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Limitations of beta diversity in conservation site selection

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ABSTRACT

Preservation of diversity is a key issue in many conservation efforts. It has recently been suggested that beta diversity should be considered in conservation planning and that sites with high local contribution to beta diversity (LCBD) may be valuable for conservation. Yet, such an approach has not been applied to freshwater mussels, a highly imperiled group of organisms. We used a dataset on freshwater mussel from the five largest rivers of southwestern Ontario, Canada to examine whether LCBD would be an efficient approach for assessing the conservation value of sites and compared it to more traditional conservation approaches (biomonitoring, high richness, high abundance). Sites with high LCBD value were associated with low mussel richness and were often characterized by mussels that are regionally widespread and usually abundant in lentic systems or smaller streams, limiting site selection based on beta diversity. Species at risk (including IUCN categories of Critically Endangered through Near Threatened) were more likely to occur in communities with high richness and abundance at sites chosen by the more traditional approaches. Thus, protecting sites with higher alpha diversity of mussels would also support higher gamma diversity of mussels. The provision of important ecosystem services by higher abundances of mussels which was also correlated with local richness should be considered as well. Our study suggests that there likely is an important link between high richness and abundance of mussels and the presence of species at risk which we argue is driven by facilitation (i.e., positive species interaction), an important, yet understudied, process that deserves more attention in conservation.

1. Introduction

Preservation of biodiversity, the diversity of life on Earth, is essential to combat ongoing environmental crises and to sustain ecosystem functions (Pereira et al., 2010; Rands et al., 2010). In 1992, at the Earth Summit held in Rio de Janeiro, or simply Convention on Biological Diversity, world leaders agreed on a comprehensive strategy for conserving biodiversity, developing national strategies for the conservation and sustainable use of biodiversity, and meeting our needs while ensuring that we leave a viable world for the future (Kats, 1992; Chandra and Idrisova, 2011). Yet, biodiversity, especially freshwater biodiversity is globally declining at an accelerated pace (Young et al., 2016). To mitigate this decline, we must accurately measure biodiversity to understand the processes that maintain species diversity and consider the organization of biodiversity in space, providing adequate means for establishing conservation targets (Dudgeon et al., 2006; Vörösmarty et al., 2010).

Diversity can be measured at different scales. Beta diversity is the change in species identities across space, which provides a direct link between local-scale (i.e., alpha diversity or local species richness) and regional-scale diversity (i.e., gamma diversity) owing to the spatial variation in community composition (Whittaker, 1960; 1972). The alpha and gamma metrics are straightforward lists of species and, as such, are relatively easy to incorporate into conservation planning. On the other hand, beta diversity incorporates a more intricate pattern as a measure of species similarity across different sites. The interest in beta diversity and its application in ecological conservation has increased significantly in recent years (e.g., Chase et al., 2020).

In an applied conservation context, beta diversity is directly related to the complementarity principle (i.e., the selection of a set of sites which are complementary to each other in terms of representing a regional species pool), a fundamental tenet in spatial conservation prioritization (Bush et al., 2016). The idea is that higher beta diversity increases gamma diversity. On the other hand, high gamma diversity can be reached with low beta diversity as long as alpha diversity is sufficiently high (Socolar et al., 2016).

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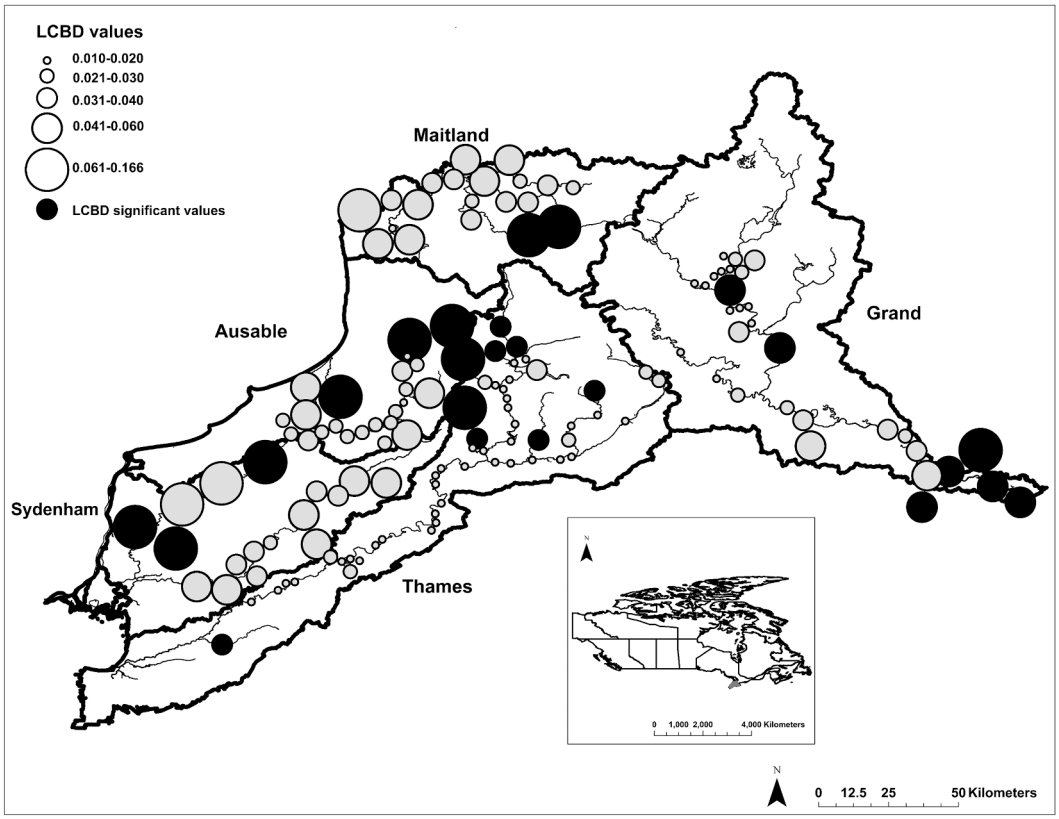

Fig. 1. Spatial distribution of sites within each watershed in Ontario and assigned LCBD values. Black colored points show significant LCBD values (LCBD sites). Number of LCBD sites recorded for each watershed: Ausable (5 sites), Grand (7 sites), Maitland (2 sites), Sydenham (3 sites), and Thames (7 sites).

Typical measures of beta diversity include nestedness and turnover (species replacement). Understanding how communities are spatially organized can facilitate and inform more effective biodiversity conservation strategies. For instance, a range of sites should be protected, when biota differ considerably between sites, i.e., high species replacement among communities. When other sites represent subsets of the most species-rich sites (nestedness), then conserving these individual species-rich sites should be a priority (Carvalho et al., 2012). Variation in biological communities within a region can be also seen as the local contribution of unique species composition to beta diversity for individual sites (Legendre et al., 2013). A measure of local contribution to beta diversity (LCBD) indicates the uniqueness of a biological community at a given site, and recent studies have suggested that uniqueness is a useful criterion for the identification of conservation priorities (Dubois et al., 2020, Heino et al., 2022, Hill et al., 2021, Niskanen et al., 2017, Vilmi et al., 2017).

The LCBD approach goes beyond typical and overall measures of beta diversity across the landscape and provides a value of the contribution to beta diversity for individual sites (Legendre et al., 2013; Heino and Grönroos, 2017). Sites with high LCBD values may indicate combinations of species with high conservation value, or degraded species-poor sites in need of ecological restoration (Legendre et al., 2013). Thus, this approach may identify sites of conservation importance that fall outside of the traditional strategies for biodiversity conservation. Sites with high contribution to beta diversity have been called ecologically unique sites (Legendre et al., 2013). Their protection may significantly increase the proportion of the regional species pool that is protected, thereby facilitating landscape-scale conservation.

Earlier studies have examined the LCBD and ecological uniqueness among freshwater communities particularly in relation to their environmental correlates (e.g., Benito et al., 2020; Pozzobom et al., 2020; Tonkin et al., 2016). However, studies taking a conservation approach have only been conducted using diatoms (Vilmi et al., 2017), macroinvertebrates (Hill et al., 2021), fish (Iacarella and Hou, 2022), and trees (Niskanen et al. 2017, Tan et al., 2019, Dubois et al. 2020) as study organisms, and to date there is no study in the literature examining the importance of ecological uniqueness in freshwater mussel conservation. The findings of these studies agree on the use of not only species-rich but also unique sites when planning effective regional conservations decisions and prioritizing management efforts.

We chose freshwater mussels as study organisms, because they are a highly imperiled group of organisms and the LCBD approach has not been applied to them yet. North America harbors the highest diversity of freshwater mussels (Order: Unionida) with roughly 300 species (Haag, 2012). Freshwater mussels can reach high abundances and as ecosystem engineers, they provide important ecosystem services such as water filtration, nutrient cycling, and habitat provision for other organisms such as benthic algae and macroinvertebrates (Vaughn, 2018). Their unique life cycle includes a parasitic stage, during which mussel larvae develop into juvenile mussels on host fish and during which they can be dispersed over larger distances. Thus, the distribution and movement of their host fish can affect the distribution and metacommunity structure of mussels, especially on a larger regional scale (Rashleigh, 2008; Schwalb et al., 2013; Schwalb et al., 2015). On a smaller spatial scale, mussel species with different life history strategies have been suggested to dominate in different types of habitats (Haag, 2012). For example, more opportunistic species tend to be abundant in lentic and/or degraded habitats (Haag, 2012).

Freshwater mussels are one of the most imperiled groups of organisms in North America and they are threatened globally (Master et al., 2000; Lopes-Lima et al., 2018). Most mussel conservation efforts are driven by species specific legislation (e.g., Species at Risk Act in Canada, Endangered Species Act in the US). Hence, sites for monitoring or conservation measures are usually determined based on the presence of

endangered or threatened species (Asaad et al., 2017). Another common approach to choosing conservation sites is to maximize alpha diversity (sites with high species richness). From a perspective of ecosystem services, high richness and high abundances of mussels would best ensure that ecosystem services are provided. In contrast, the LCBD approach would identify those sites significantly contributing to beta diversity (i.e., unique species composition), helping to distinguish sites that differ most from other sites in assemblage composition and yielding a valuable tool to base conservation decisions and restoration schemes (Legendre et al., 2013).

The goal of this study was to evaluate the characteristics of sites identified using the LCBD approach, and to compare those sites with selections of sites based on different approaches using a dataset from south-western Ontario including five river basins by contrasting: (a) biomonitoring sites (driven by legislative obligation to protect species at risk (i.e., species listed under the Species at Risk Act (SARA) in Canada, which includes IUCN categories Critically Endangered and Endangered, Vulnerable, and Near Threatened)), (b) sites with high species richness and (c) sites with high species abundance, and (d) LCBD sites (sites selected via the LCBD approach). Specifically, we wanted to (1) compare species richness and abundance between sites using different approaches (biomonitoring, high richness, high abundance, and LCBD) and examine the relationship between richness and LCBD values (value of the contribution to beta diversity for individual sites); (2) explore the spatial patterns of LCBD sites; (3) examine the proportion of sites overlapping between the approaches; (4) investigate the correlation between richness and abundance for common species and species at risk.

We predicted that (1) LCBD values and richness would show a negative relationship, assuming a trade-off between species richness and ecological uniqueness (i.e., species-poor sites harbor range-restricted species that are not found at species rich-sites); (2) because mussel beta diversity is usually lower in the headwaters, we expected to find significant LCBD sites mostly in the upstream sections of the river due to unusual species combinations at those sites; (3) significant LCBD sites would overlap minimally with the three conservation approaches (biomonitoring, high richness, and high abundance) because ecological uniqueness (localities with singular species composition) is a different measure of biodiversity; (4) based on the assumption that species at risk tend to occur at sites with high abundance and richness, thus supporting healthy mussel assemblages, we expected to find lower occurrence of species at risk at significant LCBD sites as well as low richness and low abundance of common species.

2. Methods

2.1. Study area

This study includes a compilation of data on freshwater mussel abundance from five watersheds in Ontario, Canada: Ausable, Grand, Maitland, Sydenham, and Thames rivers (Fig. 1).

2.2. Data compilation

Freshwater mussel abundance data for the five watersheds in Ontario were obtained from Fisheries and Oceans Canada's (DFO) Lower Great Lakes Unionid Database representing sites sampled between 1997 and 2009 (Ausable River 25 sites; Grand River 31 sites; Maitland River 21 sites Sydenham River 17 sites; Thames River 51 sites). 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), sampling mussels with tactile and visual searches with a search effort of 4.5 person-hours per site.

The number of selected sites varied between rivers. For the biomonitoring approach ((a), see above) we used data from a subset of sites selected for DFO's Unionid Monitoring and Biodiversity Observation network. These sites were previously selected for inclusion in DFO's monitoring network based on the presence of species at risk. The use of these sites resulted in six (Ausable, Grand, Maitland Rivers) or twelve (Sydenham and Thames River) sites in each watershed. To determine sites based on high species richness (approach (b)) and high abundance (approach (c)), for each river the same number of sites as the biomonitoring sites were used. In the Ausable, Grand and Maitland rivers the six highest abundance and the six highest richness sites were selected (matching the number of biomonitoring sites). In the Thames and Sydenham rivers the 12 highest richness and the 12 highest abundance sites were selected to match same number of biomonitoring sites for those watersheds. The LCBD approach (d) determined the number of ecological unique sites based on unique community composition, which varied among rivers according to the significance of LCBD values.

2.3. Statistical analysis

All analysis were performed in R language (R Core Team 2022). We separately calculated for each site in a watershed the LCBD values using Hellinger-transformed abundance data with the function *beta.div*. Calculations were carried out following the approach described by Legendre et al. (2013). In summary, this approach is based on the total variance (Var (**Y**)) in the community matrix (n sites $\times$ p species) estimated as beta diversity (BD_{total}). This variance is obtained by computing the total sum of squares (i.e., the sum, over all species and all sites, of the squared deviations from the species means) divided by $n - 1$, where n denotes the number of sites sampled in each watershed. The estimated measure of beta diversity based on total variance of transformed data (Var (**Y**)) can be thus partitioned into the relative contribution of single sites to total variance (LCBD), and that is calculated independently from alpha and gamma diversity. The significance of each LCBD value was assessed by 999 permutations, and the P-values were corrected for multiple testing using Holm's procedure. All functions cited above were from the 'adespatial' package (Dray et al., 2021).

It should be noted that there are different approaches to beta diversity, which are not interchangeable, although they all estimate the variation in species composition among sites. In this study, we are estimating the total variance of a community based on transformed data, which is different to the additive and multiplicative approaches partitioning gamma diversity into alpha and beta components (Chao et al., 2016). In the approach we use, data transformation is necessary to obtain ecologically meaningful variation estimates that result in the total variance quantifying the contribution of individual sites to the variation in community composition among sites (LCBD), which makes it useful for unbiased interpretation and conservation studies (Legendre et al., 2013).

To assess the relationship between LCBD and richness, we calculated site-specific taxonomic richness values with the function *specnumber* from the 'vegan' package (Oksanen et al. 2022), which we will hereafter refer to as species richness as all our taxa (33 species total) were identified to species level. Because of the nature of LCBD values (i.e., ranging from 0 to 1), we used beta regression and a logit link function (Cribari-Neto & Zeileis 2010) to model our response data using the function *betareg* from the package "BETAREG" (Cribari-Neto & Zeileis 2010). We evaluated whether LCBD values were related to species richness using beta regression analysis.

Based on the assumption that species at risk (i.e., species listed under the Species at Risk Act (SARA), Government of Canada and Species (2021) tend to occur at sites with high abundance and high alpha diversity (Eveleens, 2021), we examined for each watershed the linear relationships between overall species richness and overall abundance (predictors) and species at risk richness and abundance (response variables). For the linear regression we used the function *lm* from the the 'stats' base package in R.

Table 1
Gamma diversity and number of sites with significant ($P < 0.05$) LCBD values for watersehds studied in Ontario.

Watershed	Gamma Diversity	Number of LCBD sites
Ausable	22 species	5 sites
Grand	25 species	7 sites
Maitland	12 species	2 sites
Sydenham	28 species	3 sites
Thames	26 species	7 sites

3. Results

A total of 19,900 individuals belonging to 33 species was recorded from watersheds in Ontario with gamma diversity ranging from 28 species in the Sydenham to 12 species in the Maitland River (Table 1). The number of sites with significant ($P < 0.05$) LCBD values ranged between 7 sites (Thames and Grand River) to 2 sites (Maitland River) (Table 1). Median richness was always significantly lower at LCBD sites (range: 3 to 5 species) compared to sites selected by all other approaches (range: 6 to 14 species). However, the difference was most pronounced in watersheds with higher overall richness (i.e., > 12 mean species richness in Ausable and Sydenham, Figure A.1). Median richness at biomonitoring sites was either similar (Ausable and Sydenham) or lower (Grand and Thames) compared to the high abundance or high richness approaches (Figure A.1).

Similar to richness, median abundance was significantly lower for LCBD sites compared to all other approaches, except for the Maitland where median abundances were overall low (Figure A.2). Median

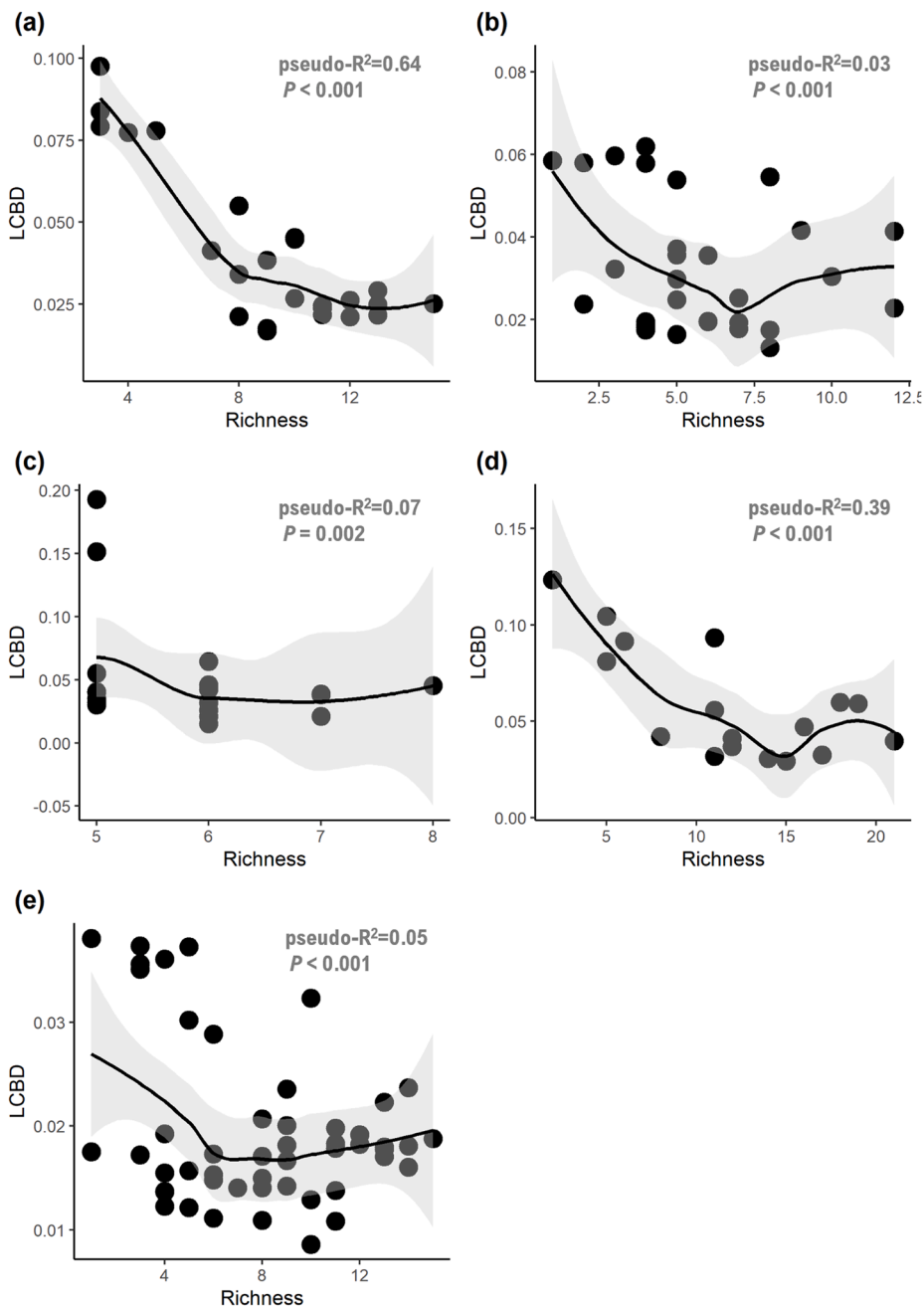

Fig. 2. Relationships between LCBD and richness for each watershed in Ontario (a = Ausable, b = Grand, c = Maitland, d = Sydenham, e = Thames). The grey shade area represents the 95% confidence interval.

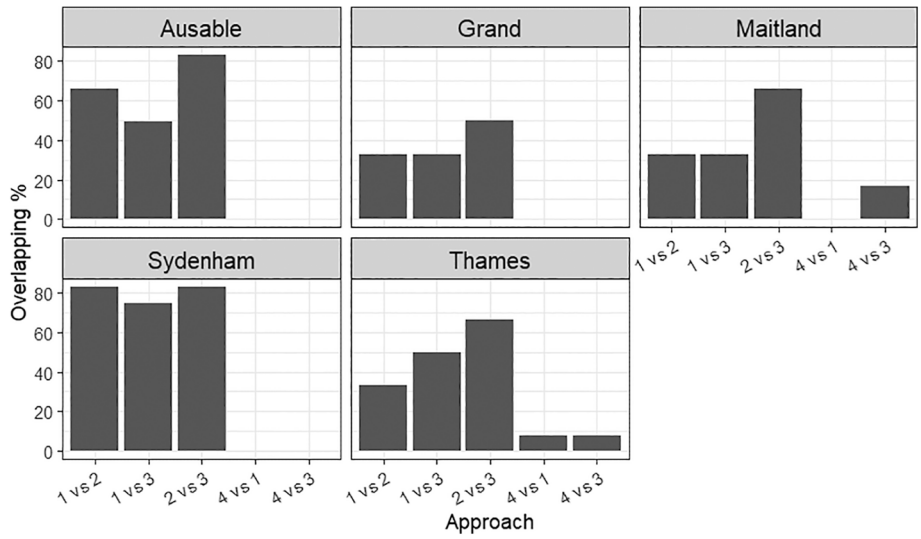

Fig. 3. Proportion of sites overlapping between the approaches within watersheds in Ontario (1. Biomonitoring, 2. High Richness, 3. High Abundance, 4. LCBD sites).

Table 2
Pearson correlation between richness and abundance for common and between richness and abundance of species at risk in each watershed.

Correlation	Ausable River	Grand River	Maitland River	Sydenham River	Thames River
All Species	0.60	0.45	−0.06	0.61	0.69
Species at risk	0.77	0.51	0.32	0.46	0.69

abundance at biomonitoring sites were either similar (Sydenham) or slightly lower compared to the high abundance approach (Grand and Thames) or the high abundance and high richness approach (Ausable, Figure A.2).

Following our first prediction, LCBD values showed a significant negative relationship with richness. The relationship was stronger in the Ausable (pseudo-$R^2 = 0.64$, $P < 0.001$) and Sydenham River (pseudo-$R^2 = 0.39$, $P = 0.003$) compared to the other rivers (Fig. 2). In accordance with our second prediction, LCBD sites tended to be mostly in the upper watersheds, except for the Grand River where LCBD sites were clustered at the most downstream sites and a few LCBD sites were also found in the lower part of the Thames and Sydenham River (Fig. 1).

The proportion of sites overlapping between approaches varied considerably between basins (objective 3, Figure A.3). The best overlap between biomonitoring sites and either high richness (83% shared sites) or high abundance (75% shared sites) was found in the Sydenham River and the lowest in the Grand and Maitland River (33% shared sites with high richness and high abundance sites) (Fig. 3). In the other two rivers, the overlap between biomonitoring sites and high richness sites ranged between 33% (Thames) to 66% (Ausable) and with high abundance sites between 49.5% (Ausable) to 50% (Thames, Fig. 3). There was generally no overlap with LCBD sites, with a few exceptions. A single LCBD site overlapped with one of the biomonitoring sites and one of the high abundance sites in the Thames and the Maitland River (Figure A.3).

In accordance with our fourth prediction, abundance of all species was positively correlated with richness in all rivers (ranging from moderate 0.45 correlation coefficient to strong 0.69), except the Maitland River. The correlation, however, was weaker in the Grand River than in the Thames, Ausable and Sydenham River when all were considered and similar to the Sydenham River when only species at risk were considered (Table 2). Richness of species at risk tended to increase with overall species richness in all rivers except the Maitland River, but the relationship was only statistically significant for the Ausable and Thames River (Fig. 4). Abundance of species at risk showed a significant positive relationship with abundance of all species in the Ausable, Thames, and Sydenham River (Fig. 5).

Most of the species present at the LCBD sites were species with broad habitat (i.e., flow and substrate) tolerances that commonly occur in areas with slow current and soft substrate, but that are otherwise considered common and widespread (in a regional species pool), e.g., *Pyganodon grandis* (Ausable, Sydenham, Thames, Grand); *Lampsilis siliquoidea* (Ausable, Maitland), *Lasmigona complanata* (Ausable, Sydenham) (Table A.1). LCBD sites in all rivers but Grand were characterized by absence of the most abundant species in that river, i.e., *Amblema plicata* (Ausable), *Lasmigona costata* (Thames Maitland, Sydenham), and *Actinonaias ligamentina* (Thames). The number of species at risk was lower at LCBD sites compared to the other approaches (Figure A.4), except for the Grand River, where the number of species at risk were higher or equal at LCBD sites compared to the sites selected by all other approaches. No species at risk was found at LCBD sites in the Ausable River (Figure A.4), whereas one species at risk was found in the Maitland and Sydenham Rivers (*Cambarunio iris*, *Quadrula quadrula*, respectively), and two species at risk in the Thames River (*Quadrula quadrula*, and *Cambarunio iris*) (Table A.1). In the Grand River, 5 species at risk were found at LCBD sites (*Quadrula quadrula*, *Lampsilis fasciola*, *Toxolasma parvum*, *Truncilla donaciformis, Obliquaria reflexa*), occurred at 5 out of 7 LCBD sites (Table A.1).

4. Discussion

Several studies using different groups of organisms such as periphyton (Vilmi et al., 2017), macroinvertebrates (Hill et al., 2021), fishes (Iacarella and Hou, 2022), and trees (Dubois et al., 2020) have shown that prioritizing sites for protection based on their unique contribution to beta diversity (identified with LCBD) would contribute to better protection of (regional) biodiversity. Yet, our study, which is the first to apply the LCBD approach to freshwater mussels, showed that this is not the case for unionid mussels (see below). Regionally rare or unique mussel species (i.e., species at risk) are more likely to occur in communities with high richness and abundance, suggesting that facilitation (i.e., positive species interactions) may be more important than competition in structuring mussel communities. Mussels are ecosystem engineers, known to enhance habitat conditions for benthic algae (e.g., Francoeur et al., 2002) and macroinvertebrates (e.g., Beckett et al., 1996) via redirecting nutrients from the water column to the benthos. Higher mussel densities may facilitate growth and survival of mussels, by making substrate more stable (Miura et al., 2021), and by attracting host fish (Firth et al., 2021), including benthic fish feeding on

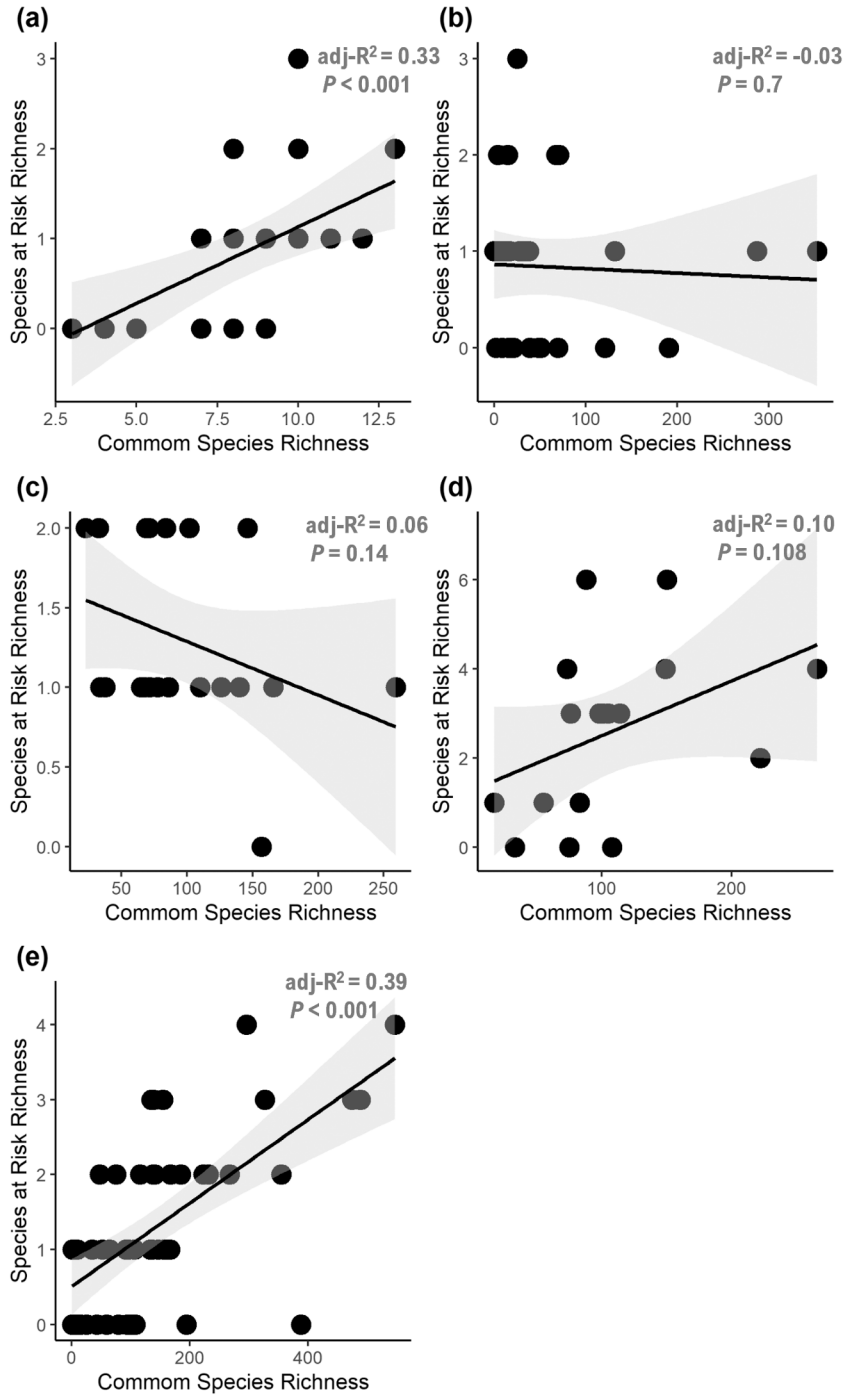

Fig. 4. Relationships between species at risk richness and commom species richness (a = Ausable, b = Grand, c = Maitland, d = Sydenham, e = Thames). Relationship considered significant when $P \leq 0.05$. The grey shade area represents the 95% confidence interval.

macroinvertebrates. The LCBD approach may also not be useful in identifying conservation sites for other group of organisms where facilitation is important, e.g., desert ecosystems where facilitation can ensure and maintain diversity and species often relay on each other to persist (Butterfield, 2009; Cavieres and Badano 2009; He et al., 2013). However, this remains to be studied.

Positive species interactions are frequently found in nature and are considered a diversity-promoting relationship driving community assembling (Boucher et al., 1982; Bronstein; 1994a, 1994b). In the last two decades, there has been an increased interest in understanding intraspecific positive species interactions (i.e., facilitation) and a variety of studies have investigated the mechanisms by which this relationship takes place (Bruno and Bertness, 2001; Brooker et al., 2008; Cardinale et al., 2002; Stachowicz and Byrnes, 2006; Vellend, 2008) and its implications for the management of ecosystems (Halpern et al., 2007). However, most of the studies on facilitation are focused on plant–plant interactions (e.g., Gómez-Aparicio et al., 2004, Maestre et al., 2005; Lortie and Callaway, 2006), and comparable attempts are lacking for freshwater systems (Holomuzki et al., 2010). Facilitation may be an important mechanism in structuring mussel communities and other aquatic organisms and deserves more attention by future studies.

Similar to previous studies investigating different groups of organisms, including fishes (Legendre et al., 2013), macroinvertebrates (Heino and Grönroos, 2017), diatoms (Vilmi et al., 2017), dung beetles

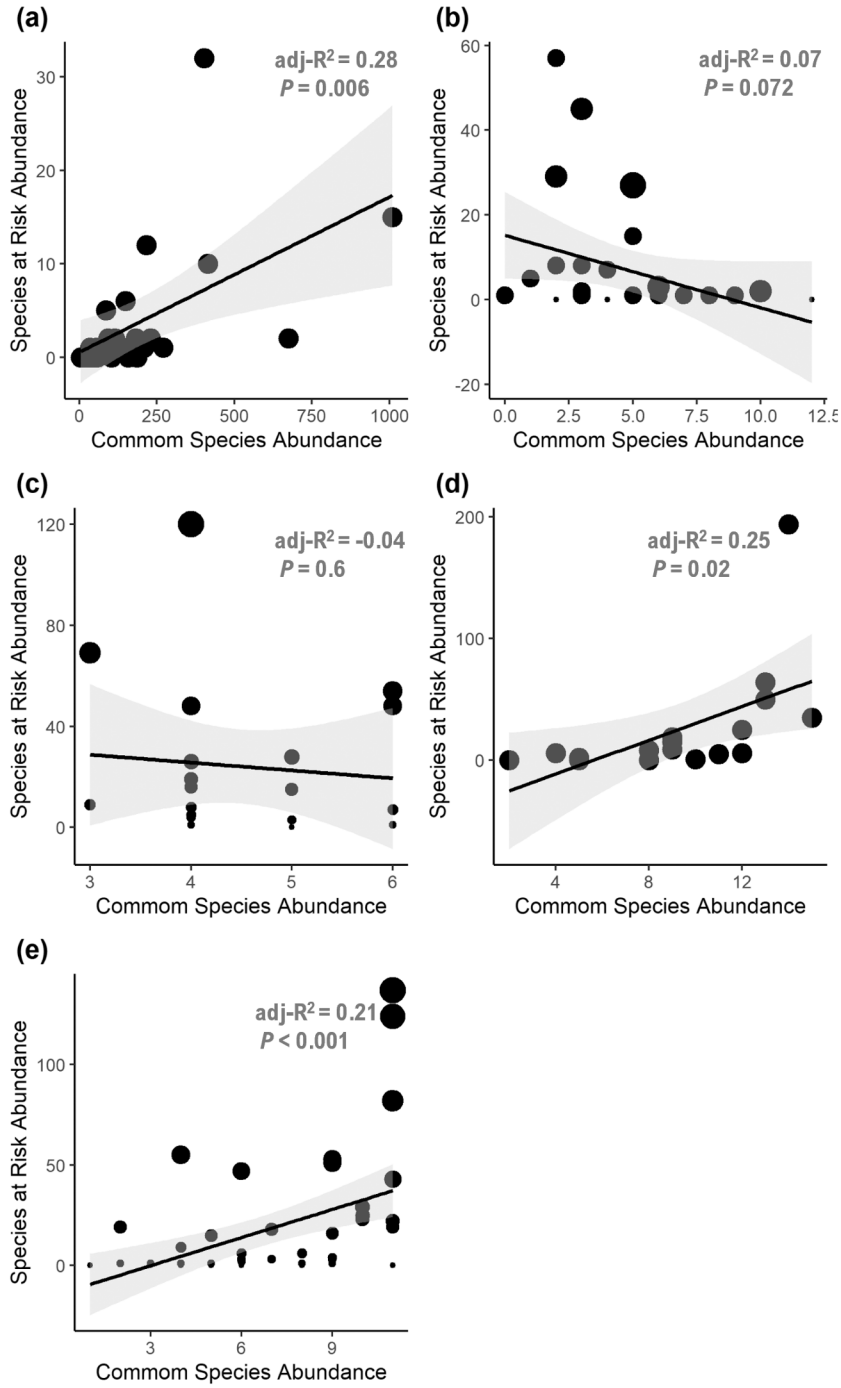

Fig. 5. Linear relationships between species at risk abundance versus commom species abundance (a = Ausable, b = Grand, c = Maitland, d = Sydenham, e = Thames). Relationship considered significant when $P \leq 0.05$. The grey shade area represents the 95% confidence interval.

(da Silva et al., 2018), and trees (Dubois et al., 2020), we found sites with high LCBD value were associated with low richness. However, in our study these low richness sites did not have a high biodiversity value as shown in these other studies. Instead, low richness sites in our study were often characterized by mussel species that are regionally widespread. These species can be abundant in lentic systems (ponds, lakes) and smaller streams (e.g., *Lampsilis siliquoidea* and *Pyganodon grandis*), although they tend to be rare at most of the riffle sites of larger rivers that were included in our study.

It can be argued that the LCBD approach may work for mussels if the dataset was not focused on rivers with potential habitat for species at risk and a truly random dataset would be gathered instead with data from different aquatic systems. Nevertheless, LCBD tends to select for sites with low richness, but in our study, higher richness of common species supported higher richness of species at risk in most of the watersheds in Ontario. There is widespread anecdotal evidence for the association of presence of protected species and high richness sites, but there a few studies that have examined this (Eveleens, 2021).

Higher local richness was not only associated with presence of species at risk, but also correlated with higher local abundances, and more mussels can provide more ecosystem services such as water filtration, nutrient cycling, and habitat provision for other organisms (see above, Vaughn 2018). Thus, protecting mussel sites with high richness and abundance not only increases the likelihood of protecting species at risk

and diversity, but also enhances ecosystem services provided by mussels. High alpha diversity may be as important as high beta diversity in mussel biodiversity conservation, demonstrating that higher beta diversity might not necessarily be a wanted outcome when maximizing regional diversity (Socolar et al., 2016).

It has also been suggested to use the LCBD approach to identify degraded sites that may be suitable for restoration (Legendre et al., 2013). It is unlikely that this approach would prove beneficial within our study systems as the LCBD approach identified sites that tended to represent peripheral (i.e., headwater sites and/or tributary) areas indicative of habitats unlike our mainstem sites. These LCBD sites could not likely be restored to represent the habitat conditions of these mainstem sites. The exception was the Grand River, where LCBD sites with a considerable number of species at risk were clustered at the most downstream sites. The Grand River may provide unique circumstances as it is the only study river where impoundment may restrict movement especially of larger host fish with larger migration distances. Hence, mussel communities in the stretch below the impoundment (where most of the LCBD sites are located) are more representative of "lake" species with limited distributions within the Grand River.

Conservation efforts must consider how biodiversity is organized in space and identifying effective conservation approaches is essential to ensure that biodiversity is sustained and when possible enhanced (e.g., Socolar et al., 2016). To best conserve biodiversity, we need to understand how locally collected data can translate into regional diversity dynamics, and how the patterns that maintain biodiversity vary from local to regional spatial scales. Monitoring of freshwater mussels is usually driven by the presence of species at risk, associated legislative obligations, and the desire to track species recovery. As a result, sites where common mussel species thrive (e.g., lentic habitats) are often under-surveyed and thus a true assessment of gamma diversity and the role of beta diversity will remain elusive. However, this study showed that biomonitoring sites selected based on expert opinion targeting species at risk showed a good agreement with site selection based strictly on high richness and abundance. Our data also indicate that there likely is an important link between high richness and abundance and the presence of species at risk, which we argue is driven by facilitation, an important, yet understudied, process that should be considered in conservation.

CRediT authorship contribution statement

Mariana Perez Rocha: Conceptualization, Formal analysis, Methodology, Project administration, Visualization, Writing – original draft, Writing – review & editing. **Todd J. Morris:** Data curation, Validation, Writing – review & editing. **Karl Cottenie:** Validation, Writing – review & editing. **Astrid N. Schwalb:** Conceptualization, Resources, Supervision, Validation, Writing – review & editing.

Declaration of Competing Interest

The authors declare that they have no known competing financial interests or personal relationships that could have appeared to influence the work reported in this paper.

Data availability

Data will be made available on request.

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Appendix A. Supplementary data

Supplementary data to this article can be found online at https://doi.org/10.1016/j.ecolind.2023.110732.

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