

Species turnover drives β -diversity patterns across multiple spatial and temporal scales in Great Lake Coastal Wetland Communities

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Abstract β dissimilarity indices have described community variation occurring from unique structuring processes: species turnover and nestedness. However, the importance of scale definition remains critical and challenging during β assessments with a need for simultaneous spatial and temporal assessment to determine ecological phenomena governing biological communities. We aim to examine the contribution of turnover and nestedness structuring processes across multiple spatial and temporal scales to demonstrate the importance of scale consideration in β assessments. Using a site-to-basin-wide spatiotemporal hierarchical design, we examined diversity patterns, testing spatial, and temporal facets of β diversity structuring Laurentian Great Lake coastal wetland fish and macroinvertebrate communities from 2000 to 2012. Both fish and

macroinvertebrate communities were analyzed using β dissimilarity indices under the same hierarchical design. Results indicated strong spatial and temporal turnover structuring with increasing β diversity and community turnover as scale localized. We suggest that high turnover is the result of inhospitable winter conditions followed by random re-colonization events in the spring. With relatively unique communities across space and time, biodiversity-oriented management of coastal wetlands should consider an all-inclusive approach as biodiversity hotspots are not apparent.

Keywords Species turnover · β Diversity · Biodiversity · Wetlands · Fish · Macroinvertebrates

Introduction

Biodiversity is a principle driver of ecosystem function (Tilman & Downing, 1994; Naeem et al., 2012) and is a fundamental concept of community and ecosystem

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ecology (Pimm & Raven, 2000; Tilman, 2012). With unprecedented rates of global biodiversity loss occurring in recent decades, an awareness of community-environmental linkages structuring biodiversity is critical to conservation and restoration initiatives.

Biodiversity assessment often requires explicit consideration of spatial and temporal variation to reveal ecological phenomena and the forces structuring them (e.g., replacement and loss of species). Spatial assessments have demonstrated unique factors structuring communities at local (Diamond, 1975; Al-Shami et al., 2013), landscape (Kays et al., 2008; Pratchett et al., 2008), and global scales (Graham et al., 2008; Leprieur et al., 2011). Temporal assessments have identified different forcing factors between short seasonal (Bhagat & Ruetz, 2011) to broad interglacial scales (Leprieur et al., 2011). No single scale captures all the dynamics present (Chase & Ryberg, 2004) and yet clearly all scales are connected and important to fully understand biodiversity patterns.

Beta (β) diversity is a revitalized area of research (Anderson et al., 2011) that conceptually addresses community compositions across scales. Generally credited to Whittaker (1960, 1972), the theory is based on discrete local communities and assesses their collective degree of uniqueness among similar communities across different spatial scales from local (α) diversity to global (γ) diversity. Whittaker's β diversity, β_w , ($\beta_w = \gamma/\alpha$), supports contrasting scenarios to reach high global diversity by promoting either 1) high site diversity (high $\gamma = \text{high } \alpha * \text{low } \beta$) or 2) high community variation (high $\gamma = \text{low } \alpha * \text{high } \beta$). However, loss in species identity during β_w transformation becomes problematic to understanding unique community structuring processes and potential environmental factors associated with specific communities (Whittaker, 2001).

Developed from β_w foundations, β dissimilarity indices address the concern of lost species identities, providing additional community-environment insights (Kessler et al., 2009; Leprieur et al., 2011; Al-Shami et al., 2013). Current state of dissimilarity indices partition β diversity into two structuring processes: turnover and nestedness (Baselga, 2010; Anderson et al., 2011; Leprieur et al., 2011). Turnover is the replacement of species between locations due to certain species being unique to discrete locations. In contrast, nestedness is the loss of species from one location due to some sites simply containing smaller subsets of a

biologically-rich site(s) elsewhere. The practice of partitioning β diversity into nestedness and turnover components is relatively new (Baselga, 2010; Anderson et al., 2011) and yet is proving to be a powerful approach in conservation and management theory. Application of such indices has tended to focus on a single biogeographical component; spatial, temporal or variation from changes in scale, suggesting the importance of all three in β diversity assessments (Angeler, 2013; Barton et al., 2013; Rádková et al., 2014). Ultimately, deciphering β diversity and its turnover and nestedness components across multiple spatial and temporal scales in combination can inform management strategies by discriminating species-diminished areas from species-replacement areas while simultaneously assessing the stability of a location through time.

The purpose of this biodiversity study was to (1) test the effects of both spatial and temporal β diversity patterns on community structuring; and (2) compare β diversity patterns among different taxonomic groups. We examined the contribution of turnover and nestedness structuring processes across multiple spatial and temporal scales to overall β diversity.

We conducted our assessment on coastal wetlands of the Laurentian Great Lakes. Coastal wetlands provide an ideal system to assess biodiversity as they often comprise a minor portion of the total surface area of the basin yet support a majority of the basin's biodiversity. For sampling and analysis practicalities, Great Lake coastal wetlands are also spatially well defined and are typically isolated habitat 'islands.' Coastal wetlands serve as important nursery, spawning, and feeding habitat for many fish, birds, mammals, invertebrates, and amphibians (Jude & Pappas, 1992; Burton et al., 1999, 2004). The biotic assemblages of coastal wetlands have been shown to be strongly structured by habitat characteristics including, vegetation, fetch, landuse, and other anthropogenic disturbances (Burton et al., 2002; Burton et al., 2004; Uzarski et al., 2004, 2005; Schock et al., 2014). However, research has generally focused on indicator species of system health and integrity with a less direct focus on biodiversity and β diversity patterns across space and particularly time. Therefore, direct assessment of patterns of biodiversity-environment structuring within the Great Lakes basin is needed. In addition to the need within this system, our study provides an approach that simultaneously addresses spatial scale, temporal scale and variation in scale definition effects on β diversity.

Methods

Model organisms

We addressed the goals of this study with two different groups of organisms: fish and aquatic macroinvertebrates. Here, after we use macroinvertebrate meaning species of aquatic macroinvertebrates from the phylum arthropoda. The use of fish and macroinvertebrates as model organisms in this study is appropriate as the groups are known to differ among various stressors within the basin (Uzarski et al., 2004, 2005; Schock et al., 2014), thus establishing observable variation in communities.

Study boundaries and data descriptions

We assessed fish richness from 174 site-level sampling efforts across coastal wetlands in Lake Michigan (92 efforts) and Lake Huron (82 efforts) from 2000 to 2012 (Fig. 1) referred to as MI/HU fish dataset. Samples were defined as ‘efforts’ since some sites were sampled multiple times over the course of the 12 years. Spatial boundaries comprised Basin (Lakes Michigan and Huron together, further denoted Basin), Lakes (Lake Michigan and Lake Huron, further denoted MI and HU, respectively), Regions (northern Lake Michigan, eastern Lake Michigan, northern Lake Huron, Saginaw Bay, further denoted NLM, ELM, NLH, and SAG, respectively) and Sites within regions (further denoted as respective region followed by Sites); (e.g., NLM Sites). These boundaries were derived from biological differences related to discrete regional patterns in physio-chemical characteristics (Uzarski et al., [in press](#)) and noted chemical/physical characteristic differences. Additionally, this design allowed hierarchical assessment across various α and γ extent combinations (Fig. 2). All sampled wetlands had a surface connection to nearshore lake waters, thus the potential to exchange individuals across all locations did exist.

Macroinvertebrate richness was partitioned into two data classifications for analytical purposes: (1) a Lake Michigan/Lake Huron (MI/HU) dataset and (2) a Laurentian Great Lakes basin (GLB) dataset. The MI/HU dataset comprised 200 (86 Lake Michigan and 114 Lake Huron) sampling efforts from 2002 to 2012 in the same hierarchical formatting as the fish dataset (Fig. 2). Efforts considered in the MI/HU dataset were not necessarily paired to fish sampling locations

due to unique sampling protocols for both fish and macroinvertebrates. The GLB dataset comprised 201 sampling efforts (23 Lake Erie, 87 Lake Huron, 44 Lake Michigan, 29 Lake Ontario, 18 Lake Superior) collected in 2011–2012. Hierarchical levels remained as previously defined with additional locations to each level, Basin (Lakes Ontario, Erie and Superior), Lake (Lake Erie, Lake Ontario, Lake Superior, further denoted ER, ON, SU, respectively), Region (northern Lake Erie, southern Lake Erie, northeast Lake Huron, northern Lake Ontario, southern Lake Ontario, and southern Lake Superior, further denoted NLE, SLE, NELH, NLO, SLO, SLS, respectively) and Site within each region (Fig. 2).

Data collection

Sampling was restricted to the summer growth period (June–August) to minimize the impacts of seasonal habitat differences, especially with respect to vegetation structure. Further, we started sampling in southern latitudes and moved northward over the course of the summer. We sampled all mono-dominant (>75% coverage) emergent vegetation zones (e.g. phragmites, lily, *Typha*, *Schoenoplectus*) for fish and macroinvertebrates communities. A submerged aquatic vegetation (SAV) habitat zone had been sampled consistently from 2000 to 2006 in the ELM region and was also included in this study. Zone size for fish sampling required a minimum continuous 100 m² patch of vegetation with a minimum of 20 m distance between net sets to ensure that catch was not influenced by adjacent nets. Zone size for invertebrate sampling required a minimum patch size of 25 m², with a minimum of 15 m between replicates. Sites with zones not clearly dominated by one type of vegetation or smaller than required size were not sampled. We sampled by vegetation zone to standardize measurements among coastal wetland sites since Uzarski et al. (2004, 2005) demonstrated that vegetation zone was the dominant driver of community composition and Cooper et al. (2012) demonstrated that biota differ among core and edge habitats.

Fish were collected via fyke nets with 4.8 mm mesh, 7.3 m lead, and 1.8 m wings which were set at 45° angles to the lead. Three replicate fyke nets were set within each dominant vegetation zone for the duration of one net-night (12–24 h). Two sizes of fyke nets, 0.5 × 1.0 m openings or 1.0 × 1.0 m openings,

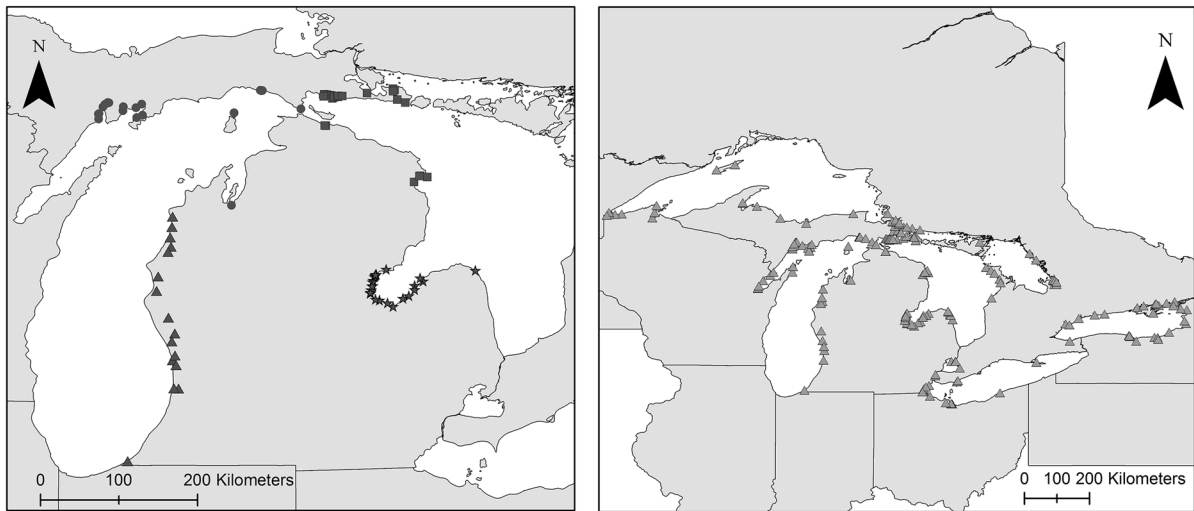


Fig. 1 (left) Location of sampled fish and macroinvertebrate sites between 2000 and 2012 used in this study. Symbols mark centroid of wetland: *Circles* represent northern lake michigan sites, *squares* represent northern lake huron sites, *triangles*

represent eastern lake michigan sites, *stars* represent saginaw bay sites. (right) Site centroid of 2011–2012 macroinvertebrate sampling locations

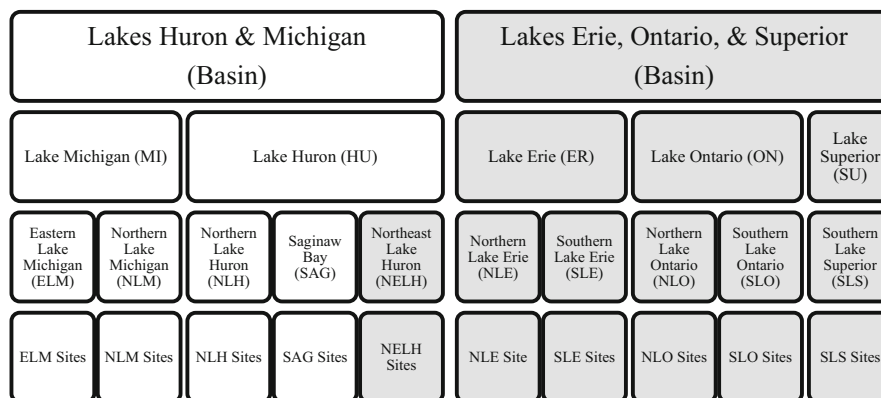


Fig. 2 Schematic representation of 4 level spatial hierarchical design. Each hierarchical level is denoted by *horizontal rows* with *each box* representing a specific boundary of interest and labeled with respective locations. *Parentheses* denote acronym

used throughout the paper. *Gray-shaded boxes* represent extents added to each hierarchical levels in the Laurentian Great Lakes Basin macroinvertebrate dataset

were utilized based on water level, with small nets set in waters ranging 0.2–0.5 m and large nets set ranging 0.5–1.0 m. Net placement was perpendicular to the targeted vegetation zone with the net lead extending into the zone, collecting fishes inhabiting both the vegetation and its edge. In cases where patch width was shorter than the leads, nets were set at acute angles to ensure nets were fishing only targeted zones. Fish were captured alive, identified to species, measured, and then released. Fish that could not be identified in the field were euthanized via MS-222 solution and

stored in formalin until further identification occurred. Fish identified as ‘unknown’ (12 occurrences) were considered to be one unique species. This was done as most unknown categorized species were a single species of young of year fishes that could not be identified to species level (e.g., sculpin species). A conservative approach in removing sites with unknown occurrence was tested and demonstrated no variation in trends and scores (unpublished).

Macroinvertebrates were sampled using a D-frame dip net that comprised 500 μm mesh size. Replicates

were taken in water depth from 0.05 to 1.0 m from targeted vegetation zones. Organisms were emptied into a 5 × 5 cm gridded white tray. All organisms were collected from the tray using forceps. All individuals were collected from a single grid cell before moving to a new cell to eliminate size and activity bias and obtain a diverse representation of organisms for each replicate. Specimens were picked for 30 person minutes/replicate or until 150 organisms were obtained. If the 30 person minutes per replicate expired before 150 organisms were collected, than the next replicate of 50 (50, 100, 150 specimens) ended collection representing a catch-per-unit-effort approach. All samples were stored in 95% ethanol solution preserved until further identification in a laboratory setting under a stereoscope. Macroinvertebrates were identified to lowest taxonomic group possible with resolution sacrificed to coarser classification if all individuals could not be identified to a similar taxonomic level. For a greater explanation of the sampling methodology implemented here please consult Uzarski et al. (2004) regarding macroinvertebrates and Uzarski et al. (2005) regarding fish.

β Dissimilarity indices

Species catch data were pooled from sample replicates/zone/site and transformed into present or absent at the site level with similar pooling made to higher hierarchical levels (e.g., replicates/zone/site/region/lake) prior to analyses. Use of dissimilarity indices followed similar methodology and reporting as Baselga, (2010). Sørensen's β dissimilarity, β_{SOR} or β_{sor} , is a measure of overall β diversity, with scores ranging 0–1, with 0 being complete community similarity and 1 being complete community dissimilarity. Case sensitivity represents multi-site or pairwise comparisons, respectively. Sørensen's β is then partitioned into 2 different indices; Simpson's β dissimilarity, β_{SIM} or β_{sim} , and the β nestedness-resultant dissimilarity, β_{NES} or β_{nes} , measures associated with species turnover and nestedness, respectively, and that summed equal Sørensen's β (Table 1). Pairwise dissimilarity indices were used in situations where only two α units were present in a γ extent (e.g., MI and HU within Basin) and the multi-site metrics were used in all other comparisons creating a composite of the observed α level (e.g., Sites within the Basin).

Due to the nature of multi-unit β measurements, all direct comparisons between areas require equal or

Table 1 Dissimilarity index and formula of measurement to determine β diversity (β_{sor}) and components of spatial turnover (β_{sim}) and nestedness (β_{nes})

Dissimilarity measure	Formula
Sørensen pairwise (β_{sor})	$\frac{b+c}{2a+b+c}$
Simpson pairwise (β_{sim})	$\frac{\min(b,c)}{a+\min(b,c)}$
Nestedness-resultant pairwise (β_{nes})	$\frac{\max(b,c)-\min(b,c)}{2a+\min(b,c)+\max(b,c)} \times \frac{a}{a+\min(b,c)}$
Sørensen multi-site (β_{SOR})	$\frac{[\sum \min(b_{ij}, b_{ji})] + [\sum \max(b_{ij}, b_{ji})]}{2[\sum (S_i - S_j) + [\sum \min(b_{ij}, b_{ji})] + [\sum \max(b_{ij}, b_{ji})]]}$
Simpson multi-site (β_{SIM})	$\frac{[\sum \min(b_{ij}, b_{ji})]}{\sum (S_i - S_j) + [\sum \min(b_{ij}, b_{ji})]}$
Nestedness-resultant multi-site (β_{NES})	$\beta_{SOR} - \beta_{SIM}$

Symbols are equivalent to: a species shared by both locations, b species only in location i , c species only in location j , S_T total number of species in all locations, S_i number of species identities in location 'S'

near equal α units, otherwise reported β values of the greater sampled areas are relatively inflated (Baselga, 2010). We corrected for sample size differences using a resampling procedure suggested by Baselga (2010) referred to as α standardizing. α standardizing occurred across all areas by randomly resampling a subset of the sampled locations at 100 iterations to determine a composite score, allowing direct comparison between areas (e.g., there were 12 SAG Sites and 5 NLH Sites, we used 100 random sample iterations of 3 MI Sites and 3 HU Sites separately to create an averaged β value for both locations). Three units became the minimum resample value used in any multi-unit comparison rather than pairwise averaging, which is noted to skew score values in large sample sizes (Baselga, 2013). All indices were analyzed using R 3.0.1 (R Development Core Team, 2006) and the 'betapart' package (Baselga & Orme, 2012).

β Dissimilarity assessments

Spatial, temporal, and boundary discrepancy assessments of β_{SOR} , β_{SIM} , and β_{NES} calculations were performed using the MI/HU fish and macroinvertebrate datasets. We conducted spatial assessment by comparing different hierarchical comparisons within a given year. Basin, lake, region, and site level assessments allowed us to compare β diversity patterns within and among spatial areas to determine the magnitude of

spatial difference on β diversity. Temporal assessment was conducted by comparing the same area across different years providing assessment without spatial influences allowing us to observe a given area through time and its community stability. Our assessment of boundary discrepancies on resulting β diversity scores was based on comparing different α units within the same γ extent (i.e., Sites within the Basin compared, Regions within the Basin, Lakes within the Basin). The simultaneous assessment of multiple boundaries allows assessment to the impact of boundary definition on perceived β diversity of an ecosystem. For example, during fine scale assessments (i.e., Sites within the Basin) we could observe very unique communities and conclude β diversity is high, while coarse scale assessment (i.e., Lakes within the Basin) we could observe very similar communities and conclude that β diversity is low. Resulting differences demonstrate how a single scale approach can limit comprehensive understanding to the complex patterns and multiple factors governing an ecosystem. The use of multi-scaled assessment can also provide insight to how habitats are perceived/utilized by the species within a community. For example, the absence of a species from a site versus a region versus a lake has different implications to the forcing that are driving biodiversity within the ecosystem. Ultimately, the coupling of spatial, temporal, and scale definition discrepancy assessment on a community aide in a greater understanding of potential mechanisms structuring β diversity and the use of habitats by communities.

To maintain hierarchical integrity only individual years containing a minimum of 3 sample efforts within every region were selected. Years 2002, 2011, and 2012 met criteria for both HU/MI datasets with 2004 also meeting the criteria in our fish dataset. Using the GLB macroinvertebrate dataset, we expanded our spatial inference by incorporating sites, regions, and lakes from the remaining areas within the Laurentian Great Lakes basin.

Additional temporal assessments were conducted within given sites to determine greater within site resolution of β diversity structuring. We implemented a two tier hierarchical design with the γ extent comprising the total species observed across all years within a given site and α units comprising the species collected within a single sampling year of that site. Our fish and macroinvertebrate temporal assessments

were conducted under different criteria due to difference in completeness and robustness of each dataset. We did not want to lose the strength of our fish dataset to maintain similarity with our macroinvertebrate dataset. Sites selected for temporal site analyses from our fish dataset contained a minimum of 4 sampling efforts (range 4–9) from 2000 to 2012, while selected macroinvertebrate sites contained a minimum of 3 sampling efforts (range 3–4) from 2001 to 2012. Seventeen and 20 sites, respectively, met our criteria with at least 3 sites/region used in both datasets.

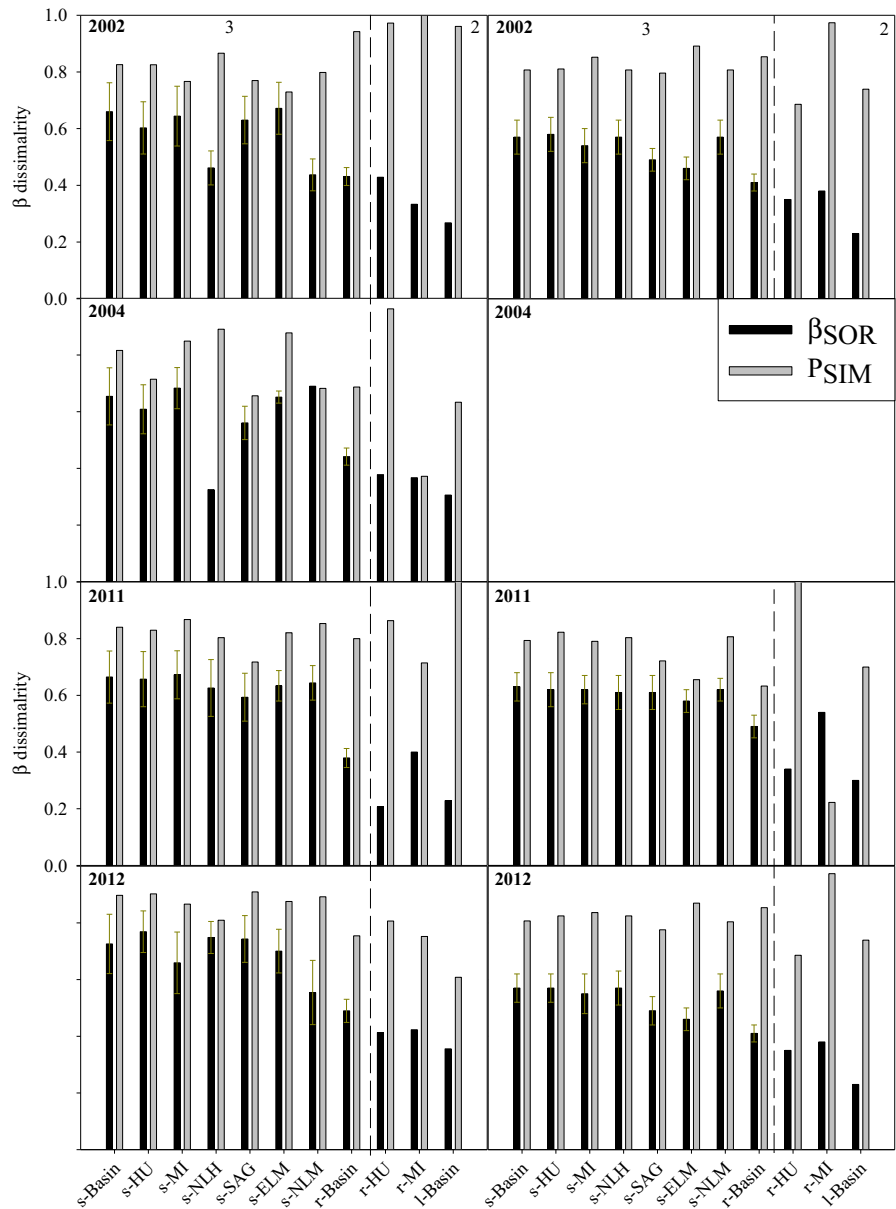
Results

There were 89 fish species identified along with 3 unknown categories (unknown fish, unknown sculpin, and unknown shiner) across all sampling efforts. The MI/HU and GLB macroinvertebrate datasets contained 287 and 260 taxonomic units, respectively. See Appendix S1 in Supporting Information for taxon locations.

β Diversity: scale discrepancy

In both MI/HU (fish and macroinvertebrate) datasets, the greatest β_{SOR} scores occurred in the most localized α scale: α Sites (annual mean = 0.67 and 0.59, respectively) > α Regions (annual mean = 0.43 and 0.44) > α Lakes (annual mean = 0.29 and 0.27, respectively). A similar trend of decreasing scores with increasing scale was observed in both fish and macroinvertebrate β_{SIM} scores with α Sites (annual mean = 0.57 and 0.47, respectively) > α Regions (annual mean = 0.35 and 0.34, respectively) > α Lakes (0.23 and 0.19, respectively). A similar scale trend in β_{NES} scores was not observed in either the fish (annual mean = 0.08, 0.08, 0.07, respectively) or the macroinvertebrate (annual mean = 0.11, 0.10, 0.07, respectively) datasets. In all scale discrepancy assessments, β_{SIM} scores comprised the greater proportion of β_{SOR} scores and in one case (fish 2011) β_{NES} displayed no contribution to diversity structuring (Fig. 3). In general, increasing locality of α scale resulted in an increase in β_{SOR} and β_{SIM} scores with little change in β_{NES} score. See Appendix S2 in Supporting Information for numerical representation of figures.

Fig. 3 β_{SOR} and P_{SIM} dissimilarity summaries of MI/HU fish (left) and macroinvertebrate (right) datasets. P_{SIM} (β_{SIM}/β_{SOR}) represents the proportion of community dissimilarity (β_{SOR}) explained by species turnover (β_{SIM}). Sites with (s-‘extent’), regions with (r-‘extent’), and lakes with (l-‘extent’) a given γ extent scores are reported 100 iteration resampled means and standard deviations to allow direct value comparison. Long hash lines note difference in α standardization values with α standardization values reported



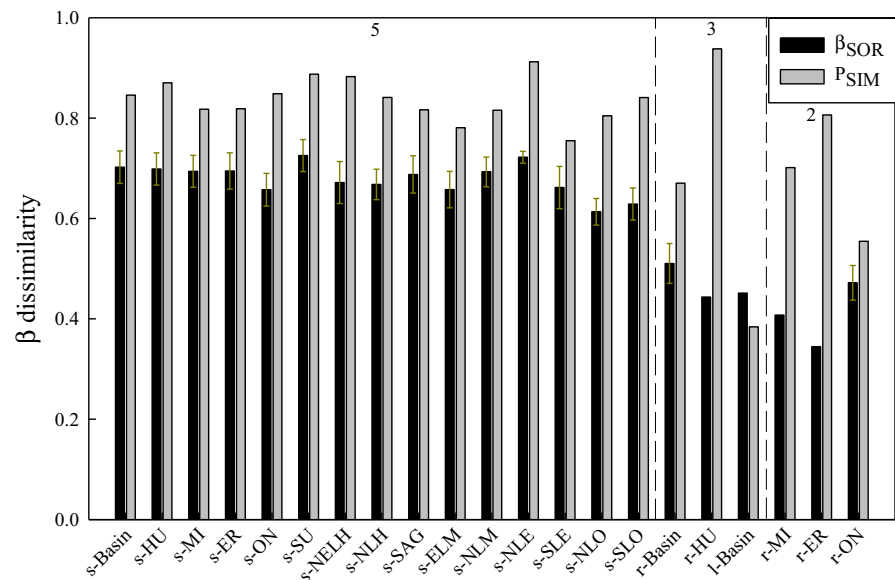
β Diversity: spatial and temporal assessments

Spatial assessment demonstrated similar trends of decreasing β_{SOR} and β_{SIM} scores and more constant β_{NES} scores as α scale became localized in both fish and macroinvertebrates within a given year. When comparing similar α units among different γ extents scores remained relatively similar to each other. Temporal assessment demonstrated relatively similar trends and dissimilarity scores across years as β_{SIM}

comprised a greater portion of the β_{SOR} in all but two assessments (α Regions within Lake Michigan 2004 (fish) and 2011(macroinvertebrate)) and no β_{NES} was observed in one assessment (α Lakes within the Basin 2011 (fish)); (Fig. 3).

The GLB macroinvertebrate dataset demonstrated similar trends of decreasing β_{SOR} and β_{SIM} scores and more constant β_{NES} scores as α scale localized. An increased prevalence of nestedness is noted at the α Lakes within Basin assessment, yet turnover was still

Fig. 4 β_{SOR} and P_{SIM} dissimilarity summarizes for GLB macroinvertebrate dataset. P_{SIM} ($\beta_{\text{SIM}}/\beta_{\text{SOR}}$) represents the proportion of community dissimilarity (β_{SOR}) explained by species turnover (β_{SIM}). Sites with (s-‘extent’), regions with (r-‘extent’), and lakes with (l-‘extent’) a given γ extent scores are reported 100 iteration resampled means and standard deviations. Long hash lines note difference in α standardized values with α standardized values reported



the greater contributor to β_{SOR} . One exception to greater β_{SIM} contribution was observed in the α Regions within Lake Michigan where $\beta_{\text{NES}} = 0.28$ was a greater contributor to $\beta_{\text{SOR}} = 0.45$ (Fig. 4).

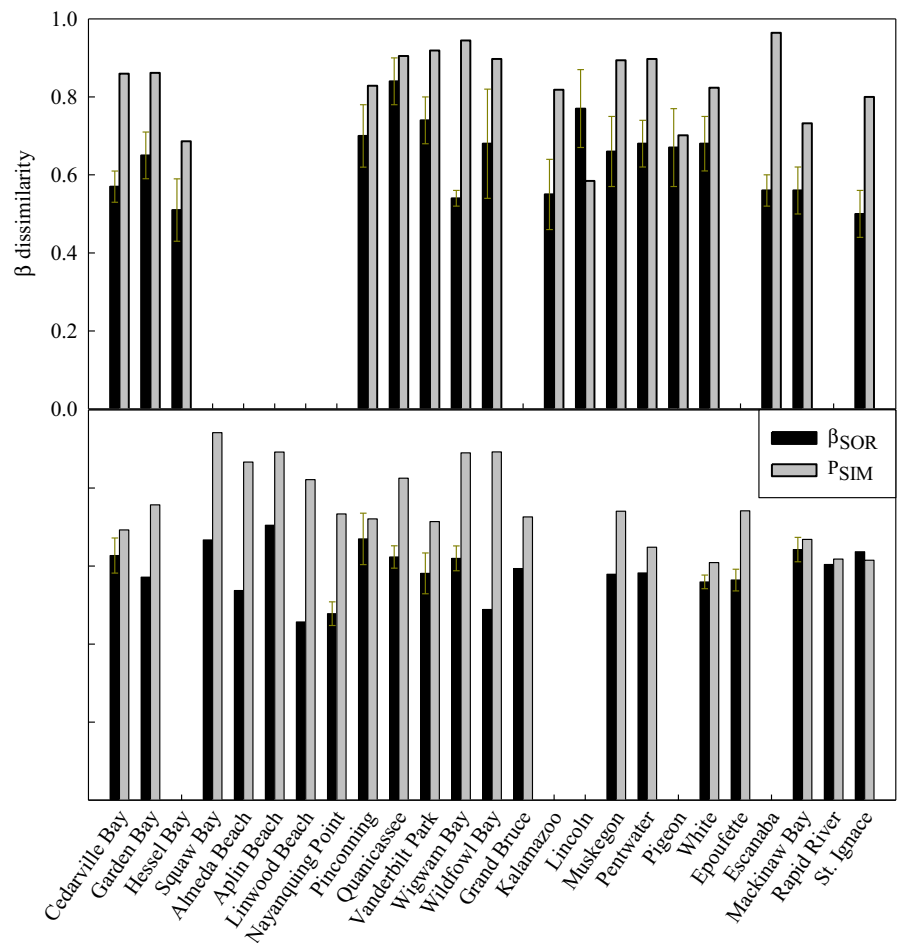
Temporal assessment within a site demonstrated β_{SIM} comprised the greater portion of β_{SOR} within a given site in all 17 fish and 20 macroinvertebrates sites (Fig. 5). However, Lincoln wetland for fish ($\beta_{\text{SIM}} = 0.45$, $\beta_{\text{NES}} = 0.32$) and White wetland for macroinvertebrates ($\beta_{\text{SIM}} = 0.34$, $\beta_{\text{NES}} = 0.22$) appeared to be possible locations that experienced relatively similar degrees of turnover and nestedness with high structuring variability.

Discussion

Species turnover was the dominant process structuring fish and macroinvertebrate communities at all spatial and temporal scales examined. A spatially turnover dominated system suggests that a given location's community is unique to other locations in space. A temporally turnover dominated system suggests a given location's community is unique to its own location through time indicating that species are replaced over time. Therefore, the results of this study suggest that a given community is relatively unique across locations and within the same location through time. Increased species dispersal ability (Baselga et al., 2012), increased

geographical scope (Keil et al., 2012), increased system productivity (Andrew et al., 2012), and relatively older geologic systems (Dobrovolski et al., 2012) have been suggested to promote species turnover structuring; however, geographical barriers and dispersal ability are the most likely drivers in Great Lake coastal wetlands. Invertebrate and phytoplankton communities have been shown to display increasing turnover structuring through time in boreal lakes due to increasing environmental variability and community dispersal limitation (Angeler, 2013). Since geographic barriers are often species specific, species mobility is also important in the prominence of turnover. Rádková et al. (2014) revealed generalist and mobile families (Chironomidae) displayed turnover structuring as they occupied many habitats with replacement between locations while habitat specialists (Plecoptera) displayed a nestedness structuring, highlighting that different mechanisms/gradients resulted in species loss. A given coastal wetland experiences a range of natural and anthropogenic disturbances at a given point in time creating a suite of intrinsic habitat conditions that possibly explain high turnover among sites due to species-specific barriers or mobility limitations. With apparent importance of geographical barriers and dispersal ability, specific insight into biotic and/or abiotic interactions influencing movement of communities/species across habitats will be important to address future β and γ diversity concerns.

Fig. 5 Temporal β_{SOR} and P_{SIM} dissimilarity summary of fish (*top*) and macroinvertebrate (*bottom*) communities within individual sites. P_{SIM} ($\beta_{\text{SIM}}/\beta_{\text{SOR}}$) represents the proportion of community dissimilarity (β_{SOR}) explained by species turnover (β_{SIM}). Reported values are 100 iteration resampled means and standard deviations α standardized at 3 sampling efforts



Coastal wetlands are extremely dynamic systems with many physical/chemical properties changing drastically at diel, seasonal, and interannual intervals (Bhagat & Ruetz, 2011). The most notable wetland habitat change is the contrast between summer and winter conditions. Many coastal wetlands are inhospitable to the majority of species over winter as relatively low water levels often dewater wetlands completely or reduce water depth to a point where the entire water column freezes. Thus, each spring is punctuated by a mass migration (or emergence from the substrate) of species into coastal wetlands, presumably to take advantage of the high productivity (Jude & Pappas, 1992). Many fish and invertebrate species inhabiting coastal wetlands throughout the summer growing season are represented by juvenile life stages arriving there via migratory adults and egg deposition delivered by water currents from upstream

spawning locations, or by winged terrestrial adults carried by winds. This predictable seasonal change in site hospitality combined with wetlands serving as a nursery largely for juveniles are likely the major forces promoting species turnover rather than nested diversity patterns; especially where natal site fidelity occurred in low frequency among the species in the global pool.

This inhospitability-colonization hypothesis may further be supported by the high degree of temporal turnover in community composition within a given location. Sites experienced relatively little change in watershed/external features during this study, and therefore, internal system factors must be contributing to observed community turnover. Extreme episodic disturbance to a system can lead to niche opportunities for new directional colonization resulting in unique communities when conditions appeared similar to

previous observations (Shea & Chesson, 2002). Temporal turnover may also suggest that ambient conditions followed by similar conditions later in time may not result in similar communities. Winter conditions often result in a system devoid of fish and benthic invertebrates, and therefore, each year a community may be the result of the unique set of initial conditions of these dynamic systems and/or random colonization events.

Our findings highlighted concerns of single scale β diversity assessments. The hierarchical approach we used clearly demonstrated the influence of changing α and γ scales on β diversity conclusions. Community assessments are often snapshot assessments that are used to extrapolate across broader spatial and temporal timescales; therefore, a multi-scale and grain assessment can alleviate opposite and conditional β diversity statements within a system (Barton et al., 2013). Most importantly, a single scale approach can misrepresent difference in landscape perception by the individuals within a given community in space and time. The use of a standardized hierarchical approach better encompassed possible human- and community-based perception difference alleviating single scale discrepancies.

The use of multiple community types is important to build a more comprehensive understanding of system processes and dynamics. Fish served as an appropriate model group to study patterns across different scales as they are often associated with both small and large geographical areas with linkages between these spatial areas often studied (Graham et al., 2008; Pangle et al., 2010). Macroinvertebrates provided another organismal community type with very different modes of dispersal and life histories in terms of how they utilize coastal wetlands (Patrick et al., 2014). With both community groups experiencing similar rates and relative degree of turnover further support the inhospitability-colonization hypothesis as similar winter conditions may be governing them.

We observed minimal variation in nestedness structuring across changes in scale. Additionally, there was an increase in β_{SOR} and β_{SIM} as scale localized suggesting minimal species richness differences among locations with an increasing degree of species replacement/rarity. This trend may suggest that temporally a given area is only capable of supporting a certain number of species regardless of which species. Alternatively, the observed turnover might be related to the

capture efficiency of rare species. Greater insight into the factors that contribute to turnover versus nested systems in relation to scale and the influence of detectability is an important yet understudied avenue of β diversity research (Segre et al., 2014).

A turnover structured system requires conservation, restoration, and protection of as many habitat locations as possible to maintain γ biodiversity. With system biodiversity widely dispersed across the landscape and supported by the entire geography rather than isolated ‘hotspots,’ the rate of habitat alteration and loss (current and historic) could have on-going incremental negative effects on regional biodiversity. Biodiversity is suggested as major driver and stabilizer of ecosystem services (Tilman, 2012). For example, declines in marine fish and invertebrate diversity have diminished the ocean’s ability to provide food, support water quality, and other services (Worm et al., 2006), with similar conclusions drawn in other systems (Tilman & Downing, 1994; Hoekstra et al., 2005; Pratchett et al., 2008). Anthropogenic and climatic activities, and still do, pose serious large-scale threats to Great Lake coastal habitats (Chow-Fraser et al., 1998). In addition to habitat threats, the increasing frequency of non-native species introductions poses another challenge to maintaining biodiversity. Global homogenization through the loss of native species results in a loss of endemic and global diversity (Toussaint et al., 2014). With multifaceted threats present, best management decisions should be cognizant of high turnover systems and take a precautionary ecosystem approach towards management. Understanding fundamental ecological structure and functioning (i.e., biodiversity patterns) is critical to combating the biodiversity crisis we currently face (Young et al., 2005; Cardinale et al., 2012).

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