



ORIGINAL PAPER

Different refuge types dampen exotic invasion and enhance diversity at the whole ecosystem scale in a heterogeneous river system

Louis Astorg · Sarah Sanderson · Virginie Côté-Gravel · Freedom Sorbara · Matthew J. S. Windle · Andrew P. Hendry · Alison M. Derry

Received: 2 December 2019 / Accepted: 24 September 2020
© Springer Nature Switzerland AG 2020

Abstract Refuges that result from environmental heterogeneity within ecosystems have an important yet under-appreciated role in maintaining native community diversity in face of exotic invasion. The objective of our study was to determine if different refuge types constrain invasion impacts on native biodiversity at the whole ecosystem-scale of the Upper St. Lawrence River. We focused on the voracious round goby fish as a sentinel exotic species whose spatial distribution within this ecosystem is also representative of the species distributions of several

other Ponto-Caspian invaders. We first explored if wetlands were acting as unknown refuges in reducing the local abundance of the round goby fish. We then tested the relative influence of a known broad-scale conductivity gradient compared with local wetlands on structuring the composition, diversity, and abundance of native macroinvertebrate and fish communities inside and outside each of these refuge types. We found that the two types of refuges, broad-scale conductivity gradient and local wetlands, limited round goby abundances at the whole ecosystem scale, and structured macroinvertebrate and fish community diversity. The broad-scale conductivity refuge was twice stronger than wetlands in limiting round goby abundance. Although wetlands were effective in constraining round goby abundance, the direct effect of wetlands rather than their indirect effects through limiting round goby abundance, were more powerful in explaining maintenance of macroinvertebrate and fish community diversity in invaded high conductivity waters. Our findings underscore the important role of environmental heterogeneity in producing different types of refuges that buffer invasion effects in freshwater ecosystems, and we advocate the preservation of wetlands as a part of this process.

Electronic supplementary material The online version of this article (<https://doi.org/10.1007/s10530-020-02374-7>) contains supplementary material, which is available to authorized users.

L. Astorg · V. Côté-Gravel · A. M. Derry
Département des sciences biologiques, Université du Québec à Montréal, Succursale Centre-Ville, C.P. 8888, Succursale Centre-Ville, Montréal, QC H3C 3P8, Canada
e-mail: derry.alison@uqam.ca

L. Astorg · S. Sanderson · A. P. Hendry · A. M. Derry
Groupe de recherche interuniversitaire en limnologie (GRIL), Montréal, Canada

S. Sanderson · F. Sorbara · A. P. Hendry
Redpath Museum and Department of Biology, McGill University, 859 Sherbrooke St. West, Montréal, QC H3A 0C4, Canada

M. J. S. Windle
St. Lawrence River Institute of Environmental Sciences, 2 St. Lawrence Dr, Cornwall, ON K6H 4Z1, Canada

Keywords Invasion · Environmental heterogeneity · Biodiversity · Refuges · Freshwater ecosystem · Wetlands

Introduction

Environmental heterogeneity, variation in physical and ecological landscape characteristics, is well known for influencing biodiversity (Cardinale et al. 2006; Stein et al. 2014) and ecosystem resilience to stressors (Oliver et al. 2015; Levine et al. 2016). Among anthropogenic stressors, biological invasions are one of the major factors that have contributed to species endangerment and extinction globally (Wilcove et al. 1998; Pejchar and Mooney 2009). Environmental heterogeneity has potential to play an important role in the preservation of native species diversity and abundances in invaded ecosystems by providing habitat refuges that limit the spread of biological invasions and constrain invasion impacts on native communities (Melbourne et al. 2007; Ricciardi et al. 2013; Vander Zanden et al. 2017). In this context, refuges can be continuous or discrete habitats with a reduced abundance of invasive species relative to native species, compared with the surrounding environment. Refuges from invasion might be especially beneficial for native biodiversity when different refuge types limit invader abundance at the whole ecosystem level. Yet, we are not aware of empirical studies that have explicitly considered the effects of environmental heterogeneity in refuge type especially within large, continuous ecosystems characterized by high connectivity and thus high potential for invasive species spread, in buffering invasion impacts on native biodiversity.

Environmental heterogeneity can generate refuges for native species in face of biological invasion by interacting with ecological tolerances and habitat preferences of the invasive species (e.g., Kestrup and Ricciardi 2009; Tamme et al. 2010; Anton et al. 2014). For example, refuges can occur when environmental conditions restrict the abundance and impact of invaders because of limits in their ecological tolerances (Kestrup and Ricciardi 2009; Iacarella and Ricciardi 2015; Latzka et al. 2016). Moreover, when abiotic heterogeneity limits invasive species survival (Iacarella and Ricciardi 2015) or competitive ability (MacDougall et al. 2006), it can contribute to biotic resistance to invasion (Elton 1977) through enhanced native species richness (Stein et al. 2014) and native predation pressure on exotic prey (Meynard et al. 2014; Stein and Kreft 2015; Yang et al. 2015). Maintaining environmental heterogeneity, by

conserving a variety of habitat types, can also potentially create refuges for native species in invaded landscapes, which become important for native species persistence (Dias, 1996) and biodiversity preservation (Stein et al. 2014) at the whole-ecosystem scale. Most of the research on the importance of environmental heterogeneity in invaded environments has been done in terrestrial ecosystems; knowledge about refuges in environmentally heterogeneous freshwater ecosystems is relatively scarce (exceptions: Kestrup and Ricciardi 2009; Iacarella and Ricciardi 2015; Latzka et al. 2016), despite that freshwater environments are among the most invaded ecosystems in the world (Richardson 2011).

At the same time, refuges can also enhance the persistence of native species that are adapted to these environments (Gelbard and Harrison 2003; Gram et al. 2004; Kobza et al. 2004; Derry et al. 2013). For example, wetlands are structurally complex highly productive aquatic habitats (Wetzel 1990) and contribute to environmental heterogeneity of shoreline aquatic habitats (Krieger 1992). Wetlands are known to promote freshwater diversity in shallow freshwater environments (Williams 1997; Gee et al. 1997; Robson and Clay 2005; Scheffer et al. 2006; Cérégino et al. 2007; Thiere et al. 2009) and seem to contribute disproportionately to regional biodiversity than other water-body types (Williams et al. 2004). Factors that increase biodiversity within wetlands are linked to the highly individual nature of physico-chemical characteristics of wetlands compared to rivers and large streams (Williams et al. 2004). In particular, structuring effects of vegetation in wetlands can create environmental conditions suitable for diverse assemblages of macroinvertebrates (Scheffer et al. 2006). The periodic flooding of certain wetlands can enhance biodiversity through the presence of egg banks that supply different macroinvertebrate species assemblages under various environmental conditions (Brendonck and Williams 2000). Furthermore, inundation of wetlands can favor genetic diversity by increasing dispersal and connectivity of wetland organisms (Rundle et al. 2002). Wetlands are highly productive environments because they host high rates of primary production, which in turn support high secondary production with rates that can exceed terrestrial ecosystems (Turner 1977). Moreover, there is a compelling yet limited number of studies that suggest that wetlands have unfavorable substrate and

hydrology for certain key aquatic invaders, including exotic zebra mussels (Bowers and Szalay 2004) and round gobies (Cooper et al. 2007, 2009; Young et al. 2010).

The objective of our study was to address if the effects of different refuge types can reduce invasion impacts on native freshwater biodiversity. We focused on the voracious round goby fish (*Neogobius melanostomus*) as a sentinel exotic species whose spatial distribution within the Upper St. Lawrence River is also representative of several other Ponto-Caspian invaders in this ecosystem (*Echinogammarus ischnus* amphipods:, Kestrup and Ricciardi 2009; dreissenid mussels: Neary and Leach 1992; Jones and Ricciardi 2005). We investigated the effects of environmental heterogeneity created by a broad-scale conductivity gradient and local wetlands in providing refuges to native fish and macroinvertebrate communities in face of Ponto-Caspian invasion in the Upper St. Lawrence River. Ponto-Caspian invaders are re-engineering littoral food webs of the Lower Great Lakes (Campbell et al. 2009), but invasion impacts on native biodiversity have been reported to be more attenuated in the Upper St. Lawrence River compared to the Lower Great Lakes (Kestrup and Ricciardi 2009; Iacarella and Ricciardi 2015). One mechanism that has been proposed to explain this difference in invasion impact is a broad-scale conductivity gradient from the joining of separate water masses from two major rivers in the Upper St. Lawrence with different calcium concentration, which has been shown to restrict Ponto-Caspian invaders (Jones and Ricciardi 2005; Whittier et al. 2008; Kestrup and Ricciardi 2009; Iacarella and Ricciardi 2015; Fig. 1). Conductivity is known to be a strong limiting factor of round goby invasion of freshwater habitats (Baldwin et al. 2012), likely because of their evolutionary history in brackish water and physiological constraints that result in reduced fitness and performance at low freshwater conductivity, especially when calcium is limiting (Iacarella and Ricciardi 2015). However, much less is known about the role of wetlands in providing refuges for native macroinvertebrate and fish communities from this exotic fish (Cooper et al. 2007, 2009; Young et al. 2010). We first explored if wetlands were acting as unknown refuges to reduce the local abundance of the round goby fish in invaded, high conductivity water of the Upper St. Lawrence River. We then tested the relative influence of the broad-scale conductivity

gradient and wetlands on structuring the composition, diversity, and abundance of native macroinvertebrate and fish communities inside and outside of these refuges. We provide one of the few freshwater studies to date to address the unexplored yet important role of environmental heterogeneity in buffering invasion effects on native biodiversity. More specifically, our study provides support for the importance of preserving different refuge types, including wetlands, for their effects in dampening the negative impacts of exotic invasion on freshwater biodiversity.

Materials and methods

Study system

At a broad, river-wide scale in the Upper St. Lawrence River, Canada (Fig. 1), Ponto-Caspian invaders such as the round goby fish are limited to areas that receive high conductivity water (30–40 mg/L of calcium) flowing from the Great Lakes (Kestrup and Ricciardi 2009; Baldwin et al. 2012; Iacarella and Ricciardi 2015). The confluence of the Upper St. Lawrence River and the Ottawa River at Lake St. Louis (N45°22'12", W73°49'12"), a lacustrine widening of the St. Lawrence River, has created a conductivity gradient in which the north side of Lake St. Louis receives low conductivity water (10–15 mg/L of calcium) from the Ottawa River whereas the south side receives high-conductivity water (30–40 mg/L of calcium) from the St. Lawrence River (Hudon et al. 2003) (Fig. 1). The Ponto-Caspian invasive exotics are absent from areas that receive low conductivity water (10–15 mg/L of calcium) from the Ottawa River (Kestrup and Ricciardi 2009; Iacarella and Ricciardi 2015). Within these water masses and along the conductivity gradient in the Upper St. Lawrence River, wetlands provide productive aquatic habitats that are structurally complex compared to adjacent shoreline habitats and contribute to environmental heterogeneity of shoreline aquatic habitats (Wetzel 1990; Krieger 1992). The environmental heterogeneity created by wetlands has the previously unexplored potential to generate numerous local refuges for native species in the face of exotic invasion within the high conductivity water of the Upper St. Lawrence River.

Between spring and fall of 2017 and 2018, we collected macroinvertebrate and fish community data,

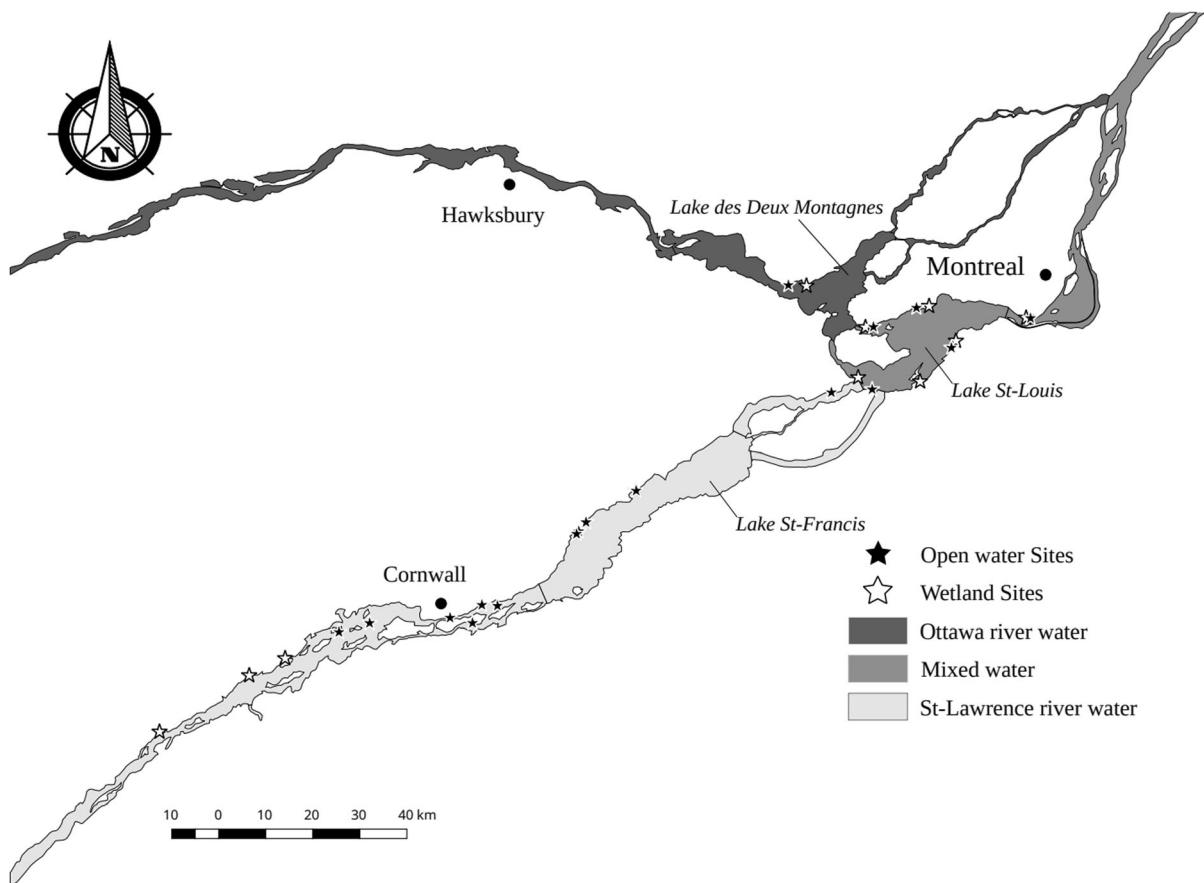


Fig. 1 Map of the sampled area in the Upper St. Lawrence River. White background represents land, the light grey color is high conductivity water from the St. Lawrence River, and the dark grey color represents low conductivity water from the Ottawa River. The intermediate grey color represents an area of

mixing of water masses. Note that the water mixing is not homogeneous in the mixing zone; water near the shore is less mixed. The solid stars represent open-water shore sampling sites while open stars represent wetland sampling sites

as well as environmental data, from wetland sites and from open-water (non-wetland) shore sites in the Upper St. Lawrence River (Lake St. Francis and upstream), Ottawa River (Lac des Deux Montagnes), and in Lake St. Louis in Québec and Ontario, Canada (Fig. 1). Wetland sites were identified and chosen using information from Ducks Unlimited Canada (Powers et al. 2012) and Land Information Ontario (LIO). A total of 27 sites were sampled for this study: 9 wetland sites and 17 open-water shore sites (Fig. 1). Of the 27 total sampling sites, eight sites were located in low conductivity water and 19 sites were in high conductivity water; the purpose of sampling a greater number of high conductivity sites was to focus the effort on the potential yet unknown attenuating effects of wetlands on biological invasion for native

freshwater biodiversity in invaded areas of the Upper St. Lawrence River. The importance of low conductivity water in limiting round goby abundance has already been established by other previous studies (Kestrup and Ricciardi 2009; Baldwin et al. 2012; Iacarella and Ricciardi 2015).

Of the 27 sampling sites, 12 were located in Lake St. Louis (Fig. 1). Wetlands along each of the north and south shores of Lake St. Louis were sampled for a total of 6 wetlands and 6 open-water shore sites. In the low conductivity water refuge in Lake des Deux Montagnes, which receives low conductivity water from the Ottawa River that prevents round goby invasion (Iacarella and Ricciardi 2015), we sampled 1 wetland site and 1 open-water shore site. In the highly invaded high conductivity waters of Lake St. Francis,

we sampled 4 open-water shore sites. In the St. Lawrence River upstream of Lake St. Francis, we sampled 3 wetlands and 6 open-water shore sites. The selection of wetlands for sampling was based on maximizing the number of accessible wetlands while keeping a sampling design as balanced as possible.

Community data collection

For macroinvertebrate collection, three transects were randomly established to collect three samples at each site. Sampling was performed by the sweep method (“Kick and Sweep”) with a 500- μm “D-net” as recommended by the Ontario Benthos Biomonitoring Network (OBBN; Ontario, Dorset Environmental Science Centre, and Jones 2007). The collected samples were stored in 100% ethanol and brought back to the laboratory at the Université du Québec à Montréal (UQAM) for identification. Identification was done up to the Family level using Moisan (2010). For each sample, 100 mL sub-sample was taken and counted until the 100th individual was reached. If the 100th individual was not reached within the initial 100 mL, an additional 100 mL was counted. When the 100th individual was reached, the remaining part of the sub-sample was counted, and the total sub-sampled volume calculated. A ratio was then calculated between the total sub-sampled volume and the sample total volume to estimate the taxon-specific abundance of macroinvertebrates. The abundance in each site was estimated using the mean abundance of the three samples collected at every site. All macroinvertebrate samples were identified using SZX10 stereo microscopes (Olympus) with varying magnification ($\times 6.3$ – $\times 10$). For fish collection, each site was seined three times consecutively for replication, with short (< 1 h) intermission periods between seining times. The dimensions of the seine were 114 cm by 407 cm with 5 mm mesh. After seining, all fish were placed into bins, sorted by species according to Bernatchez and Giroux (2000), and counted for species-specific abundance.

Environmental data collection

Dissolved oxygen (DO; mg L⁻¹), pH, water temperature (°C) and conductivity ($\mu\text{S cm}^{-2}$) were measured using a Professional Plus Model YSI multi-parameter sonde (model 10102030; Yellow Springs Inc.).

Dissolved organic carbon (DOC; mg L⁻¹) and water calcium (Ca; mg L⁻¹) were measured from water samples for a subset of the sites around Lake St. Louis where there are important gradients of DOC and water Ca. We also collected water samples to quantify total nitrogen (TN; mg L⁻¹), and total phosphorous (TP; $\mu\text{g L}^{-1}$). Detailed analytical methods for measured water chemistry variables are provided in Appendix 1. We provide a Principal Component Analysis (PCA) to visualize how study sites are distributed across the environmental gradients (Appendix 2; Fig. 6 and 7). PCA of the all sites had missing values; we imputed the missing data using an iterative PCA algorithm (Josse and Husson 2012).

Data analyses

Diversity indices

Diversity indices were calculated using total abundances for the macroinvertebrate and fish community assemblages separately. We calculated taxon richness, Shannon diversity (Shannon 1948) and Pielou’s evenness (Pielou 1969). These diversity indices and total abundances were included as response variables in different generalized linear models that tested the influence of wetlands, conductivity and round goby abundance together in each model (see section below). Conductivity and water Ca correlated highly (Regression Calcium-Conductivity: $R^2 = 0.87$, P value = 1.364e–06), and conductivity was selected for the generalized linear models as it had the most complete dataset across all sampling sites. Local Contribution to Beta Diversity (LCBD) was computed from a percentage difference dissimilarity matrix for each site for both macroinvertebrate and fish in order to distinguish sites that contributed the most to overall beta diversity. LCBD represents the degree of uniqueness of a site in terms of species composition (Legendre 2014).

Generalized linear models

We investigated the effect of the broad-scale conductivity gradient and wetland on round goby abundance. The effect of water conductivity, wetlands, and round goby abundance were tested on diversity indices (Shannon index, taxon richness and Pielou’s evenness, and LCBD) as well as on the total abundance for each

of macroinvertebrate and fish communities. The different variables included in generalized linear models required different probability distributions. Count data such as round goby abundance and total abundance of macroinvertebrates and fish were first assigned a Poisson distribution. The equi-dispersion hypothesis of Poisson models was tested using the AER package in R 3.6.3 (R Core Team 2018), and this indicated that all models in which a Poisson distribution was applied were over-dispersed. We therefore next applied a zero-inflated Poisson model to investigate the effect of the broad-scale conductivity gradient and wetland on round goby abundance because wetland sites inflated the number of sites with null round goby abundance (Appendix S2: Fig. 8). For each of macroinvertebrate and fish communities, we applied negative binomial distributions to models to the total abundance data. Zero-inflated models and negative binomial models all showed improvement over Poisson distribution models using Vuong test (Vuong 1989). For Shannon index, taxon richness and Pielou's evenness, and LCBD that are positive continuous variables, we used Gamma distributions that best fitted the data. For all generalized linear models, we performed backward model selection, removing interaction and variables from a full model in a step-wise manner. We selected the most parsimonious model using model AIC values (Aho et al. 2014). Following model selection, model residuals were investigated for non-linear patterns (residuals vs fitted values), distribution fit (qqplot), equal spread (scale location) and outliers (residuals vs leverage and sites outside 1.5 times the interquartile range above the upper quartile and below the lower quartile). Model diagnostics detected outliers in round goby abundances and in macroinvertebrate taxonomic abundances that influenced model outcomes; these sites were therefore removed from these models.

Effect size

To compare the relative importance of conductivity and wetlands on the abundance of invasive fish at each site, Cohen's D effect sizes (Cohen 2013) were computed. The effect size of wetlands on round goby abundance were computed for the full dataset, for only high conductivity sites, and for only low conductivity to determine if the effect of wetland on round goby abundance was consistent throughout the conductivity

gradient. We used the effsize package in R 3.6.3 (R Core Team 2018) to compute the different Cohen's D effect sizes.

Structural equation modelling

We wanted to determine if the effects of wetlands in invaded landscape (high-conductivity sites) were direct or mediated by reduced round goby abundance. We applied mediation analysis using structural equation models (SEMs) (Grace 2006; Gunzler et al. 2013) to test for indirect correlations between wetland presence and community diversity (Shannon index, taxon richness, Pielou's evenness, LCBD and Abundance) mediated by round goby abundance in high-conductivity sites only. This was done for each of macroinvertebrates and fish communities diversity indices on which the effect of wetlands was potentially mediated by round goby abundance (Fig. 2). We therefore tested the total, direct and indirect effect of wetland on community composition and diversity indices (Fig. 2). The total effect c (Fig. 2a) tests the effect of wetland without an indirect or mediation path in the model structure (i.e., the unstandardized slope of the regression of wetland on community composition and diversity indices). The direct effect c' (Fig. 2b) represents the effect of wetland on community composition and diversity indices after controlling for the proposed mediator variable, here round goby abundance. The effect of wetland on round goby abundance is represented by the path a (Fig. 2b), and the effect of round goby abundance on community composition and diversity indices, controlling for wetland, is represented by the path b (Fig. 2b). Finally, the indirect effect is the product of a*b = ab (Fig. 2b). The indirect effect (ab) is generally equivalent to c-c', the difference between the total effect and the direct effect, but it is easier to test the significance of ab because these coefficients are drawn from a single model, whereas c and c' are from separate models (Rucker et al. 2011). Each metric was analyzed in separate models for macroinvertebrates and fish. The SEM analysis was performed using the Lavaan package in R (R Core Team 2018).

Redundancy analysis

Redundancy analysis (RDA) is a canonical ordination procedure that examines relationships among response

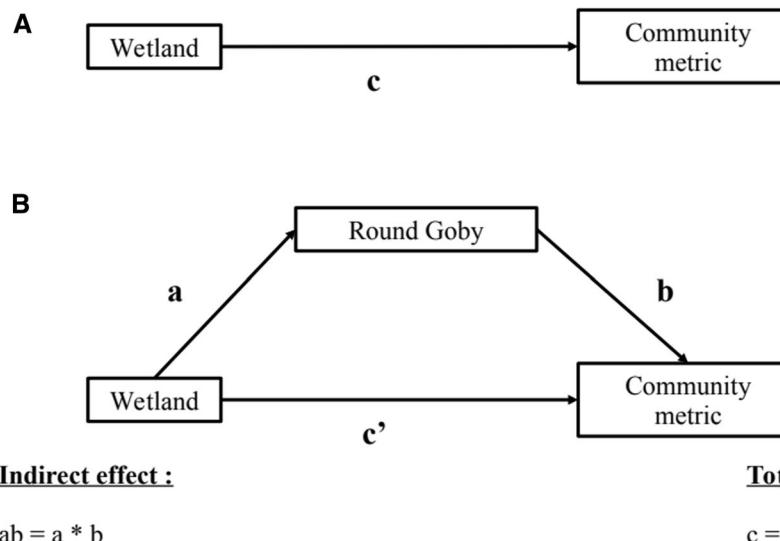


Fig. 2 Structural equation models (SEMs) of hypotheses to test total, direct and indirect effects of wetlands on macroinvertebrate and fish community diversity and composition: **a** Model without an indirect effect mediating wetland influence on community indices; path c represents the total effect of wetlands on community diversity and composition. The total effect includes the direct effect and all possible indirect effects of wetlands on community diversity and composition. **b** Model with an indirect effect of wetlands on community indices via

reduced round goby abundance; path a is the effect of wetland on the mediator variable (round goby abundance), path b is the effect of round goby abundance on community diversity and composition, and path c' represents the direct effect of wetland on community diversity and composition; Path $ab = a*b$ is the product of path a and path b and represents the indirect effect of wetlands on community diversity and composition via round goby abundance

variables and predictor variables in multivariate space (ter Braak and Verdonschot 1995). The resulting RDA diagrams summarize the major environmental variables structuring biological communities while showing the approximate species composition for the different samples (Blanchet et al. 2014). We used RDA to evaluate environment-taxon relationships for macroinvertebrate and fish assemblages. We used forward selection to determine which environmental variables were related to response metrics. Forward selection (Blanchet et al. 2008) of the explanatory variables was achieved using the `ordistep{vegan}` function in R 3.6.3 (R Core Team 2018) ($\alpha = 0.05$). Prior to RDA, community data was Hellinger transformed to down-weight the influence of rare species (Legendre and Gallagher 2001). RDAs were performed on the full broad-scale scale data set of sites in the Upper St. Lawrence River, as well as on St. Lawrence River and Ottawa River sites separately to test if different environmental variables structure the fish and macroinvertebrate communities with and without the broad-scale scale refuge. All statistical

analyses were performed in R 3.6.3 (R Core Team 2018).

Results

Broad-scale conductivity gradient and local wetland refuges reduce invader abundance

We detected broad-scale conductivity and local wetland refuges for macroinvertebrate and fish communities in the face of round goby invasion in the Upper St. Lawrence River. In accord with other studies in this system (Kestrup and Ricciardi 2009; Iacarella and Ricciardi 2015), we found a positive relationship between round goby abundance and conductivity at a broad spatial scale in the Upper St. Lawrence River (Table 1, Line 3, Fig. 3a, generalized linear model). Wetlands provided local refuges that limited round goby abundance: round goby abundances were lower inside wetlands compared to outside wetlands within invaded high conductivity waters (Table 1, Line 2, Fig. 3a, generalized linear model). The effect of

Table 1 Generalized linear model results for the influence of the broad-scale conductivity gradient, wetlands, and round goby abundance as predictors of community diversity indices: Shannon diversity (Shannon), Pielou Evenness (Evenness),

taxon or species richness (Richness), Local Contribution to Beta Diversity (LCBD), and total abundance of macroinvertebrate and fish communities (Abundance)

Line	Response variable	Predictor	Estimate (s.e.)	Df	T-value	P value
1	Round goby	Intercept	1.625 (0.452)	8	3.591	0.0003
2		Wetland	1.619 (0.479)	8	3.379	0.0007
3		Conductivity	0.005 (0.001)	8	3.199	0.001
4		Wet:Cond	- 0.004 (0.001)	8	- 2.37	0.0177
5	Shannon Macro	Intercept	0.932 (0.082)	25	11.317	2.5e-11
6		Conductivity	- 0.0007 (0.0002)	25	- 3.227	0.003
7	Evenness Macro	Intercept	1.99 (0.177)	25	11.241	2.88e-11
8		Conductivity	- 0.0013 (0.0005)	25	- 2.708	0.012
9	Richness Macro	Intercept	0.085 (0.006)	25	12.912	1.47e-12
10		Wetland	0.028 (0.009)	25	3.167	0.004
11	Abundance Macro	Intercept	7.287 (0.35)	23	20.809	< 2e-16
12		Wetland	- 0.567 (0.284)	23	- 1.997	0.045
13		Conductivity	- 0.002 (0.001)	23	- 2.901	0.003
14	Shannon Fish	Intercept	0.77 (0.079)	25	9.629	6.85e-10
15		Wetland	- 0.052 (0.095)	25	- 0.551	0.586
16	Evenness Fish	Intercept	1.755 (0.183)	25	9.551	8.04e-10
17		Conductivity	- 0.0007 (0.0005)	25	- 1.33	0.196
18	Richness Fish	Intercept	6.002e-02 (2.089e-02)	23	2.874	0.008
19		Wetland	7.994e-02 (2.856e-02)	23	2.782	0.011
20		Conductivity	2.513e-04 (2.856e-02)	23	2.730	0.011
21	Abundance Fish	Wet:Cond	3.115e-04 (1.084e-04)	23	- 2.873	0.008
22		Intercept	4.816 (0.289)	25	16.665	4.75e-15
23		Wetland	0.355 (0.354)	25	1.004	0.325
24	LCBD Macro	Intercept	21.722 (3.193)	25	6.803	3.94e-07
25		Wetland	9.013 (4.516)	25	1.996	0.057
26	LCBD Fish	Intercept	22.004 (1.423)	25	15.464	2.63e-14
27		Wetland	8.454 (1.991)	25	4.246	0.0002

The influence of conductivity and wetland on round goby abundance are reported. In each model, variables and interactions were selected using AIC values. Both macroinvertebrate and fish diversity indices were included in generalized linear models; these are referred to as Macro and Fish, respectively. Bold P values are < 0.05. Interaction between wetland and conductivity is referred to as Wet:Cond in the table. Significant findings are summarized in Fig. 3 for round goby abundance and Fig. 4 for macroinvertebrate and fish community diversity indices and composition

wetlands in dampening round goby abundance was dependent on water conductivity, and only apparent in the high conductivity water and absent at low water conductivity sites (The wetland: conductivity interaction; Table 1, Line 4, generalized linear model; Fig. 3a). Conductivity and the presence of wetlands were therefore the two major environmental variables that structured round goby abundance across the

Upper St. Lawrence River in our study. The effect size of conductivity on round goby abundance was approximately twice as large as the effect size of wetlands, but the effect size of wetland on round goby abundance was strongly negative in high conductivity water (Fig. 3b). The effect size of wetlands on round goby abundance was slightly negative with wide error bars in low conductivity water (Fig. 3b).

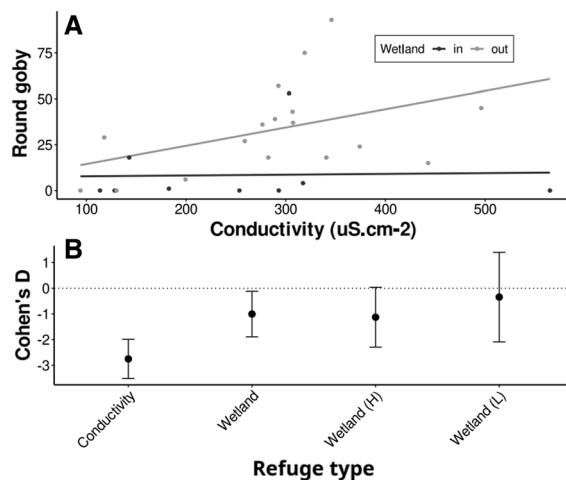


Fig. 3 Identification of different refuge types in the Upper St. Lawrence River, and their relative influences in reducing round goby abundance. **a** Linear positive relationship between broad-scale water conductivity gradient and round goby abundance, excluding wetland sites (generalized linear model, Table 1, Line 2); **b** The difference in round goby abundance inside and outside local wetlands within invaded, high-conductivity water (generalized linear model, Table 1, Line 4); **c** Cohens' D effect size of conductivity and wetlands on round goby abundance: all sites, only high conductivity wetland sites (H), and only low conductivity wetland sites (L)

Broad-scale conductivity gradient and local wetland refuges enhance community diversity

Conductivity and the presence of wetlands were two major environmental variables that structured the macroinvertebrate (Fig. 4a–d) and fish (Fig. 4e, f) diversity in the Upper St. Lawrence River (Table 1, generalized linear models). High conductivity water, where exotic round gobies are well established, had a higher Shannon diversity (Table 1, Line 6, Fig. 4a) and Pielou's Evenness (Table 1, Line 8), but lower total abundance of macroinvertebrate communities (Table 1, Line 13, Fig. 4c). For the native fishes, however, conductivity had positive effects on the fish community species richness (Table 1, Line 20). Across the conductivity gradient, sites within wetlands had, relative to sites outside wetlands, higher macroinvertebrate taxon richness (Table 1, Line 10, Fig. 4c), higher macroinvertebrate abundance (Table 1, Line 12, Fig. 4d) and lower fish species richness (Table 1, Line 26). Local Contribution to Beta Diversity (LCBD) of fish (Table 1, Line 27, Fig. 4f) was also higher inside wetlands. We found a significant interaction of wetland and conductivity on species richness

of the native fish community: fish species richness was lower in wetlands within invaded high conductivity waters compared to in wetlands at low water conductivity sites (Table 1, wetland x conductivity Line 21, 4e). We found support for the positive effects of wetlands on taxon richness of macroinvertebrates (Table 2, Line 8), the negative effects of wetlands on fish species richness (Table 2, Line 38), and the positive effect of wetlands on LCBD of the fish community (Table 2, Line 78) at high water conductivity sites. Enhanced community diversity, richness, evenness, and LCBD of macroinvertebrate and fish communities were directly accounted by the habitat provisioning of wetlands; while wetlands provided refuges by limiting round goby abundance, positive community diversity effects were not explained by lessened round goby impact in wetlands (Table 2, SEMs, Fig. 2b).

Broad-scale conductivity gradient and local wetland refuges structure community composition

There were pronounced effects of conductivity and wetlands on macroinvertebrate and fish community composition (Fig. 5a, b, RDAs). The strong clustering of samples on the conductivity axis in both macroinvertebrate and fish communities confirmed that conductivity was the main driver of community differences between the low-conductivity and high-conductivity shoreline habitats. To identify structuring variables of macroinvertebrate and fish communities at local scales within water types, only sites from either the Ottawa or St. Lawrence River were used in a subset of RDAs. Among low-conductivity sites, no variable was selected by the forward selection procedure. Thus, wetlands influenced macroinvertebrate and fish community composition only in the high conductivity, invaded waters of the Upper St. Lawrence River (Fig. 5c, d, RDAs). Details on specific macroinvertebrate and fish community taxon differences across the conductivity and wetland refuges are provided in Appendix S2. Figures 9–12.

Discussion

Our study supports the presence of different refuge types that constrain exotic round goby abundance and promote native freshwater biodiversity at the

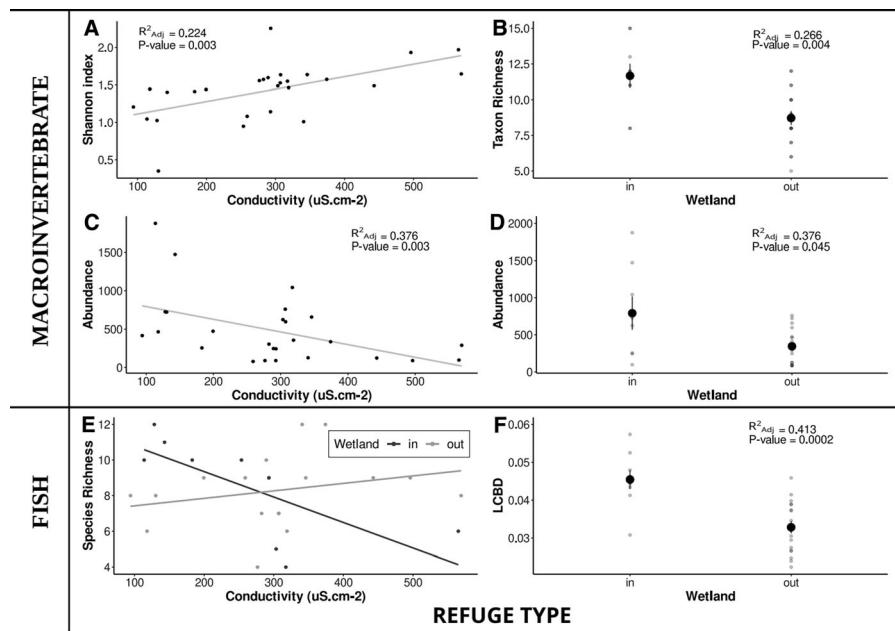


Fig. 4 Broad-scale conductivity gradient and local wetland refuges enhance native community diversity. The top panels display linear relationships between the conductivity gradient across the Upper St. Lawrence River and Shannon indices of the **a** macroinvertebrate and **b** fish communities. The middle panels indicate taxon richness inside and outside wetlands for **c** macroinvertebrate and **d** fish communities. The bottom panels show Local Contribution to Beta Diversity (LCBD) scores

inside and outside wetlands for **e** macroinvertebrate and **f** fish communities. For the **c**, **e** and **f** mean and standard error are represented (dark) over raw data (grey). For all panels, the grey dots and grey linear regression lines represent open-water shore sites, while black dots and black linear regression line represent wetland sites. Statistical results for generalized linear models associated with each of these panels are summarized in Table 1

ecosystem scale in the Upper St. Lawrence River. The conductivity gradient had a twice as strong effect as wetlands in excluding round gobies from low conductivity habitats. Wetlands were effective in limiting round goby abundances in invaded waters. Wetlands, and not solely ecological interactions through reduced round goby abundances, increased the diversity of macroinvertebrate and to a lesser effect, fish, communities within invaded waters. Our findings suggest that environmental heterogeneity in producing different refuge types has an important yet under-appreciated role in combining to maintain native community diversity at a whole-ecosystem scale in face of exotic invasion.

Broad-scale conductivity gradient and local wetland refuges reduce invader abundance

Our results support the findings of other previous studies that found that low conductivity waters exclude round gobies (Baldwin et al. 2012; Iacarella

and Ricciardi 2015), as well as other Ponto-Caspian exotics (*Echinogammarus ischnus* amphipods; Kestrup and Ricciardi 2009; dreissenid mussels: Neary and Leach 1992; Jones and Ricciardi 2005), and thus represent an important refuge in the Upper St. Lawrence River. However, we also detected previously underappreciated refuges from round goby invasion in wetlands along shoreline environments. The refuge effect from wetlands in reducing round goby abundance could be the result of substrate preferences of this benthic fish species. Round gobies preferentially colonize, and are found in greater densities, on rock and cobble substrates (Ray and Corkum 2001; Young et al. 2010). Soft-bottomed wetlands with high biological productivity appear to be less hospitable for this invasive fish in the Lower Great Lakes (Cooper et al. 2007; Coulter et al. 2015), although their role as a refuge for native aquatic species has not previously been fully explored. Local refuges provided by wetlands could be of particular importance because of their role in locally reducing

Table 2 Results of mediation analysis using structural equation models (SEMs) to test for total, direct and indirect (mediated by round goby abundance) effects of wetlands on community diversity and composition for macro (macroinvertebrates) and fish

Line	Response variable	Path	Estimate	SE	Z	Ci lower	Ci upper	P value
1	Shannon macro	a	36.100	13.547	2.665	5.928	59.312	0.008
2		b	0.001	0.002	0.636	-0.004	0.004	0.525
3		c'	-0.197	0.238	-0.828	-0.726	0.225	0.408
4		ab	0.045	0.071	0.644	-0.104	0.179	0.520
5		c	-0.152	0.231	-0.658	-0.609	0.319	0.511
6	Richness macro	a	36.100	13.547	2.665	5.928	59.312	0.008
7		b	0.027	0.015	1.771	0.006	0.064	0.076
8		c'	-3.909	1.250	-3.127	-5.903	-0.771	0.002
9		ab	0.981	0.546	1.795	0.108	2.314	0.073
10		c	-2.929	1.257	-2.330	-5.140	-0.137	0.020
11	Evenness macro	a	36.100	13.547	2.665	6.028	59.312	0.008
12		b	0.000	0.001	-0.276	-0.003	0.001	0.783
13		c'	0.023	0.095	0.244	-0.176	0.202	0.807
14		ab	-0.008	0.026	-0.308	-0.081	0.033	0.758
15		c	0.015	0.093	0.166	-0.159	0.213	0.869
16	Abundance macro	a	36.100	13.547	2.665	5.928	59.313	0.008
17		b	-0.482	1.211	-0.398	-3.502	0.916	0.690
18		c'	40.010	104.196	0.384	-289.596	197.290	0.701
19		ab	-17.410	42.727	-0.407	-133.529	40.346	0.684
20		c	22.600	96.282	0.235	-226.425	177.310	0.814
31	LCBD macro	a	36.100	13.547	2.665	5.928	59.312	0.008
32		b	0.000	0.000	-1.324	0.000	0.000	0.186
33		c'	-0.011	0.010	-1.129	-0.035	0.006	0.259
34		ab	-0.005	0.004	-1.299	-0.017	0.000	0.194
35		c	-0.016	0.009	-1.729	-0.038	0.000	0.084
36	Shannon fish	a	36.100	13.547	2.665	6.028	59.312	0.008
37		b	-0.004	0.003	-1.254	-0.014	0.000	0.210
38		c'	0.564	0.235	2.403	0.059	0.996	0.016
39		ab	-0.156	0.118	-1.322	-0.516	0.003	0.186
40		c	0.408	0.215	1.901	-0.018	0.861	0.057
41	Richness fish	a	36.100	13.547	2.665	6.028	59.312	0.008
42		b	-0.017	0.018	-0.976	-0.065	0.008	0.329
43		c'	2.252	1.400	1.609	-0.927	4.797	0.108
44		ab	-0.624	0.590	-1.057	-2.395	0.147	0.291
45		c	1.629	1.276	1.277	-0.969	4.162	0.202
46	Evenness fish	a	36.100	13.547	2.665	5.928	59.312	0.008
47		b	-0.002	0.001	-1.294	-0.005	0.000	0.196
48		c'	0.156	0.118	1.323	-0.092	0.376	0.186
49		ab	-0.057	0.040	-1.452	-0.166	-0.001	0.147
50		c	0.099	0.119	0.832	-0.129	0.337	0.405
51	Abundance fish	a	36.100	13.547	2.665	5.928	59.313	0.008
52		b	-0.482	1.211	-0.398	-3.502	0.916	0.690
53		c'	40.010	104.196	0.384	-289.596	197.290	0.701
54		ab	-17.410	42.727	-0.407	-133.529	40.346	0.684

Table 2 continued

Line	Response variable	Path	Estimate	SE	Z	Ci lower	Ci upper	P value
55		c	22.600	96.282	0.235	- 226.425	177.310	0.814
76	LCBD fish	a	36.100	13.454	2.683	7.358	59.336	0.008
77		b	0.000	0.000	- 0.315	0.000	0.000	0.753
78		c'	- 0.015	0.005	- 2.654	- 0.026	- 0.006	0.008
79		ab	- 0.001	0.003	- 0.364	- 0.007	0.004	0.716
80		c	- 0.016	0.005	- 3.232	- 0.023	- 0.003	0.001

The path c is the total effect of wetlands on community diversity and composition. The total effect includes the direct effect and all possible indirect effects of wetlands on community diversity and composition (Fig. 2a). Path a is the effect of wetland on the mediator variable (round goby abundance), path b is the effect of round goby abundance on community diversity and composition, and path c' represents the direct effect of wetland on community diversity and composition; Path ab = a*b is the product of path a and path b and represents the indirect effect of wetlands on community diversity and composition via round goby abundance (Fig. 2b). The transformation used for each community is specified after each response variable in the table. Bold P-values are < 0.05

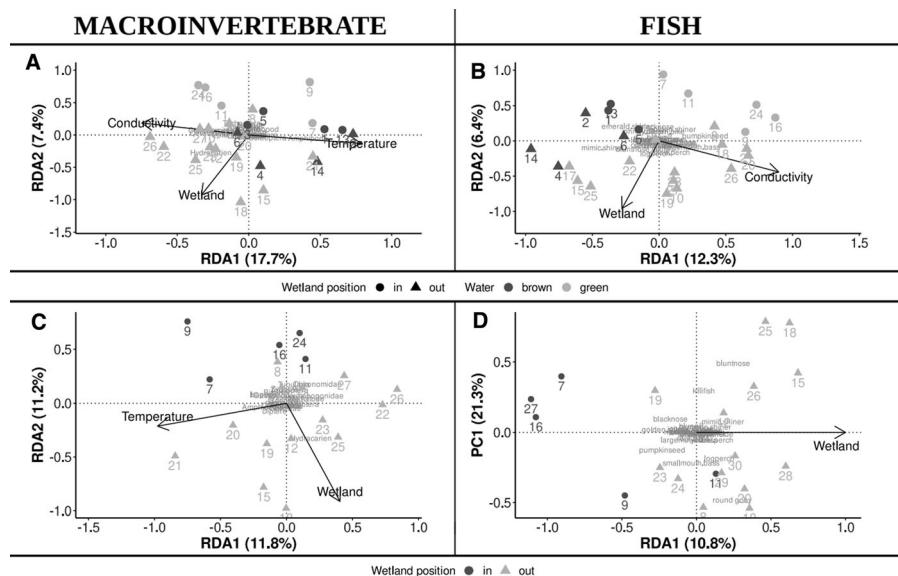


Fig. 5 Broad-scale conductivity gradient and local wetland refuges structure communities: RDA biplots with the full dataset for **a** macroinvertebrate and **b** fish communities and RDA biplots with a reduced dataset of only St. Lawrence River sampling sites (high conductivity) for **c** macroinvertebrate and **d** fish communities. In all panels, arrows represent forward

selected environmental variables; numbers represent sampling sites. The grey solid symbols represent sampling sites in the high conductivity water and dark solid symbols represent sampling sites in the low conductivity water. The triangles represent sampling sites within wetlands and circles represent sampling sites outside wetlands

invasive round goby abundance, especially in the invaded high conductivity waters of the Upper St. Lawrence River. Given that dispersal between communities is higher at smaller spatial scales than at larger spatial scales, local refuges from invasive species in patchy wetlands could potentially provide

important demographic subsidies of individuals belonging to native species in surrounding areas (Melbourne et al. 2007), enhancing native community resilience in more heavily invaded areas of ecosystems (Strayer et al. 2006).

Local wetland refuges enhance community diversity

Wetlands generally have different substrate, organic matter load, dissolved oxygen levels, nutrient concentrations and environmental complexity from other surrounding shorelines (Wetzel 1990; Krieger 1992), which can enhance the diversity of macroinvertebrate communities (Nelson et al. 2000). These characteristics of wetlands likely contributed to the positive effects on community diversity that we observed in wetland macroinvertebrate communities in our study (Fig. 4). We did not detect indirect benefits of the wetlands on native macroinvertebrate and fish community biodiversity through reduced round goby abundances (Table 2, Fig. 2b). The SEMs and RDAs (Fig. 5) with only high-conductivity sites also indicated that wetland habitats enhanced macroinvertebrates taxon richness, fish community Shannon index and LCBD, as well as structured fish communities. Our study therefore confirms that wetland habitats can be of crucial importance for the preservation of aquatic biodiversity in invaded freshwater landscapes (Bowers and Szalay 2004; Cooper et al. 2007, 2009; Young et al. 2010).

Wetlands had a direct positive effect in increasing the diversity of macroinvertebrate communities, but less so in fish communities (Fig. 4). Wetlands in high conductivity water hosted lower fish species richness compared to wetlands in low conductivity water (Table 1, wetland x conductivity Line 21, 4e). Following their establishment in aquatic ecosystems over several decades, round gobies have become a key food source of piscivorous fish species in the Lower Great Lakes (Crane et al. 2015) and in the St. Lawrence River (Morissette et al. 2018). The lower abundance of round gobies inside wetlands may therefore be a limiting prey resource for piscivorous fish that is more plentiful at open-water shore sites in high conductivity waters. The difference in round goby abundance between wetland and open-water shore sites may therefore potentially cause certain fish species to favor open-water shore habitats over wetlands in invaded, high conductivity water. Further, different fish species utilize wetlands in various manners: some species are permanent resident of wetlands (e.g., *Ameiurus nebulosus* (brown bullhead), *Umbra limi* (central mudminnow) and *Lepisosteus osseus* (longnose gar)), while other fish species only spawn in wetlands and

then leave them for open-water areas (e.g., *Esox lucius* (northern pike), *Cyprinus carpio* (common carp), and *Notropis hudsonius* (spottail shiner)) (Jude and Pappas 1992). The dynamic nature of fish communities in wetlands may have limited our ability to properly estimate their alpha diversity at a given point in time. Although fish alpha diversity was reduced in high conductivity water wetlands, fish beta diversity was increased by wetlands. Therefore, high conductivity water wetlands in the Upper St. Lawrence River have relatively species-poor fish communities, yet also host to unique fish assemblages compared with open-water shore sites.

Different refuges dampen invasion and enhance diversity at the whole ecosystem scale

Wetlands presented refuges that both reduced local round goby abundance, and also directly increased both alpha and beta diversity of macroinvertebrate and beta diversity of fish within invaded, high conductivity waters. Interestingly, wetlands did not have strong effects on macroinvertebrate and fish community structure in the low conductivity water of the Ottawa River when community data from the high-conductivity water of St. Lawrence River and low-conductivity water from the Ottawa River were analyzed separately. The low-conductivity water is a refuge from invasion, therefore local wetlands seems to be less important for native species when nested within a spatially broader refuge. A caveat is that more wetlands and open-water shore sites were sampled in high conductivity water than in low conductivity water, which could have reduced our ability to detect wetland effects in low conductivity water. However, taken altogether, local refuge inside wetlands enabled diverse assemblages of macroinvertebrates and unique assemblages of fish, making these critical habitats for aquatic diversity, especially within invaded, high conductivity waters. The environmental heterogeneity provided by wetlands had a strong positive effect on macroinvertebrate community diversity, and also to a lesser extent for fish communities. Environmental heterogeneity has been shown to increase species diversity in many groups (Tews et al. 2004), but it can also decrease species diversity in some cases (Sullivan and Sullivan, 2001). The effect of environmental heterogeneity can vary depending on how the studied

animal guild perceives this heterogeneity and the spatial scale of the study (Tews et al. 2004).

Most of research on environmental heterogeneity in invaded environments to date has been done in terrestrial ecosystems; our study joins a handful of papers that have addressed this topic in freshwater ecosystems (Kestrup and Ricciardi 2009; Iacarella and Ricciardi 2015; Latzka et al. 2016). Refuges to invasion at local scales (Holway et al. 2002; Leprieur et al. 2006; Menke and Holway 2006; Krassoi et al. 2008) and at broad scales (Menke et al. 2007; Kestrup and Ricciardi 2009; Anton et al. 2014) have been recognized as important driver of invasive abundance and native community diversity. Our results confirm the results of other studies that environmental heterogeneity can locally decrease invasion impact in invaded areas (Melbourne et al. 2007; Ricciardi et al. 2013; Vander Zanden et al. 2017). Our findings uniquely highlight that environmental heterogeneity from different types of refuges can dampen invasion impact and enhance aquatic community diversity at the whole ecosystem scale. In our study, broad-scale environmental heterogeneity, such as the conductivity gradient across the Upper St. Lawrence River, can allow native species to be sheltered from invasive species and create diversity of communities by structuring composition of organisms. Local scale heterogeneity, such as the patchy wetlands within the invaded, high conductivity waters, have the potential to reduce invasive species abundance and increase local community diversity. Freshwater ecosystems are among the most invaded ecosystems in the world (Richardson 2011), and our findings are reported from one of the most economically and culturally important invaded bodies of freshwater in North America, the St. Lawrence River (Vincent and Dodson 1999; Carignan and Lorrain 2000; Kavcic 2016).

Caveats

Other previous research has investigated macroinvertebrate diversity patterns in the Upper St. Lawrence River, and this research found contrasting patterns to what we report in our study (Kipp and Ricciardi 2012; Kipp et al. 2012). These previous other studies focused on round goby impacts on macroinvertebrate communities in relation to invasion history, and in contrast with our results, found that round goby abundance was negatively correlated with macroinvertebrate diversity

(Kipp and Ricciardi 2012), especially for molluscs (Kipp et al. 2012). These other studies used macroinvertebrate sampling methods that targeted sessile organisms such as molluscs, but these methods were not optimal for sampling the rapidly swimming invertebrates. Our field sampling methods targeted swimming macroinvertebrates, such as amphipods and insect larvae, and we found that macroinvertebrate community Shannon diversity was higher, not lower, in high conductivity water where round gobies are well-established and abundant. This finding can be explained because the evenness of the overall community assemblage is negatively affected by conductivity ($P = 0.012$, $R^2 = 0.179$, Appendix S2: Fig. 13); amphipod relative abundance was lower at heavily invaded sites with higher evenness ($P = 4.42e - 05$, $R^2 = 0.482$, Appendix S2: Fig. 14). Therefore, amphipods dominated in low conductivity refuges where macroinvertebrate community evenness and Shannon index were lower. The lack of detected effects of round goby abundance on macroinvertebrate diversity could be the result of not specifically sampling for gastropods in our study. In lentic habitats, round gobies favor molluscs and chironomids, but they have very high diet diversity and are capable of adapting to locally abundant food sources (Kornis et al. 2012). Our study suggests that amphipods are likely an important food resource for round gobies at invaded, high conductivity sites in the Upper St. Lawrence River, which has been shown to be an important prey item of round gobies in other systems (Raby et al. 2010; Tarkan et al. 2019).

A long-term survey (1995 to 2017) of fish community diversity in the St. Lawrence River, with areas overlapping with our study (Morissette et al. 2018), found no effects of the round goby on fish species diversity indices but rather specific local effects on certain fish species abundances such as the tessellated darter (*Etheostoma olmstedi*). We found that fish community Shannon diversity was reduced at high round goby abundance. Our study focused on lentic waters; Morissette et al. (2018) sampled both lentic and lotic habitats with different sampling gear over wider a geographic area. Round gobies prefer warmer water (optimum around 26 °C) (Kornis et al. 2012); they could therefore be more abundant and have stronger impacts in lentic waters. The results we show in this manuscript indicate that round goby continue to have negative effects on fish diversity in

certain areas of the Upper St. Lawrence River. No other studies to our knowledge investigated patterns of fish diversity inside wetlands in the Upper St. Lawrence River, which we show here to host unique fish assemblages with high LCBD values (Fig. 4e, f). None of these other studies of fish and macroinvertebrates in the St. Lawrence River explored community patterns across different refuge types that amount to a net effect of constraining round goby invasion and enhancing aquatic biodiversity at the whole ecosystem scale.

Conclusions

We found that different refuge types damped invasion impact and favored aquatic biodiversity at a whole-ecosystem scale in a complex, environmentally-heterogenous river system. Our findings suggest that conservation efforts will likely have greater effect if they focus on the maintenance of environmental heterogeneity outside of large protected areas, by protecting a wide variety of local patches of habitats that provide key refuges for the persistence of diverse native communities. The low conductivity Ottawa River water provided a strong refuge that excluded round goby presence, and so the relative importance of wetlands in structuring native communities was reduced in these waters. Local heterogeneity created by habitat patches could therefore be less important in maintaining native species diversity in face of exotic invasion when nested inside broader scale refuges. Within invaded habitats, other studies have shown that high levels of native diversity at small local spatial scales can reduce invasive species success because of biotic resistance (Byers and Noonburg 2003; Davies et al. 2005; Melbourne et al. 2007). The maintenance of diverse communities across spatially environmentally heterogeneous habitats also has the added potential benefit of providing compensatory dynamics through a diversity of ecological responses that could further buffer impacts from exotic invasion and other environmental change (Gonzalez and Loreau 2009). More empirical work is needed to understand the role of different refuges in combining to maintain native population and community diversity, and their importance in promoting ecological and evolutionary processes for native species co-existence with invasive

species at whole ecosystem and landscape-level scales.

Acknowledgements This research was supported by a team grant awarded by the Fonds de recherche du Québec - Nature et technologies (FRQNT) to AMD and APH, a NSERC discovery grant to AMD, CFI infrastructure grant to AMD, and the NSERC Create ÉcoLac Training program that provided scholarship funds to LA. We also acknowledge financial support from the Groupe de recherche interuniversitaire en limnologie (GRIL), a strategic cluster of FRQNT. We thank A.Paccard and anonymous reviewers of this manuscript for their generous efforts in improving its quality.

References

- Aho K, Derryberry D, Peterson T (2014) Model selection for ecologists: the worldviews of AIC and BIC. *Ecology* 95(3):631–636. <https://doi.org/10.1890/13-1452.1>
- Anton A, Simpson MS, Vu I (2014) Environmental and biotic correlates to lionfish invasion success in Bahamian coral reefs. *PLoS ONE* 9(9):e106229. <https://doi.org/10.1371/journal.pone.0106229>
- Baldwin BS, Carpenter M, Rury K, Woodward E (2012) Low dissolved ions may limit secondary invasion of inland waters by exotic round gobies and dreissenid mussels in North America. *Biol Invasions* 14(6):1157–1175. <https://doi.org/10.1007/s10530-011-0146-0>
- Bernatchez L, Giroux M (2000) Les poissons d'eau douce du Québec et leur distribution dans l'est du Canada. Éditions Broquet Inc, 350
- Blanchet FG, Legendre P, Borcard D (2008) Forward selection of explanatory variables. *Ecology* 89(9):2623–2632
- Blanchet FG, Legendre P, Bergeron JAC, He F (2014) Consensus RDA across dissimilarity coefficients for canonical ordination of community composition data. *Ecol Monogr* 84(3):491–511. <https://doi.org/10.1890/13-0648.1>
- Bowers R, Szalay FAD (2004) Effects of hydrology on Unionids (Unionidae) and Zebra Mussels (Dreissenidae) in a Lake Erie Coastal Wetland. *Am Midland Nat* 151(2):286–300. [https://doi.org/10.1674/0003-0031\(2004\)151%5b0286:ehouuu%5d2.0.co;2](https://doi.org/10.1674/0003-0031(2004)151%5b0286:ehouuu%5d2.0.co;2)
- Brendonck L, Williams WD (2000) Biodiversity in wetlands of dry regions (drylands). Backhuys Publishers
- Byers JE, Noonburg EG (2003) Scale dependent effects of biotic resistance to biological invasion. *Ecology* 84(6):1428–1433. <https://doi.org/10.1890/02-3131>
- Campbell LM, Thacker R, Barton D, Muir DCG, Greenwood D, Hecky RE (2009) Re-engineering the eastern Lake Erie littoral food web: the trophic function of non-indigenous Ponto-Caspian species. *J Great Lakes Res* 35(2):224–231. <https://doi.org/10.1016/j.jglr.2009.02.002>
- Cardinale BJ, Srivastava DS, Duffy JE, Wright JP, Downing AL, Sankaran M, Jouseau C (2006) Effects of biodiversity on the functioning of trophic groups and ecosystems. *Nature* 443(7114):989–992. <https://doi.org/10.1038/nature05202>

- Carignan R, Lorrain S (2000) Sediment dynamics in the fluvial lakes of the St Lawrence River: accumulation rates and characterization of the mixed sediment layer. *Can J Fish Aquat Sci* 57(S1):63–77. <https://doi.org/10.1139/f99-246>
- Céréghino R, Biggs J, Oertli B, Declerck S (2007) The ecology of European ponds: defining the characteristics of a neglected freshwater habitat. In: Pond conservation in Europe (pp 1–6). Springer, Dordrecht. https://doi.org/10.1007/978-90-481-9088-1_1
- Cohen J (2013) Statistical power analysis for the behavioral sciences. Routledge, London
- Cooper MJ, Ruetz CR, Uzarski DG, Burton TM (2007) Distribution of round gobies in Coastal Areas of Lake Michigan: are wetlands resistant to invasion? *J Great Lakes Res* 33(2):303–313. [https://doi.org/10.3394/0380-1330\(2007\)33%5b303:dorgic%5d2.0.co;2](https://doi.org/10.3394/0380-1330(2007)33%5b303:dorgic%5d2.0.co;2)
- Cooper MJ, Ruetz CR, Uzarski DG, Shafer BM (2009) Habitat use and diet of the round goby (*Neogobius melanostomus*) in Coastal Areas of Lake Michigan and Lake Huron. *J Freshw Ecol* 24(3):477–488. <https://doi.org/10.1080/02705060.2009.9664321>
- Coulter DP, Murry BA, Uzarski DG (2015) Relationships between habitat characteristics and round goby abundance in Lakes Michigan and Huron. *J Great Lakes Res* 41(3):890–897. <https://doi.org/10.1016/j.jglr.2015.06.001>
- Crane DP, Farrell JM, Einhouse DW, Lantry JR, Markham JL (2015) Trends in body condition of native piscivores following invasion of Lakes Erie and Ontario by the round goby. *Freshw Biol* 60(1):111–124. <https://doi.org/10.1111/fwb.12473>
- Davies KF, Chesson P, Harrison S, Inouye BD, Melbourne BA, Rice KJ (2005) Spatial heterogeneity explains the scale dependence of the native–exotic diversity relationship. *Ecology* 86(6):1602–1610. <https://doi.org/10.1890/04-1196>
- Derry AM, Kestrup Åsa M, Hendry AP (2013) Possible influences of plasticity and genetic/maternal effects on species coexistence: native *Gammarus fasciatus* facing exotic amphipods. *Funct Ecol* 27(5):1212–1223. <https://doi.org/10.1111/1365-2435.12105>
- Dias PC (1996) Sources and sinks in population biology. *Trends Ecol Evol* 11(8):326–330. [https://doi.org/10.1016/0169-5347\(96\)10037-9](https://doi.org/10.1016/0169-5347(96)10037-9)
- Elton CC (1977) The ecology of invasions by animals and plants. Springer, Netherlands. <https://doi.org/10.1007/978-94-009-5851-7>
- Gee JH, Smith BD, Lee KM, Griffiths SW (1997) The ecological basis of freshwater pond management for biodiversity. *Aquat Conserv: Mar Freshw Ecosyst* 7(2):91–104. [https://doi.org/10.1002/\(SICI\)1099-0755\(199706\)7:2<91::AID-AQC221>3.0.CO;2-O](https://doi.org/10.1002/(SICI)1099-0755(199706)7:2<91::AID-AQC221>3.0.CO;2-O)
- Gelbard JL, Harrison S (2003) Roadless habitats as refuges for native grasslands: interactions with soil aspect and grazing. *Ecol Appl* 13(2):404–415. [https://doi.org/10.1890/1051-0761\(2003\)013%5b0404:rharfn%5d2.0.co;2](https://doi.org/10.1890/1051-0761(2003)013%5b0404:rharfn%5d2.0.co;2)
- Gonzalez A, Loreau M (2009) The causes and consequences of compensatory dynamics in ecological communities. *Annu Rev Ecol Evol Syst* 40:393–414. <https://doi.org/10.1146/annurev.ecolsys.39.110707.173349>
- Grace JB (2006) Structural equation modeling and natural systems. Cambridge University Press, Cambridge
- Gram WK, Borer ET, Cottingham KL, Seabloom EW, Boucher VL, Goldwasser L, Burton RS (2004) Distribution of plants in a California serpentine grassland: are rocky hummocks spatial refuges for native species? *Plant Ecol (Formerly Vegetatio)* 172(2):159–171. <https://doi.org/10.1023/b:vege.0000026332.57007.7b>
- Gunzler D, Chen T, Wu P, Zhang H (2013) Introduction to mediation analysis with structural equation modeling. *Shanghai Arch Psychiatry* 25(6):390. <https://doi.org/10.3969/j.issn.1002-0829.2013.06.009>
- Holway DA, Suarez AV, Case TJ (2002) Role of abiotic factors in governing susceptibility to invasion: a test with argentine ants. *Ecology* 83(6):1610–1619. [https://doi.org/10.1890/0012-9658\(2002\)083%5b1610:roafig%5d2.0.co;2](https://doi.org/10.1890/0012-9658(2002)083%5b1610:roafig%5d2.0.co;2)
- Hudon C, Patoine A, Armellin A (2003) Water temperature variability in the St. Lawrence River Near Montreal. McGill
- Iacarella JC, Ricciardi A (2015) Dissolved ions mediate body mass gain and predatory response of an invasive fish. *Biol Invasions* 17(11):3237–3246. <https://doi.org/10.1007/s10530-015-0949-5>
- Ontario, Dorset Environmental Science Centre, & Jones, CF (2007) Ontario benthos biomonitoring network: protocol manual. Dorset Environmental Science Centre
- Jones LA, Ricciardi A (2005) Influence of physicochemical factors on the distribution and biomass of invasive mussels (*Dreissena polymorpha* and *Dreissena bugensis*) in the St. Lawrence River. *Can J Fish Aquat Sci* 62(9):1953–1962. <https://doi.org/10.1139/f05-096>
- Josse J, Husson F (2012) Handling missing values in exploratory multivariate data analysis methods. *J de la Société Française de Stat* 153(2):79–99
- Jude DJ, Pappas J (1992) Fish utilization of Great Lakes coastal wetlands. *J Great Lakes Res* 18(4):651–672. [https://doi.org/10.1016/S0380-1330\(92\)71328-8](https://doi.org/10.1016/S0380-1330(92)71328-8)
- Kavcic R (2016) Connecting across borders: a special report on the Great Lakes and St. Lawrence Regional Economy. <http://www.gsgp.org/>
- Kestrup AM, Ricciardi A (2009) Environmental heterogeneity limits the local dominance of an invasive freshwater crustacean. *Biol Invasions* 11(9):2095–2105. <https://doi.org/10.1007/s10530-009-9490-8>
- Kipp R, Ricciardi A (2012) Impacts of the Eurasian round goby (*Neogobius melanostomus*) on benthic communities in the upper St. Lawrence River. *Can J Fish Aquat Sci* 69(3):469–486. <https://doi.org/10.1139/f2011-139>
- Kipp R, Hébert I, Lacharité M, Ricciardi A (2012) Impacts of predation by the Eurasian round goby (*Neogobius melanostomus*) on molluscs in the upper St. Lawrence River. *J Great Lakes Res* 38(1):78–89. <https://doi.org/10.1016/j.jglr.2011.11.012>
- Kobza RM, Trexler JC, Loftus WF, Perry SA (2004) Community structure of fishes inhabiting aquatic refuges in a threatened Karst wetland and its implications for ecosystem management. *Biol Conserv* 116(2):153–165. [https://doi.org/10.1016/s0006-3207\(03\)00186-1](https://doi.org/10.1016/s0006-3207(03)00186-1)
- Kornis MS, Mercado Silva N, Vander Zanden MJ (2012) Twenty years of invasion: a review of round goby *Neogobius melanostomus* biology, spread and ecological implications. *J Fish Biol* 80(2):235–285. <https://doi.org/10.1111/j.1095-8649.2011.03157.x>

- Krassoi FR, Brown KR, Bishop MJ, Kelaher BP, Summerhayes S (2008) Condition-specific competition allows coexistence of competitively superior exotic oysters with native oysters. *J Anim Ecol* 77(1):5–15. <https://doi.org/10.1111/j.1365-2656.2007.01316.x>
- Krieger KA (1992) The ecology of invertebrates in great lakes coastal wetlands: current knowledge and research needs. *J Great Lakes Res* 18(4):634–650. [https://doi.org/10.1016/s0380-1330\(92\)71327-6](https://doi.org/10.1016/s0380-1330(92)71327-6)
- Latzka AW, Hansen GJA, Kornis M, Vander Zanden MJV (2016) Spatial heterogeneity in invasive species impacts at the landscape scale. *Ecosphere* 7(3):e01311. <https://doi.org/10.1002/ecs2.1311>
- Legendre P (2014) Interpreting the replacement and richness difference components of beta diversity. *Glob Ecol Biogeogr* 23(11):1324–1334. <https://doi.org/10.1111/geb.12207>
- Legendre P, Gallagher ED (2001) Ecologically meaningful transformations for ordination of species data. *Oecologia* 129(2):271–280. <https://doi.org/10.1007/s004420100716>
- Leprieur F, Hickey MA, Arbuckle CJ, Closs GP, Brosse S, Townsend CR (2006) Hydrological disturbance benefits a native fish at the expense of an exotic fish. *J Appl Ecol* 43(5):930–939. <https://doi.org/10.1111/j.1365-2664.2006.01201.x>
- Levine NM, Zhang K, Longo M, Baccini A, Phillips OL, Lewis SL, Feldpausch TR (2016) Ecosystem heterogeneity determines the ecological resilience of the Amazon to climate change. *Proc Natl Acad Sci* 113(3):793–797. <https://doi.org/10.1073/pnas.1511344112>
- MacDougall AS, Boucher J, Turkington R, Bradfield GE (2006) Patterns of plant invasion along an environmental stress gradient. *J Veg Sci* 17(1):47–56. <https://doi.org/10.1111/j.1654-1103.2006.tb02422.x>
- Melbourne BA, Cornell HV, Davies KF, Dugaw CJ, Elmendorf S, Freestone AL, Yokomizo H (2007) Invasion in a heterogeneous world: resistance, coexistence or hostile takeover? *Ecol Lett* 10:77–94. <https://doi.org/10.1111/j.1461-0248.2006.00987.x>
- Menke SB, Holway DA (2006) Abiotic factors control invasion by Argentine ants at the community scale. *J Anim Ecol* 75(2):368–376. <https://doi.org/10.1111/j.1365-2656.2006.01056.x>
- Menke SB, Fisher RN, Jetz W, Holway DA (2007) Biotic and abiotic controls of argentine ant invasion success at local and landscape scales. *Ecology* 88(12):3164–3173. <https://doi.org/10.1890/07-0122.1>
- Meynard CN, Lavergne S, Boulangeat I, Garraud L, Es JV, Mouquet N, Thuiller W (2014) Disentangling the drivers of metacommunity structure across spatial scales. *J Biogeogr* 40(8):1560–1571. <https://doi.org/10.1111/jbi.12116>
- Moisan J (2010) Guide d'identification des principaux macroinvertébrés benthiques d'eau douce du Québec, 2010: surveillance volontaire des cours d'eau peu profonds. Développement durable, environnement et parcs Québec
- Morissette O, Paradis Y, Pouliot R, Lecomte F (2018) Spatio-temporal changes in littoral fish community structure along the St. Lawrence River (Québec, Canada) following round goby (*Neogobius melanostomus*) invasion. *Aquat Invasions*. <https://doi.org/10.3391/ai.2018.13.4.08>
- Neary BP, Leach JH (1992) Mapping the potential spread of the zebra mussel (*Dreissena polymorpha*) in Ontario. *Can J Fish Aquat Sci* 49(2):406–415. <https://doi.org/10.1139/f92-046>
- Nelson SM, Roline RA, Thullen JS, Sartoris JJ, Boutwell JE (2000) Invertebrate assemblages and trace element bioaccumulation associated with constructed wetlands. *Wetlands* 20(2):406–415. [https://doi.org/10.1672/0277-5212\(2000\)020%5b0406:iaateb%5d2.0.co;2](https://doi.org/10.1672/0277-5212(2000)020%5b0406:iaateb%5d2.0.co;2)
- Oliver TH, Heard MS, Isaac NJ, Roy DB, Procter D, Eigenbrod F, Proença V (2015) Biodiversity and resilience of ecosystem functions. *Trends Ecol Evol* 30(11):673–684. <https://doi.org/10.1016/j.tree.2015.08.009>
- Pejchar L, Mooney HA (2009) Invasive species, ecosystem services and human well-being. *Trends Ecol Evol* 24(9):497–504. <https://doi.org/10.1016/j.tree.2009.03.016>
- Pielou EC (1969). An introduction to mathematical ecology. An introduction to mathematical ecology
- Powers RP, Hay GJ, Chen G (2012) How wetland type and area differ through scale: a GEOBIA case study in Alberta's Boreal Plains. *Remote Sens Environ* 117:135–145. <https://doi.org/10.1016/j.rse.2011.07.009>
- R Core Team (2018) R: A language and environment for statistical computing. R Foundation for Statistical computing, Vienna, Austria. <http://www.R-project.org/>
- Raby GD, Gutowsky LF, Fox MG (2010) Diet composition and consumption rate in round goby (*Neogobius melanostomus*) in its expansion phase in the Trent River, Ontario. *Environ Biol Fishes* 89(2):143–150. <https://doi.org/10.1007/s10641-010-9705-y>
- Ray WJ, Corkum LD (2001) Habitat and site affinity of the round goby. *J Great Lakes Res* 27(3):329–334
- Ricciardi A, Hoopes MF, Marchetti MP, Lockwood JL (2013) Progress toward understanding the ecological impacts of nonnative species. *Ecol Monogr* 83(3):263–282. <https://doi.org/10.1890/13-0183.1>
- Richardson DM (2011) Fifty years of invasion ecology: the legacy of Charles Elton. Wiley, London
- Robson BJ, Clay CJ (2005) Local and regional macroinvertebrate diversity in the wetlands of a cleared agricultural landscape in south western Victoria, Australia. *Aquatic Conser: Mar Freshw Ecosyst* 15(4):403–414. <https://doi.org/10.1002/aqc.675>
- Rucker DD, Preacher KJ, Tormala ZL, Petty RE (2011) Mediation analysis in social psychology: current practices and new recommendations. *Soc Pers Psychol Compass* 5(6):359–371. <https://doi.org/10.1111/j.1751-9004.2011.00355.x>
- Rundle SD, Foggo A, Choisuel V, Bilton DT (2002) Are distribution patterns linked to dispersal mechanism? An investigation using pond invertebrate assemblages. *Freshw Biol* 47(9):1571–1581. <https://doi.org/10.1046/j.1365-2427.2002.00886.x>
- Scheffer M, Van Geest GJ, Zimmer K, Jeppesen E, Søndergaard M, Butler MG, De Meester L (2006) Small habitat size and isolation can promote species richness: second order effects on biodiversity in shallow lakes and ponds. *Oikos* 112(1):227–231. <https://doi.org/10.1111/j.0030-1299.2006.14145.x>
- Shannon CE (1948) A mathematical theory of communication. *Bell Syst Tech J* 27(3):379–423

- Stein A, Kreft H (2015) Terminology and quantification of environmental heterogeneity in species-richness research. *Biol Rev* 90(3):815–836. <https://doi.org/10.1111/brv.12135>
- Stein A, Gerstner K, Kreft H (2014) Environmental heterogeneity as a universal driver of species richness across taxa biomes and spatial scales. *Ecol Lett* 17(7):866–880. <https://doi.org/10.1111/ele.12277>
- Strayer DL, Evner VT, Jeschke JM, Pace ML (2006) Understanding the long-term effects of species invasions. *Trends Ecol Evol* 21(11):645–651. <https://doi.org/10.1016/j.tree.2006.07.007>
- Sullivan TP, Sullivan DS (2001) Influence of variable retention harvests on forest ecosystems. II. Diversity and population dynamics of small mammals. *J Appl Ecol* 38(6):1234–1252. <https://doi.org/10.1046/j.0021-8901.2001.00674.x>
- Tamme R, Hiiesalu I, Laanisto L, Szava-Kovats R, Pärtel M (2010) Environmental heterogeneity species diversity and co-existence at different spatial scales. *J Veg Sci*. <https://doi.org/10.1111/j.1654-1103.2010.01185.x>
- Tarkan AS, Tepeköy EG, Karakuş U, Top N, Vilizzi L (2019) Plasticity in the feeding ecology of native Ponto-Caspian gobies suggests establishment success in their nonnative range. *Int Rev Hydrobiol* 104(3–4):57–67. <https://doi.org/10.1002/iroh.201801974>
- ter Braak CJF, Verdonschot PFM (1995) Canonical correspondence analysis and related multivariate methods in aquatic ecology. *Aquat Sci* 57(3):255–289. <https://doi.org/10.1007/bf00877430>
- Tews J, Brose U, Grimm V, Tielbörger K, Wichmann MC, Schwager M, Jeltsch F (2004) Animal species diversity driven by habitat heterogeneity/diversity: the importance of keystone structures. *J Biogeogr* 31(1):79–92. <https://doi.org/10.1046/j.0305-0270.2003.00994.x>
- Thiere G, Milenkovski S, Lindgren PE, Sahlén G, Berglund O, Weisner SE (2009) Wetland creation in agricultural landscapes: biodiversity benefits on local and regional scales. *Biol Conserv* 142(5):964–973. <https://doi.org/10.1016/j.biocon.2009.01.006>
- Turner RE (1977) Intertidal vegetation and commercial yields of penaeid shrimp. *Trans Am Fish Soc* 106(5):411–416. [https://doi.org/10.1577/1548-8659\(1977\)106<411:IVACYO>2.0.CO;2](https://doi.org/10.1577/1548-8659(1977)106<411:IVACYO>2.0.CO;2)
- Vander Zanden MJ, Hansen GJA, Latzka AW (2017) A framework for evaluating heterogeneity and landscape-level impacts of non-native aquatic species. *Ecosystems* 20(3):477–491. <https://doi.org/10.1007/s10021-016-0102-z>
- Vincent WF, Dodson JJ (1999) The St Lawrence River, Canada-USA: the need for an ecosystem-level understanding of large rivers. *Jpn J Limnol (Rikusuigaku Zasshi)* 60(1):29–50. <https://doi.org/10.3739/rikusui.60.29>
- Vuong QH (1989) Likelihood ratio tests for model selection and non-nested hypotheses. *Econom: J Econom Soc*. <https://doi.org/10.2307/1912557>
- Wetzel RG (1990) Land-water interfaces: metabolic and limnological regulators. *Int Vereinigung für theoretische und angewandte Limnologie: Verhandlungen* 24(1):6–24. <https://doi.org/10.1080/03680770.1989.11898687>
- Whittier TR, Ringold PL, Herlihy AT, Pierson SM (2008) A calcium-based invasion risk assessment for zebra and quagga mussels (*Dreissena* spp). *Front Ecol Environ* 6(4):180–184. <https://doi.org/10.1890/070073>
- Wilcove DS, Rothstein D, Dubow J, Phillips A, Losos E (1998) Quantifying threats to imperiled species in the United States. *Bioscience* 48(8):607–615. <https://doi.org/10.2307/1313420>
- Williams DD (1997) Temporary ponds and their invertebrate communities. *Aquat Conserv: Mar Freshw Ecosyst* 7(2):105–117. [https://doi.org/10.1002/\(SICI\)1099-0755\(199706\)7:2<105:AID-AQC222>3.0.CO;2-K](https://doi.org/10.1002/(SICI)1099-0755(199706)7:2<105:AID-AQC222>3.0.CO;2-K)
- Williams P, Whitfield M, Biggs J, Bray S, Fox G, Nicolet P, Sear D (2004) Comparative biodiversity of rivers, streams, ditches and ponds in an agricultural landscape in Southern England. *Biol Conserv* 115(2):329–341. [https://doi.org/10.1016/S0006-3207\(03\)00153-8](https://doi.org/10.1016/S0006-3207(03)00153-8)
- Yang Z, Liu X, Zhou M, Ai D, Wang G, Wang Y, Lundholm JT (2015) The effect of environmental heterogeneity on species richness depends on community position along the environmental gradient. *Sci Rep* 5:10. <https://doi.org/10.1038/srep15723>
- Young JAM, Marentette JR, Gross C, McDonald JI, Verma A, Marsh-Rollo SE, Balshine S (2010) Demography and substrate affinity of the round goby (*Neogobius melanostomus*) in Hamilton Harbour. *J Great Lakes Res* 36(1):115–122. <https://doi.org/10.1016/j.jglr.2009.11.001>

Publisher's Note Springer Nature remains neutral with regard to jurisdictional claims in published maps and institutional affiliations.