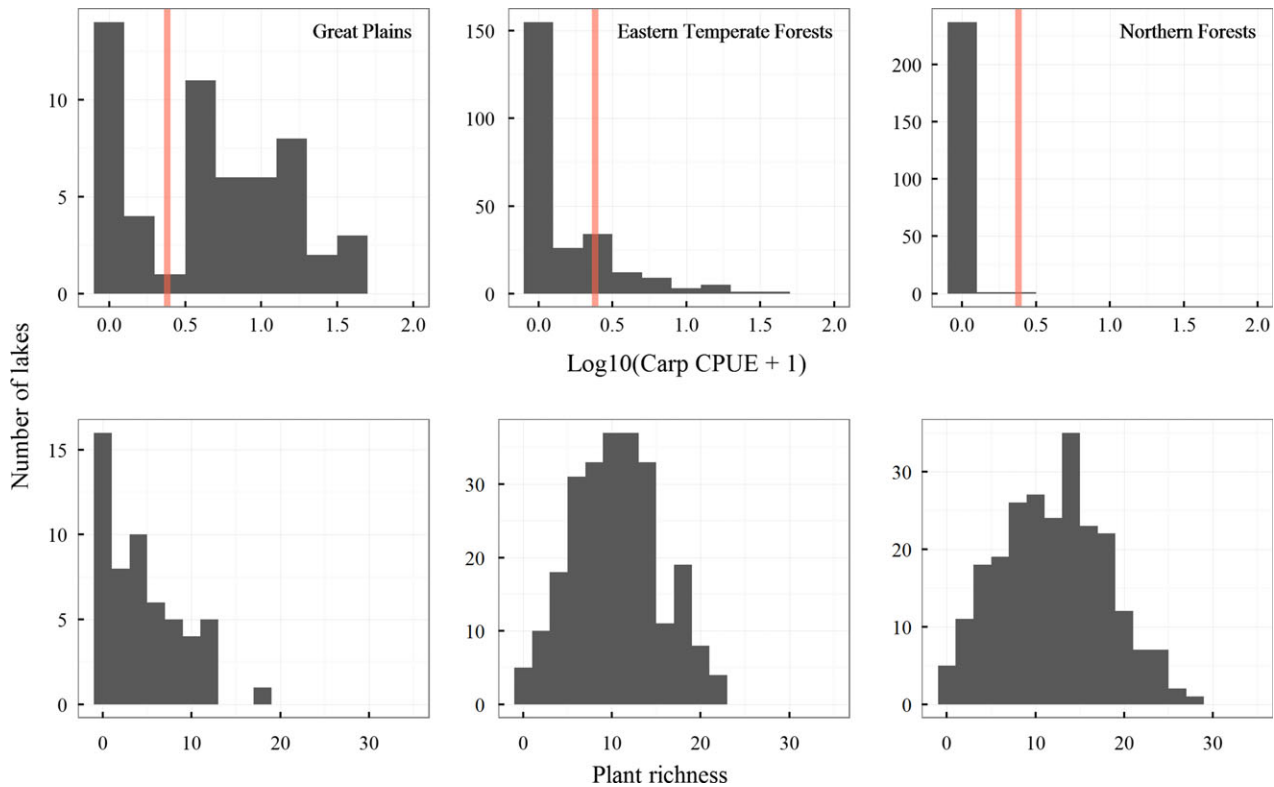
Fig. 3 Frequency histograms of common carp gillnet catch per unit of effort (CPUE, kg net^{-1}) (top panels) and plant species richness (bottom panels) in lakes of the Great Plains (left), Eastern Temperate Forests (middle), and Northern Forests (right) ecoregion. Red line represents threshold in carp biomass that causes severe damage to aquatic plants. In total, 2422 lakes were sampled for carp and 717 lakes were sampled for plants. Only some lakes were sampled both for carp and plants during the same year (Fig. 4).

Temperate Forests ecoregions showed relatively normal distributions (Fig. 3).

Model selection analysis conducted across the three ecoregions showed that the most parsimonious model of plant species richness included carp biomass, Secchi depth, lake area, human development of the watershed and their interactions with ecoregion (Table 1). Carp had a negative effect on species richness and this effect was consistent across the Great Plains and Eastern Temperate Forests ecoregions where this species was present (Table S7; Fig. 4). Secchi depth had a positive effect on species richness, but this effect declined in lakes of the Northern Forests ecoregion (Fig. 4; Table S7). Lake area had a positive effect on species richness especially across the Northern Forests and Eastern Temperate Forests ecoregions (Fig. 4; Table S7). The effect of human development was overall insignificant, but it had a positive effect on species richness in lakes of the Northern Forests ecoregion (Fig. 4; Table S7). Of the variables included in the most parsimonious model, all had importance values above 0.99 (scale from 0 to 1) showing little evidence of model overfitting. Removal of any of these variables significantly reduced model support (ΔAIC $\geq$10; Table 1)

showing that they all contributed important information to the model. Our most parsimonious model explained 54% of the overall variability in plant richness ($r^2 = 0.54$; $F_{14, 359} = 32.01$; $P < 0.001$).

Model selection analyses conducted separately for each ecoregion supported the trends identified in the across-ecoregion analysis. For Great Plains lakes, the most parsimonious model included carp and Secchi, both of which had similar variable importance (carp 0.74, Secchi 0.72) (Tables 1; S8). For the Eastern Temperate Forests lakes, the most parsimonious model included carp, Secchi, lake area, percent under human development and maximum depth (Tables 1; S9), of which the first three had variable importance of 1.0. For Northern Forests lakes, where carp were absent, the most parsimonious model included lake area, percent under human development and maximum depth (Tables 1; S10) all of which had variable importance >0.75.

Discussion

Our study provides support for the hypothesis that biological invasions can drive large-scale declines in biodiversity (richness) and ecosystem function in freshwater

Table 1 Results of model selection analysis to explain trends in aquatic plant species richness across three ecoregions (Great Plains, Eastern Temperate Forests and Northern Forests). Predictor variables include: log10 (common carp catch rate+1), log10 (Secchi depth), shoreline development (irregularity) index (SDI), log 10 (percent human development of the watershed + 1), log10 (lake area), log10 (lake maximum depth), watershed area and ecoregion. Model parameters are shown in Table S7

| Model	Variables	AIC	ΔAIC
Best model	(Carp, Secchi, Area, Phuman) × Ecoregion	2071.2	0.0
Best model without carp	(Secchi, Area, Phuman) × Ecoregion	2083.3	12.1
Best model without Secchi	(Carp, Area, Phuman) × Ecoregion	2116.3	45.1
Best model without area	(Carp, Secchi, Phuman) × Ecoregion	2192.3	121.1
Best model without Phuman	(Carp, Secchi, Area) × Ecoregion	2090.2	19.0
Best model without ecoregion	Carp, Secchi, Area, Phuman	2093.6	22.4
Model with carp × Secchi interaction	(Carp x Secchi, Area, Phuman) × Ecoregion	2073.5	2.3
Full model	(Carp, Secchi, Area, Depth, Phuman, SDI, Watershed area) × Ecoregion	2082.7	11.5
Best model for Great Plains only	Carp, Secchi	184.5	–
Best model for Eastern Temperate Forests only	Carp, Secchi, Area, Phuman, Depth	1001.3	–
Best model for Northern Forests only (Carp absent)	Area, Phuman, Depth	874.4	–

lakes (Sala *et al.*, 2000). A century after its introduction, the common carp is excessively abundant in approximately 70 percent of Great Plains lakes and a large proportion of Eastern Temperate Forests lakes in Minnesota, where it has contributed to a severe decline in aquatic plant cover and richness. Although our study is restricted to Minnesota, these impacts are likely to be representative of a much larger area because Great Plains and Eastern Temperate Forests are among the largest ecoregions of North America extending from Canada to the Gulf of Mexico and carp have been reported to be abundant throughout the entire region (Zambrano *et al.*, 2006; Jackson *et al.*, 2010; Kulhanek *et al.*, 2011a). The impacts of carp likely extend beyond plants and include amphibians (Kloskowski, 2009), invertebrates (Stewart & Downing, 2008) fish (Egertson & Downing, 2004) and waterfowl (Haas *et al.*, 2007). Nutrient and sediment export is also likely to increase from lakes invaded by carp and stripped of aquatic plants (Engelhardt & Ritchie, 2001).

Aquatic plant cover and richness followed an exponential decline in response to increases in carp biomass. Consequently, lakes with moderate carp biomass will likely exhibit intermediate levels of plant cover and richness and perform ecological services (e.g., providing habitat for waterfowl, maintaining water clarity) with intermediate efficacy (Haas *et al.*, 2007). While many lakes are moderately impacted, it is also important to identify those in which severe and abrupt changes, such as switching to a turbid state (Scheffer *et al.*, 2001; Matsuzaki *et al.*, 2009), are likely to occur as a result of high carp biomass. Defining the values of a threshold in carp, or benthivorous fish in general, biomass that drives such severe changes has received considerable attention worldwide (Vilizzi *et al.*, 2015; Bernes *et al.*, 2015). We

used a relatively high threshold (190 kg ha^{-1}) while estimating the number of lakes severely impacted by carp in each ecoregion. The threshold we used caused a 90% reduction in plant cover in our whole-lake manipulations and was almost twice that (100 kg ha^{-1}) we previously showed to be already causing strong effects on plants in a shallow lake in Illinois and a stratified lake in Minnesota (Bajer *et al.*, 2009; Bajer & Sorensen, 2015). It is also similar to a tipping point estimate (198 kg ha^{-1}) independently quantified by a review of carp impacts on lakes worldwide (Vilizzi *et al.*, 2015) and values for benthivorous fishes suggested by the European biomanipulation literature that range between 120 and 200 kg ha^{-1} (Meijer *et al.*, 1990; Williams *et al.*, 2002; Haas *et al.*, 2007; Søndergaard *et al.*, 2008). Because our threshold represents lake ecosystems that are severely impacted by the carp, lake restoration efforts should aim for a considerably lower carp biomass (probably <100–120 kg ha^{-1}) to ensure that this species is not significantly impacting plants, other biota or ecosystem functions (Haas *et al.*, 2007; Bajer *et al.*, 2009).

Synergistic stressors often confound the effects of invasive species on freshwater ecosystems (Gurevitch & Padilla, 2004). This is particularly relevant in our region where the introduction of carp coincided with anthropogenic eutrophication and corresponding increases in phosphorus concentrations and reduced water clarity in many south-central Minnesota lakes (Ramstack *et al.*, 2003). Disentangling the effects of carp from those of cultural eutrophication is important for directing appropriate lake restoration strategies. This process is complex due to positive feedback mechanisms: lake productivity (lower Secchi) appears to increase the chance that a lake will be invaded and dominated by carp (Kulhanek *et al.*, 2011a,b; Bajer *et al.*,
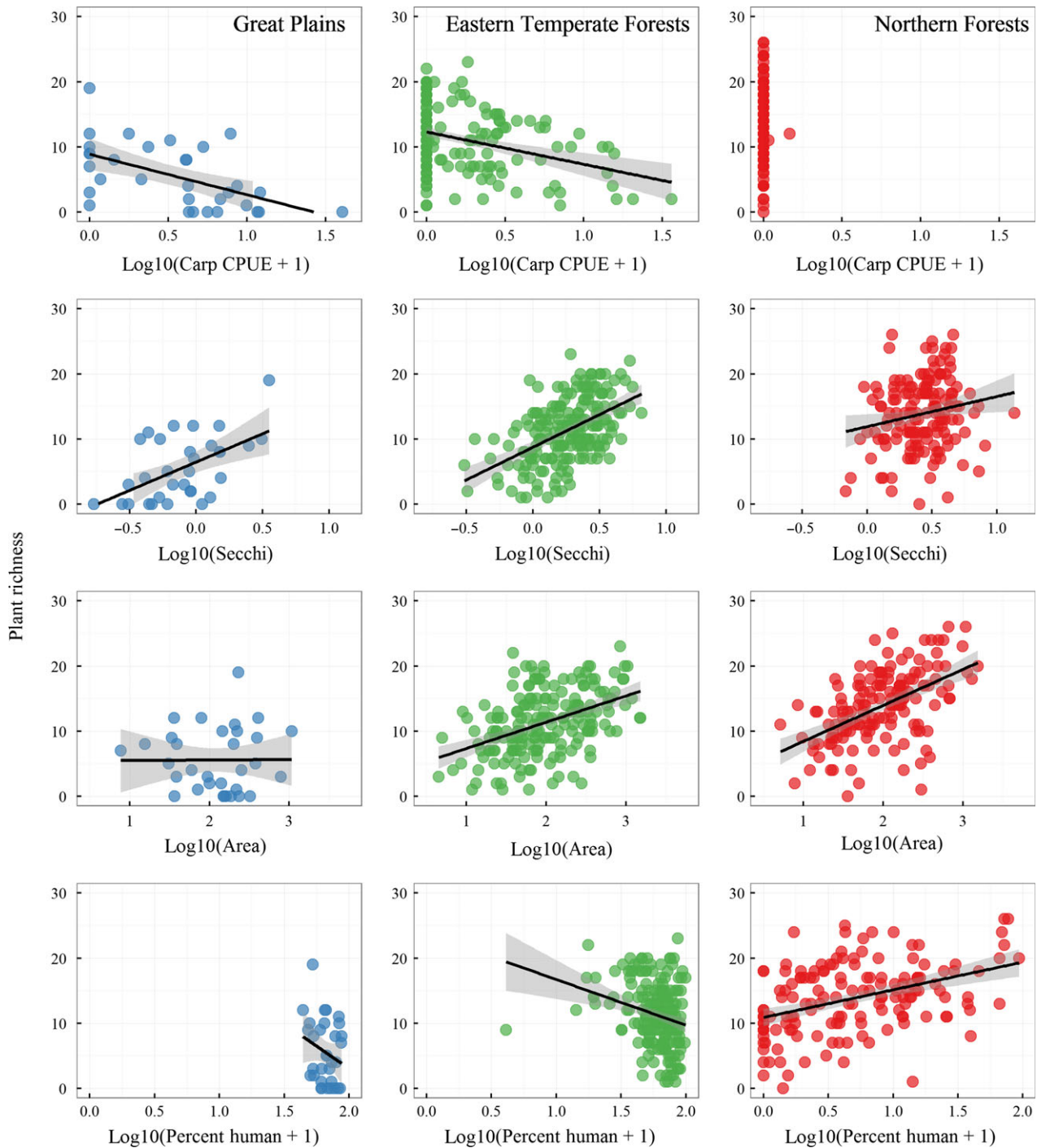
Fig. 4 Relationships between common carp gillnet catch per unit of effort (CPUE, kg net^{-1}), Secchi depth (m), lake area (ha), proportion of watershed under human development (Percent Human) and plant species richness in lakes of the three ecoregions (Great Plains, Eastern Temperate Forests, Northern Forests). Gray shading represents 95% confidence intervals around the linear model in each panel.

2015), who can then reduce Secchi depths even more through nutrient release and sediment resuspension (Vilizzi *et al.*, 2015). Our model selection analysis showed that both carp and Secchi could independently explain variation in plant species richness and that their effects were additive. This was supported by post hoc analyses that showed that Secchi significantly affected plant richness in lakes with and without carp (Fig. S4).

Similarly, carp had a significant effect in lakes with lower and higher Secchi depths (Fig. S5). Auxiliary analyses also showed that Secchi depths were driven primarily by phosphorus concentrations and secondarily by carp whose presence reduced Secchi by ~0.75 m across a wide range of phosphorus concentrations (Figs S6, S7). Gorman *et al.* (2014) have also shown synergistic effects of phosphorus and fish biomass on Secchi in Minnesota lakes. Clearly, many lakes can have poor species richness of aquatic plants due to low water clarity driven by, for example, anthropogenic eutrophication. Introduction of carp to such systems will exacerbate these conditions through uprooting and reduced clarity (additional nutrient release and sediment resuspension). Nevertheless, the additive nature of the carp – Secchi effect suggests that significant improvements in plant species richness (at least in shallower areas) can be achieved by removing carp, even if water clarity does not improve appreciably. This was corroborated by our whole-lake experiments where rapid increases in littoral (<2 m depth) plant richness and cover occurred despite only modest gains in Secchi depth and modest declines in phosphorus (Table S2).

Lake area and percent of watershed under human development had important effects on plant species richness in our models. Lake area had a positive effect on species richness, particularly in the Eastern Temperate Forests and Northern Forests ecoregions. This may be attributable to the often-documented effect of habitat patch size on species diversity in both aquatic and terrestrial habitats (Kohn & Walsh, 2004). However, the increased importance of the area effect in lakes with clearer water (Eastern Temperate Forests and Northern Forests) than in those with more turbid water (Great Plains) is more intriguing. A similar pattern was reported from Danish lakes (Vestergaard & Send-Jensen, 2000) and was attributed to increased habitat diversity (depth, slope, sediment type, fetch) that is more likely to occur in larger lakes, and which will have a positive effect on plant richness, except in eutrophic, turbid lakes typical of agricultural landscapes (Moss, 1998). It is also possible that increased species richness in larger lakes was to some extent caused by a greater number of sampling transects in such systems, although the number of transects per hectare was consistent across all lakes. Regardless of its cause, the effect of lake area was unlikely to confound the effect of carp on species richness because the latter was strong and similar in both small and large lakes (Fig. S8). The effect of human development of watersheds was overall insignificant in Great Plains and Eastern Temperate Forests lakes, but this might be attributable to the fact that nearly all lakes in those ecoregions were located in watersheds in which human development exceeded 50%. Further, some of the effect of human development of watersheds was probably already accounted for by the Secchi depth effect. Human development had a positive effect on species richness in Northern Forests lakes, which are nutrient limited (Heiskary *et al.*, 1987).

The common carp is one of the '100 world's worst invasive alien species' (Lowe *et al.*, 2000), and its impacts may be more severe than those of most invaders. However, there are several more recently introduced ecosystem engineers that are demonstrating similar capacity to spread and impact aquatic ecosystems. These include filter-feeding silver carp (*Hypophthalmichthys molitrix*) and bighead carp (*H. nobilis*) that are rapidly expanding throughout the Mississippi and Missouri watersheds and which are capable of modifying planktonic communities (Tsehaye *et al.*, 2013), zebra mussels (*Dreissena polymorpha*) that are capable of driving fundamental changes in water clarity (Caraco *et al.*, 1997) and which have been implicated in extinctions of native bivalves (Ricciardi *et al.*, 1998) or rusty crayfish (*Orconectes rusticus*) that can cause large-scale declines in aquatic vegetation (Matsuzaki *et al.*, 2009; Hansen *et al.*, 2013). Many of the currently expanding invasive species might ultimately have similar impacts on aquatic ecosystems across large geographic areas as those demonstrated for common carp in this study. Freshwater lakes, ponds and rivers comprise a small but very important biome (Downing *et al.*, 2006). Many have already lost their regional identity due to introductions of non-native species (Garcia-Berthou & Moreno-Amich, 2000). We hope that this work will demonstrate the value of curbing the introductions of non-native species to lakes and rivers worldwide.

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Supporting Information

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

Table S1 Size, maximum depth and mixing conditions in lakes where we examined the relationship between carp biomass and aquatic plant cover and species richness. All lakes were located in the Eastern Temperate Forests ecoregion.
Table S2 Carp biomass, total phosphorus (growing season mean), Secchi depth (springtime mean), aquatic plant cover and plant species richness in the lakes in which carp biomass was estimated using mark-recapture analyses.
Table S3 Lakes used to estimate the relationship between carp biomass (kg ha^{-1}) and gillnet catch rate (kg net^{-1}).
Table S4 Species of aquatic plants present in lakes that were used in whole-lake carp removal experiments.
Table S5 Parameter values of a linear model describing the effects of common carp biomass (kg ha^{-1}), Secchi depth (m), and total phosphorus (TP; µg L^{-1}) on plant cover (%) in whole-lake experiments.
Table S6 Parameter values of a linear model describing the effects of common carp biomass (kg ha^{-1}), Secchi depth (m), and total phosphorus (TP; µg L^{-1}) on plant richness in whole-lake experiments.
Table S7 Parameter coefficients for the most parsimonious (lowest AIC) model to explain submersed aquatic plant species richness across lakes of the Great Plains, Eastern Temperate Forests, and Northern Forests ecoregions.
Table S8 Best model for Great Plains ecoregion.
Table S9 Best model for Eastern Temperate Forests ecoregion.
Table S10 Best model for Northern Forests ecoregion.
Figure S1 Relationship between carp biomass estimates using mark-recapture and gillnet catch rates in lakes.
Figure S2 Diagnostics of variables used in model selection analysis for vegetation species richness in lakes of Great Plains, Eastern Temperate Forests, and Northern Forests ecoregions.
Figure S3 Diagnostics of variables used in model selection analysis for vegetation species richness in lakes of Great Plains, Eastern Temperate Forests, and Northern Forests ecoregions in which common carp were not detected (catch rate = zero).
Figure S4 Relationship between Secchi depth and submersed plant species richness in lakes without carp (catch rate = 0; left) and with carp (right) in Great Plains (red), Eastern Temperate Forests (black) and Northern Forests (green) ecoregions.
Figure S5 Relationship between carp catch rate and submersed plant species richness in lakes that had poor water clarity (Secchi <1 m; left) and good water clarity (Secchi >1 m; right).
Figure S6 Relationship between total phosphorus (µg L^{-1}) and Secchi depth (m) in lakes with (black circles, black line) and without (red circles, red line) carp (kg net^{-1}).
Figure S7 Relationship between common carp catch rate and total phosphorus concentration in lakes of Great Plains (red, $n = 47$), Eastern Temperate Forests (black, $n = 251$) and Northern Forests (green, $n = 178$) ecoregions.
Figure S8 Effects of carp abundance (log10 carp kg net^{-1} +1) on species richness of submersed plants in small (<95 ha; left) and large (>95 ha; right) lakes; 95 ha was the median lake size in our analysis.