BIODIVERSITY RESEARCH

Distribution of unionid freshwater mussels depends on the distribution of host fishes on a regional scale

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ABSTRACT

Aim The successful conservation of endangered mussel communities requires, in part, a thorough understanding of the processes that shape their distribution. Therefore, we tested the prediction that (1) the distribution of host fishes explains a significant amount of variation in mussel community composition. In addition, because mussel distribution also depends on spatial processes and environmental variables, we predicted that (2) the distribution and community composition of mussels in Ontario varies across eight contiguous watersheds, flowing into three different basins of the Great Lakes (Huron, St. Clair and Erie); and (3) environmental variables also explain part of the mussel distribution.

Location Watersheds in south-western Ontario, North America, Great Lakes Region.

Methods Existing data on the distribution of mussels and fishes, and environmental and spatial information were compiled. Variation partitioning with redundancy analysis was used to examine what proportion of the variation in mussels' community composition was explained by watershed (as a spatial component), environmental differences and host fish presence. Redundancy analysis for mussel abundances was used to illustrate the similarities in the distributions of mussels and fishes, and the association of differences in community composition of mussels among watersheds with certain mussel species and environmental variables.

Results Host fish presence explained 44%, watershed identity 28% and environmental factors 23% of the variation in mussel species composition. However, much of the explained variation was shared among these components, and all three components together explained 55% of the total variation in species composition. Even after statistically eliminating the other explanatory variables, host fish distribution was the most important group of predictor variables, although we used a subset of relevant environmental variables because of the scale of the study.

Main conclusions Our results highlight the important role played by host fishes in shaping current distributions of freshwater mussels and underscore the necessity of incorporating these relationships in conservation efforts and management actions.

Keywords

dispersal, fish, freshwater mussel conservation, Great Lakes, metacommunity, molluscs, Unionidae.

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Diversity and Distributions

INTRODUCTION

South-western Ontario has the highest diversity of native freshwater mussels (Bivalvia: Unionidae) in Canada (Metcalfe-Smith *et al.*). Unfortunately, native freshwater mussels are highly imperilled and their populations have declined severely, which has been attributed to changes in land use, habitat modification and destruction, pollution and the invasion of dreissenid mussels (Bogan, 1993; Lydeard *et al.*, 2004; Morris & Burridge, 2006). The successful conservation and management of these endangered mussel communities requires a thorough understanding of their distribution and habitat needs as well as the relative importance of processes that shape these at local and regional scales (Strayer, 2006, 2008).

The current distributions of species are the result of both historical and environmental processes. Because unionid mussels depend on fish for their dispersal, they are unable to overcome terrestrial barriers among watersheds. Consequently, dispersal among rivers and post-glacial colonization depend on historical drainage connections, which is reflected in current distributions of mussels (van der Schalie, 1945; Strayer & Jirka, 1997; Graf, 2002). Many previous studies on the distribution of freshwater mussels have focused on environmental microhabitat variables, such as substrate composition, with varying degrees of success and sometimes with contradictory findings (reviewed in detail by Strayer, 2008). Both historical (e.g. Hocutt & Wiley, 1986) and environmental (e.g. Matthews, 1998) processes have been well studied in freshwater fishes. For example, the current distributions of freshwater fishes in Ontario were shaped by current climate (Mandrak, 1995) and colonization from glacial refugia after the Wisconsin glacial period ended 10,000 years ago (Mandrak &

Crossman, 1992a). It is likely that the present-day distributions of unionid mussels in Ontario are similarly related to post-glacial invasion patterns as early life stages of unionid mussels are known to be parasitic on freshwater fishes. Long-distance dispersal of mussels depends on fish movement (Newton *et al.*, 2008), and movement of fishes into the newly formed Great Lakes following the glacial retreat must have provided an important dispersal avenue.

Several previous studies have recognized the importance of host fish for the distribution of mussels (Watters, 1992; Vaughn, 1997; Haag & Warren, 1998; Schwalb *et al.*, 2011).

Environmental and spatial effects were found to be significant in explaining the variation in mussel community structure in the Red River watershed in south-central Unites States, but fish richness was considered to be the most important factor (Vaughn & Taylor, 2000).

Sepkoski & Rex (1974) examined the relationship between variables such as watershed size and species richness in a river on a regional scale, but an analysis that quantifies the relative contribution of environmental and spatial processes on the community composition of mussels is lacking at a regional scale across several contiguous watersheds.

The watersheds in our study area (Fig. 1) were initially recolonized by aquatic organisms from southern refugia during the early formation of the Great Lakes following the melting of the Wisconsin ice sheet (14,000 YBP; Dyke *et al.*, 2003). As the continental ice sheet receded northward, its meltwaters formed a series of ephemeral waterbodies along the southern ice margin, which overflowed into the Mississippi basin and acted as dispersal corridors (see Mandrak & Crossman, 1992a for a detailed chronology). As the Great Lakes evolved over the next several thousand years, the extent and outlet of the Great Lakes varied based on the
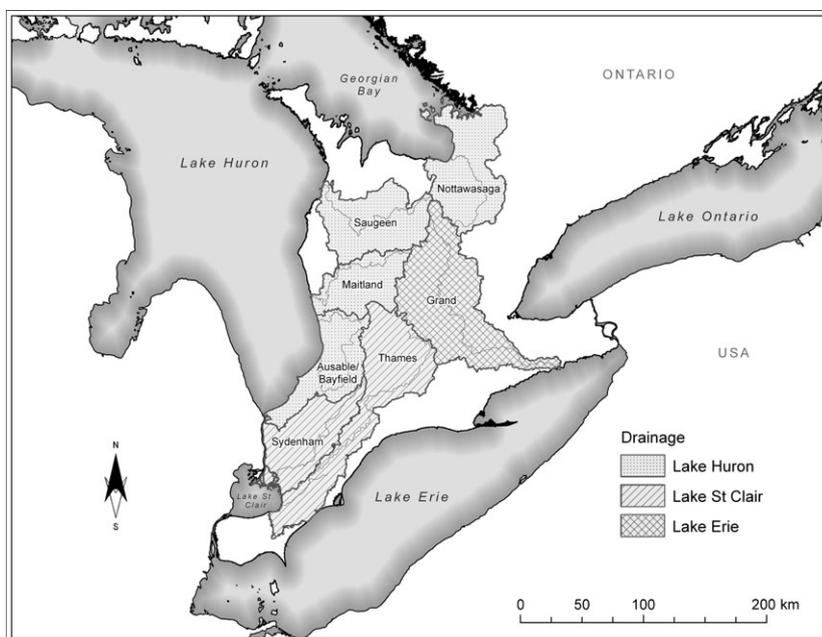
Figure 1 The eight watersheds in south-western Ontario used in this study: Ausable, Bayfield, Maitland and Nottasawaga watersheds flowing into Lake Huron, Grand River flowing into Lake Erie; and Sydenham and Thames River flowing in to Lake St. Clair.

position of the ice sheet and isostatic rebound (Dyke *et al.*, 2003). In periods when glacial Lake Algonquin and subsequent lakes in the Huron basin drained across southern Ontario rather than into the Erie basin, ca. 11,000–7,200 YBP, the watersheds in the Huron basin were likely still connected to each other, but separated from those in the St. Clair and Erie basins (Dyke *et al.*, 2003). During that time, the watersheds in the St. Clair and Erie basin may have also been intermittently separated because of low water levels in those basins (Dyke *et al.*, 2003). The lower reaches of adjacent watersheds within each basin would have been connected to varying degrees based on lake water levels, but nothing is known about potential connections higher in the watersheds (e.g. headwater captures) (Chapman & Putnam, 1984).

Many mussel species may have colonized Lake Erie as recently as 6000–4000 years ago through modern-day headwater connections between the Erie (Maummee River) and Mississippi (Wabash River) basins, whereas only a few species likely colonized Lake Erie earlier via glacial Lake Maumee, ca. 10,000 years ago (Graf, 2002).

Genetic studies (e.g. Kelly & Rhymer, 2005) can provide insight into the importance of post-glacial events, and gene flow in population genetics can be considered the equivalent to dispersal in community ecology (Vellend, 2010). Recently, genetic studies have examined post-glacial dispersal and the degree of gene flow among populations within and across watersheds of both fishes and mussels in the Great Lakes region. For example, differences in genetic patterns of smallmouth bass (*Micropterus dolomieu*) populations among Great Lake basins were best explained by several and sequential colonization events from multiple refugia (Borden & Krebs, 2009). A low genetic divergence found between populations of greenside darter (*Etheostoma blennioides*) in contiguous watersheds of the Thames and Sydenham rivers – both flowing into Lake St. Clair – could be due to historical or ongoing gene flow through Lake St. Clair (Beneteau *et al.*, 2008). Greenside darter populations in a contiguous watershed, the Ausable River, which flows into Lake Huron, were found to be more genetically distinct (Beneteau *et al.*, 2008). The genetic structure of populations of Mucket mussel (*Actinonais ligameninta)* and Threeridge (*Amblema plicata*) in Lake Erie and Ohio watersheds indicated that populations of *A. ligamentina* originated from two genetically distinct glacial refugia (Elderkin *et al.*, 2008) and those of *A. plicata* from at least two refugia (Elderkin *et al.*, 2007). While these genetic studies provide insight into potential glacial refugia and historical or ongoing gene flow of individual species, they do not inform about patterns in community composition within and among watersheds.

Although several studies have indicated the significance of historical dispersal processes to freshwater fishes and mussels, the importance of dispersal via host fishes for the distribution and community composition of mussels in south-western Ontario has not yet been examined. The objective of this study is to investigate the link between current mussel and fish distributions at the regional scale. We predicted that (1) the distribution of host fishes explains a significant amount of variation in mussel community composition. In addition, because mussel distribution also depends on spatial processes and environmental variables, we predicted that (2) the distribution and community composition of mussels in Ontario varies across eight contiguous watersheds, flowing into three different basins of the Great Lakes (Huron, St. Clair and Erie); and (3) environmental variables also explain part of the mussel distribution.

METHODS

Study area

This study includes eight watersheds in Ontario flowing into different Great Lakes basins: (1) Ausable, Bayfield, Maitland, Saugeen and Nottasawaga watersheds of Lake Huron; (2) Sydenham and Thames watershed of Lake St. Clair; and (3) Grand River watershed of Lake Erie (Fig. 1). The spatial extent of the total study area is *c.* 30,000 km^2.

Compilation of data

Freshwater mussel abundance data for the eight watersheds were obtained from Fisheries and Oceans Canada's Lower Great Lakes Unionid database representing a total of 199 collection sites sampled between 1997 and 2009 by different researchers (Table 1, Table S1). Although collected by different researchers/organizations, all mussel data were collected following a standardized semi-quantitative sampling protocol developed in southern Ontario for the purpose of detecting rare species (Metcalfe-Smith *et al.*, 2000) and employing a fixed 4.5 person-hour effort. Sites were selected to cover the range of wadable habitats (1–1.25 m) available in each system, and mussel assemblages were surveyed using a range of techniques appropriate to local conditions [most sites were searched manually using underwater viewers and tactile sampling, whereas rakes and scoops were only used at few sites with soft substrate and low visibility (high turbidity)]. When sites had been sampled repeatedly in different years, only the first year was used. A number of environmental variables were measured following the Ontario Ministry of Natural Resources (OMNR) stream habitat assessment guides (Dodge *et al.*, 1987). Several of the environmental variables used for the analyses were converted to categorical data (Table S4). Twenty-one environmental variables (Table S3, S4) and abundance data for 33 mussel species (Table S1) were used.

Of more than 200 fish species that occur in south-western Ontario, only 57 are known host species for the local mussel species (Table S2). These data had been previously gathered and were primarily derived from host fish studies that identified host fish species based on the transformation of

Table 1 Summary of mussel sampling efforts in south-western Ontario between 1997 and 2009. Data from Fisheries and Oceans Canada Lower Great Lakes Unionid Database. Mussel data were collected using standard 4.5 person-hours timed searches.

Watershed	Code	Years sampled (# sites considered here)	Number of sites	Number of species
Ausable River	AR	1998 (8), 2002 (7), 2004 (10)	25	22
Bayfield River	BF	2007 (18)	18	16
Grand River	GR	1997 (17), 1998 (9), 2001 (1), 2004 (6), 2005 (1), 2006 (1)	35	25
Maitland River	MR	1998 (1), 2003 (10), 2004 (10)	21	12
Nottasawaga River	NR	2009 (22)	22	11
Saugeen River	SG	2006 (8)	8	8
Sydenham River	SR	1997 (9), 1998 (8)	17	28
Thames River	TR	1997 (11), 1998 (5), 2004 (25), 2005 (12),	53	26

glochidia into juveniles, but also from a few field observations of glochidia infestations on fish for those mussel species for which these data were lacking (see Schwalb *et al.*, 2011 for details). Occurrence data for host fishes of mussels in south-western Ontario (Table S2, see also Appendix S2 in Schwalb *et al.*, 2011) were obtained for segments identified by the Aquatic Landscape Inventory Software (ALIS, Wichert *et al.*, 2004), which divides streams into segments based on a number of different natural features such as surficial geology, adjoining streams, wetlands, and lakes and artificial barriers such as dams. The minimum length of each segment is defined as 50 m. The fish distribution data were derived from a database containing over 400,000 collection records for Ontario fishes primarily from the Ontario Ministry of Natural Resources and Royal Ontario Museum, 1920s–1990 (see Mandrak & Crossman, 1992b for description), and primarily from Fisheries and Oceans Canada and the Royal Ontario Museum, 1991-present (Mandrak, N.E. unpubl. data).

Statistical analysis

We used variation partitioning to examine how much of the variation in community composition among different sites could be explained by environmental and spatial variables, host fish presence and watershed identity (Legendre & Legendre, 1998). All analyses were performed in R (R Development Core Team, 2011). The variation decomposition was based on redundancy analysis (RDA) following the procedure described in Cottenie (2005). RDA is the multivariate extension of multiple regressions (Legendre & Legendre, 1998). Similar to multiple regressions, it provides an estimate of the amount of variation in multiple dependant variables based on multiple predictor variables or explained variation. The computed percentage of explained variation was adjusted for the number of explanatory variables (Peres-Neto *et al.*, 2006), just as in a multiple regression. The dependent mussel abundances were fourth-root transformed to normalize the data and Hellinger transformed to minimize the disproportional influence of rare species on the redundancy analysis (Legendre & Gallagher, 2001).

The three sets of explanatory variables consisted of host fish data, watershed identity and environmental data (Tables S1–S4). Variation decomposition using RDA (Legendre & Legendre, 1998) determines different types of explained variation: (1) the explained variation by each group of explanatory variables, (2) the amount of variation explained by the three groups after eliminating the effects of the other groups of variables (e.g. the amount of variation associated with host fish distribution after removing the effect of watershed identity and environmental data from the dependant variables), and (3) the variation shared by the different combinations of the three groups of variables. Randomization procedures compute the significances of these variation components, but only for variations of types (1) and (2) (Legendre & Legendre, 1998), and we used alpha = 0.05 as our cut-off for significance.

Mussel data were available from 199 sites, but only 157 of these could be linked to available fish segment data. The watershed identity of each sampling point was coded with an indicator matrix, with a column for each watershed (1 = site is part of watershed, otherwise 0).

RESULTS

Host fish presence explained 44% of the variation in mussel species composition, watershed identity 28% and environmental factors 23%. However, much of the explained variation was shared among these components (Fig. 2). For example, 12% of the variation was shared by all three components. All three components together explained 55% of variation in species composition, and all effects were significant ($P = 0.001$) except for the environmental variation alone explaining 2% of the variation ($P = 0.18$).

Mussel community composition was similar in rivers flowing into the same basin of the Great Lakes and differed significantly between rivers flowing into different basins of the Great Lakes (Fig. 3a). A similar pattern was observed for fish communities (Fig. S1). The exceptions were the Ausable and Saugeen watersheds, in which the community composition of the mussels was different from each other and from the Maitland, Bayfield and Nottasawaga watershed, although all rivers flow into Lake Huron (Fig. 3a).

Differences in mussel community composition among watersheds were associated with certain species and some environmental variables, although correlations with environmental
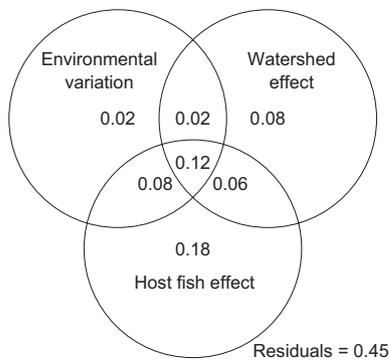
Figure 2 Results of the variation decomposition. All effects were significant ($P = 0.001$) except for the environmental variation alone explaining 2% of the variation ($P = 0.18$). Overlapping circles contain the percentage of variation that was shared between the components. For example, all three components together explained 12% of the variation in mussel community composition.

variables were rather weak (Fig. 3b,c). *Lampsilis fasciola* was most abundant in the Grand River, whereas both the Grand and Saugeen watershed were characterized by the dominance of *Elliptio dilatata* (Fig. 3a,b, Table S1). *Actinonaias ligamentina* and *Quadrula pustulosa* were most abundant in the Thames watershed (Fig. 3a,b, Table S1). Several species occurred primarily in the Thames and Sydenham watersheds: *Cyclonaias tuberculata*, *Lasmigona complanata*, *Leptodea fragilis*, *Truncilla truncata* and *Quadrula quadrula*, whereas *Ligumia recta* and *Amblema plicata* were most abundant in the Ausable watershed (Fig. 3a,b, Table S1). *Lampsilis cardium* and *Villosa iris* were most prevalent in the Maitland watershed, and both the Bayfield and the Maitland watersheds had high abundances of *Lampsilis siliquoidea* (Fig. 3a,b, Table S1). Sandy, gravel substrate and riffles were predominant in the Thames and the Sydenham watersheds, whereas pools and increased algae growth were predominant in the Maitland and Bayfield watersheds (Fig. 3c). Siltation and silt substrate were predominant in the Ausable watershed (Fig. 3a,c).

DISCUSSION

This is the first study to demonstrate that both the mussel and fish community composition in Ontario rivers differ significantly among watersheds flowing into different Great Lakes. It also shows congruence between host fish and mussel community structure. Giving the range of potentially confounding factors, the surprising strong correlation between mussel and fish distribution at the regional scale supports the hypothesis that fish distributions strongly influences mussel distributions. In addition, this study confirms the importance of environmental factors to mussels, which has been previously shown (e.g. McRae *et al.*, 2004).

A considerable amount of variation is shared by host fish presence, watershed identity and environmental variables, which makes it difficult to definitively associate a causal
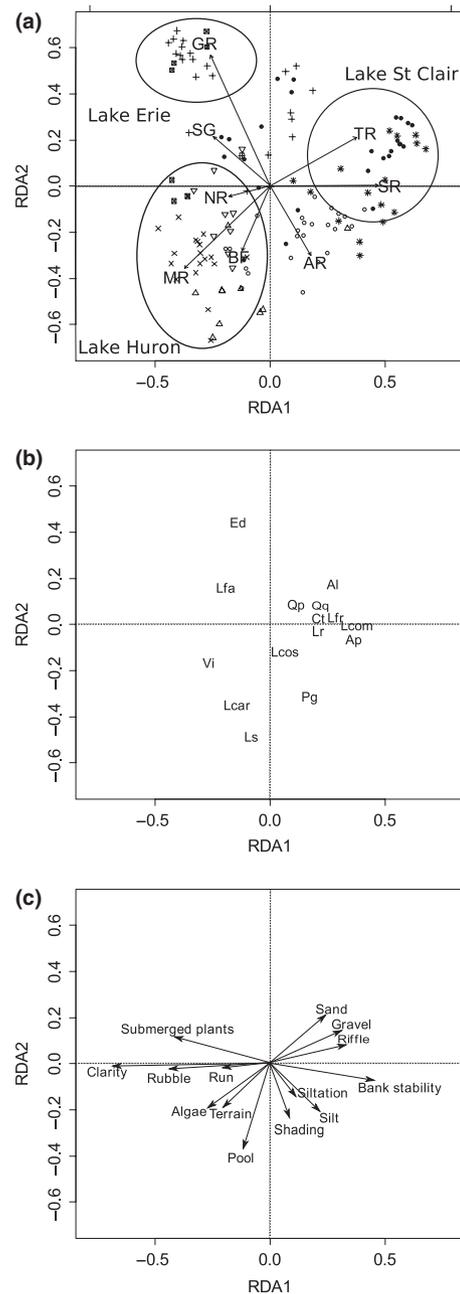
Figure 3 Biplots of redundancy analysis. (a) Mussel data; Symbols represent sites: AR: empty circles, BF: triangles pointing up, GR: +, MR: x, NR: triangle pointing down, SG: square with x, SR = asterisk, TR: black circles. See Table 1 for watershed coding. Ellipsoids enclose vectors of watersheds flowing into the same Great Lakes basins. (b) mussel species; we only show the species that distinguished between different watersheds; Al, *Actinonaias ligamentina*; Ap, *Amblema plicata*; Ct, *Cyclonaias tuberculata;* El, *Elliptio dilatata*; Lcar, *Lampsilis cardium*; Lfa, Lampsilis fasciola; Lcom, *Lasmigona complanata*; Lcos, *Lasmigona costata*; Lfr, *Leptodea fragilis*; Lr, *Ligumia recta*; Ls, *Lampsilis siliquoidea*; Qp, *Quadrula pustulosa*; Qq, *Quadrula quadrula*; Vi, *Villosa iris*. *Truncilla truncata* not visible (behind Ct), (c) Significant ($P < 0.05$) environmental variables.

process with the differences in mussel communities (Fig. 2). However, host fish presence explained most of the variation, including 18% of the mussel variation on its own. In addition, the differences in mussel community composition found among watersheds may have been shaped by differences in fish communities among watersheds and directly (via constraints on mussel survival) or indirectly (via constraints on fish survival) by differences in environmental conditions among watersheds. The idea that the distribution of mussels depends on those of their host fish is supported by several previous studies that found evidence for the importance of fish in structuring mussel communities (Watters, 1992; Vaughn, 1997; Vaughn & Taylor, 2000; Rashleigh, 2008; Schwalb *et al.*, 2011).

Differences in fish communities and, consequently, mussel communities between watersheds that flow into different Great Lakes could be the results of low connectivity and limited dispersal between these watersheds that became separated with the formation of the current Great Lakes 4000 years ago. Alternatively, mussel communities in different Great Lakes tributaries could have become isolated only recently through the local extinction of unionid populations in the Great Lakes (potential stepping stones) because of the invasion of zebra mussels (Zanatta *et al.*, 2007) or through an increased fragmentation by dams (Strayer, 2008) in the Great Lakes tributaries. While this could potentially explain differences in mussel community composition between rivers flowing into different Great Lakes, it would fail to explain the similarities between rivers flowing into the same Great Lakes (e.g., Sydenham and Thames, Fig. 3a).

The differences in fish and mussel communities we found are consistent with a recent genetic study on greenside darter, which found a low genetic divergence of populations of greenside darter between the Sydenham and the Thames River flowing into Lake St. Clair (Beneteau *et al.*, 2008). On the other hand, populations of greenside darter were found to be genetically distinct in the Ausable River flowing into Lake Huron (Beneteau *et al.*, 2008), which suggests isolation since the last Ice Age and is consistent with our findings of a distinct fish community composition in that watershed. Similarly, populations of the mussels *Lampsilis fasciola* in the Grand River (flowing into Lake Erie) were genetically distinct from those of the Thames (flowing into Lake St. Clair) and the Maitland River (flowing into Lake Huron, Zanatta *et al.*, 2007).

The exceptions from the general spatial pattern that mussel and fish communities differ between watersheds flowing into different Great Lakes suggest that environmental factors may also be important. Fish and mussel communities in the Ausable watershed likely differed from all other watersheds (Fig. 3a and S1) because the lower Ausable River has a distinct geomorphology related to the presence of a dune complex. Much of the lower Ausable is of low gradient and historically covered by a large wetland complex not present in other watersheds. In addition, the Ausable is the most agriculturally degraded stream in Ontario and has the greatest amount of buried headwaters and drains (Stammler, 2011). Fish

communities in the upper Grand River were different from all other rivers, but the lower Grand River was similar to the Sydenham and the Thames River (Fig. S1). This could be due to environmental conditions in the lower Grand River being more similar to the Sydenham and the Thames River, and habitat in the upper Grand River being distinct (headwater habitat) compared to the lower Grand River.

Some differences among watersheds can be attributed to species' habitat preferences. For example, many unionid species prefer gravel riffles (Staton *et al.*, 2003). The Thames and Sydenham have sandy, gravel substrate and riffles, and higher abundances of many species. On the other hand, *Lampsilis siliquoidea*, which was most abundant in the Bayfield and the Maitland watersheds (Fig. 3a,b, Table S1), is known to occur in slow-flowing waters, including lakes and margin of pools (Clarke, 1981). Siltation and silty substrate were associated with the species *Lasmigona costata* and *Pyganodon grandis* (Fig. 3b,c). Both species belong to the tribe Anodontini, which are believed to be more pollution tolerant (Metcalfe-Smith & Lane, 1998). However, habitat preferences alone fail to explain other associations, for example, the high abundances of *Villosa iris* in the Maitland River (Fig. 3a,b, Table S1). It should be noted that many of the environmental variables that were available have been shown to poorly predict mussel distribution (e.g. substrate, Table S3; Strayer, 2008). Unfortunately, several variables that have been shown to be important for the distribution of mussels such as complex hydraulic variables, for example, those indicating substrate stability under high flow conditions (Steuer *et al.*, 2008; Allen & Vaughn, 2010), but also water chemistry (e.g. ammonia, Augspurger *et al.*, 2003), were not available for our sampling sites. Consequently, it is possible that our study underestimates the importance of environmental variables in determining the distribution of mussels. The inclusion of crucial environmental variables could increase the amount of variation explained by environmental variables and also the total amount of variation explained by all components.

Similarly, our host fish data are limited by the available research studies. Although a lot of progress has been made, not all host fish for all mussels have been identified yet. In addition, the relative importance of identified host fish in the field is unclear and more research on host fish is needed (Schwalb *et al.*, 2011). Thus is possible that improved knowledge on host fish will also help to better explain distribution of mussels.

Our results showcase how the distribution of a parasite (mussel) depends on the distribution of its host (fish) on a regional scale. This is consistent with a genetic study of the mussel *Epioblasma triquetra* and its host fish, the logperch (*Percina caprodes*), in which a considerable congruency over a large spatial scale was found for the genetic population structures of both species (Zanatta & Wilson, 2011). However, the interaction between mussels and fishes is more similar to a transport phenomenon rather than parasitism (Barnhart *et al.*, 2008). Thus, the dependence of the

distribution of mussels on the dispersal via their host fishes may be comparable with the importance of seed-dispersing animals (e.g. frugivores) for the distribution and structure of tropical forests (e.g. Holbrook & Smith, 2000; Bleher & Bohning-Gaese, 2001) but also with the importance of dispersal by animals for post-glacial dispersal of terrestrial plants (Vellend *et al.*, 2003).

This study is the first to demonstrate the relative contributions of host fishes, watershed location and microhabitat variables on the spatial distribution of freshwater mussels. Our results highlight the important role played by host fishes in shaping current distributions of freshwater mussels and underscore the necessity of incorporating these relationships in management actions as suggested by Clark *et al.* (2010). To effectively manage these critically imperilled taxa (Williams *et al.*, 1993) and to ensure the long-term persistence of many species, it will be necessary to continue to develop and refine our understanding of the factors shaping their distributions.

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SUPPORTING INFORMATION

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

Figure S1 Biplot of constrained analysis of principal coordinates (CAP) for fish presence/absence.

Table S1 Average abundances of mussel species in the eight watersheds used in the analysis.

Table S2 Presence/absence data of host fish species in the watersheds used in the analysis.

Table S3 Average values for environmental data in the watersheds used in the analysis. Note: Environmental data were not available for the Nottasawaga River.

Table S4 Summary table of environmental variables that were used in this study.

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BIOSKETCH

Astrid N. Schwalb received her PhD from the University of Guelph, Canada. Her research interests include the dispersal of freshwater mussels, their host infection strategies, their conservation and the impact of benthic communities on ecological processes.

Author contributions: ANS and KC conceived the ideas; TJM and NM provided the data; ANS and KC analysed the data; and ANS led the writing. All co-authors commented on and contributed to the manuscript.

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