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Patterns of biodiversity and co-occurrence of native and nonindigenous species at Great Lakes coastal margins

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PATTERNS OF BIODIVERSITY AND CO-OCCURRENCE OF NATIVE AND NONINDIGENOUS SPECIES AT GREAT LAKES COASTAL MARGINS

by
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I hereby declare that this thesis incorporates material that is result of joint research, as follows:

This thesis also incorporates the outcome of a joint research undertaken in collaboration with Jan J.H. Ciborowski and Lucinda B. Johnson. The collaboration is covered in Chapter 2 of the thesis. In all cases, the key ideas, primary contributions, experimental designs, data analysis and interpretation, were performed by the author, and the contribution of co-authors was primarily through the provision of data.

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ABSTRACT

Studies that assess the ecological processes that allow establishment by a nonindigenous species in the Laurentian Great Lakes can help elucidate general ecological processes. The Great Lakes has such varied habitats that observations of any general patterns in ecological processes, involving both native species and nonindigenous species, likely pertain elsewhere. Studies relating biotic interactions and interaction-neutral processes to invasibility are numerous, but they have been largely inconclusive.

This thesis evaluates hypotheses linking biotic interaction (i.e., richness, evenness, and dominance) and neutral-interaction (i.e., dispersal/propagule pressure) processes of several taxonomic groups (birds, diatoms, fishes, macroinvertebrates, and wetland vegetation) to invasibility at various spatial scales and sample sizes. These hypotheses were assessed using synoptic sample collections from various locations throughout the US Laurentian Great Lakes coastal margins influenced by varying types and levels of anthropogenic disturbance.

I tested hypotheses relating biotic resistance versus habitat suitability to invasion by a nonindigenous amphipod. Results supported the view that biotic facilitation by dreissenid mussels and distribution of suitable habitats better explain the distribution of the nonindigenous amphipod than anthropogenic disturbance and biotic resistance.

I evaluated hypotheses relating richness, evenness, and relative species dominance to invasibility and the occurrence of native and nonindigenous species using data compiled for various taxonomic groups from several hundred locations along the US coastline of the Laurentian Great Lakes. Across taxonomic groups, trends of native and nonindigenous species distributions were inconsistent with regulation by biotic interaction related processes. Regulation by neutral processes, such as propagule pressure or habitat suitability may better explain patterns. Native species distributions were correlated with habitat suitability and habitat hydrogeomorphology, and ranges reflect biogeographic history. The factors that constrain nonindigenous species are arguably a variation

of those that constrain native species distributions, thus indicating that similar factors constrain both native and nonindigenous species.

The general accuracy of these synoptic findings was assessed by comparing biodiversity estimation performance of data resulting from intensive sampling protocols. A method proposed by Olszewski (2004), which is alternative to rarefaction and statistical estimators for species richness, was also tested. This method uses the evenness component of biodiversity and requires a limited number of samples for estimations. My findings indicated that true biodiversity measures cannot be attained efficiently from surveys. Since such measures are unattainable, interpretation of biodiversity studies would benefit from closer examination of detectable species (i.e., common species) that likely have a stronger impact on community processes, than rare and/or transient species.

Nonindigenous species that become widespread and abundant are likely governed by the same factors that regulate common native species. Ecology would benefit from linking studies of the factors that regulate the distribution and abundances of common species, both native and nonindigenous, and the dynamics between biodiversity and ecosystem properties and processes.

For My Family

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CHAPTER 1: GENERAL INTRODUCTION

The Laurentian Great Lakes collectively cover 24.5 million ha and are the largest freshwater system in the world. They carry more shipping than any other freshwater system on Earth, and their shores have seen some of the continent's heaviest industrial and agricultural development while the lakes support a set of fisheries worth $4 billion annually (Bright, 1998). A growing number of fish, mollusks, plants, plankton, and assorted other organisms have entered the system, either as a result of human planning and intensive management (e.g. coho salmon, *Oncorhynchus kisutch*) or through unintentional introductions (e.g. sea lamprey, *Petromyzon marinus*). Establishment is said to have occurred when a nonindigenous population persists by means of local reproduction and recruitment (Vermeij, 1996). At least 182 nonindigenous organisms have established in the Great Lakes or on their shoreline (Ricciardi, 2006), and the current rate of invasion is estimated at ~1.8 species per year (Ricciardi, 2006). The movement of organisms beyond their natural range can have consequences that are ecologically or even economically devastating. However, most nonindigenous species never establish self-sustaining populations and most of those that do have little discernable impact on community structure or dynamics. Ecologists have attempted to understand why some nonindigenous species are able to invade while others are unsuccessful (Mooney and Drake, 1986; Drake *et al*., 1989), so they often examine the interaction between the nonindigenous species and its new habitat (i.e., the physical surroundings and group of species living in that area). Many have tried to understand the attributes of habitats that make them vulnerable to invasion (Elton, 1958; Drake *et al*., 1989; Lodge, 1993). The study of the ecological processes involved in invasions offers a unique opportunity to examine general drivers of ecological processes that regulate communities. Studying the factors that regulate populations of a nonindigenous species after it first enters a new habitat allows ecologists to examine the key drivers that determine its successful establishment and dispersal.

Historically, ecological research has focused on how the distribution and co-occurrence of multiple species in an area determines biodiversity (i.e., richness and evenness). The ecological questions most often investigated have

involved the possible factors that drive biodiversity (Hutchinson, 1959). Classic studies have explored the roles of factors such as competition (Gause, 1934; MacArthur, 1960), predation (Paine, 1966), environmental heterogeneity (Hutchinson, 1961), dispersal (MacArthur and Wilson, 1967), and disturbance (Dayton, 1971). These and other studies have formed the foundation for two main models that explain ecological processes, biotic interaction based and neutral-interaction based theories, which are often viewed as opposing one another.

The implied meaning of the term 'niche' has changed over time, from representing the habitat in which an organism resides (Grinnell 1917, 1924, 1928), to representing the ecological role an organism performs within a community (Elton 1927), to the intersection of ranges of abiotic and biotic tolerances for a set of resources utilized by an organism (Hutchinson 1957). The Hutchinsonian niche was comprised of an “n-dimensional hypervolume” of environmental limits within which an organism is able to survive and reproduce (Hutchinson 1957). This niche could include any number of dimensions or environmental axes (Holt et al. 2005). Since the response of an organism to all possible environmental factors is difficult to determine, most ecologists study a smaller set of dominant factors. The "fundamental" niche was thus defined as the hypervolume created in the absence of interaction with other species, and represents a species' potential to use available resources (Holt et al. 2005). The fundamental niche is determined by a species’ physiological tolerances in the absence of predators and competitors. The “realized” niche is then the hypervolume created in the presence of interactions with other species, such as competition, predation, and facilitation (Hutchinson 1957, Holt et al. 2005). Biotic interactions between species can affect the breadth of a species' niche along one or several niche axes. For example, competition could decrease the breadth of the food niche axis of a species if the availability of a food item decreased in the presence of a competitor. A species’ realized niche may vary from location to location because of the presence of different sets of predators, and competitors (Leibold 1995, Pulliam 2000).

Niche-based theories assert that biological interactions and environmental heterogeneity underly species coexistence and community structure (e.g., Tilman 1982, Cornell, 1992). Advocates believe that species can only coexist when they differ from each other in the resources they use most efficiently, or in their adaptation to the local environmental conditions (Ostling 2005). These theories assume that coexisting species must have different niches.

In contrast, neutral-based theories claim that chance, history, and dispersal explain species coexistence (Hubbell 1997, Bell 2001, Hubbell 2001). These theories suggest that historical dispersal by chance, rather than the outcome of biotic interactions, determine coexistence of species (Ostling 2005). Dispersal to the same habitable region is the main criterion for coexistence (Ostling 2005). Neutral-based theories assume that all species are competitively equivalent to see if observed patterns can be duplicated. They also assume that regional abundances are determined by dispersal driven by demographic stochasticity (Hubbell, 2001).

The path of the study of invasions has overall followed the same route as general ecological research. Invasion has variously been linked to factors such as competition (Elton, 1958; MacArthur, 1970; Fox and Fox, 1986; Pimm, 1991; Rejmanek, 1996; Lonsdale, 1999), facilitation (Levine 1976; Case, 1991; Simberloff and Von Holle, 1999; Ricciardi, 2001; Kang *et al*., 2007), individual species dominance in communities (Crawley *et al.,* 1999; Smith and Knapp 1999; Wilsey and Polley, 2002; Callaway *et al.,* 2003; van Ruijven *et al.,* 2003; O'Connor and Crowe 2005, Wilsey *et al.,* 2005; Smith *et al*. 2004), environmental heterogeneity (Baltz and Moyle 1993; Moyle and Light, 1996; Harrison 1999; Hood and Naiman 2000; Fausch *et al*. 2001), disturbance (Elton 1958; Hobbs and Huenneke 1992; D'Antonio 1993; Burke and Grime 1996), and propagule pressure (Simberloff, 1989; Williamson, 1996; Lonsdale, 1999; Levine, 2000; Fine, 2004; Lockwood, 2005; VonHolle and Simberloff, 2005). The biotic interaction based and neutral-interaction based theories related to these factors and invasibility of communities are discussed further in the introduction sections of chapters 2 and 3.

Thesis Objectives

The main objective of my thesis was to study factors that may govern how the distribution and co-occurrence of multiple species in an area determines biodiversity (i.e., richness and evenness) of nonindigenous species at Great Lakes coastal margins. I compared the distribution and occurrence of nonindigenous species with that of native species to determine whether biotic interaction based or neural-interaction based theories could better account for trends and whether factors influence native and nonindigenous species differently.

Data Sources

Data that were used for analyses of chapters 2 and 3 were a result of the efforts of the Great Lakes Environmental Indicators (GLEI) project (Niemi *et al*., 2004, Danz *et al*., 2005) whose goal is to develop and test biological indicators (of amphibians, birds, diatoms, fishes, macroinvertebrates, and vegetation) of anthropogenic stressors of Great Lakes coastal margin ecosystems at several scales (Niemi *et al*., 2004, Danz *et al*., 2005). I contributed to the collection of fish and aquatic invertebrate data.

Between 2002 and 2004, seven suites of response variables (birds, wetland emergent vegetation, amphibians, fishes, zoobenthos, diatoms, and water quality characteristics) were sampled at a total of 160 locations within 2 km of the shoreline of each of the Laurentian Great Lakes following a synoptic approach. Site locations had been preselected from among 762 second-order or higher drainage basins bordering the US Great Lakes coastline. A stratified-random design was used such that the total number of sites encompassed the full range of each of 7 classes of stress ascertained from geospatially referenced measurements of 229 stressor variables at each watershed (Danz *et al*., 2005). The stress classes were those related to agriculture and agricultural chemicals, atmospheric deposition, land use and land cover, point and non-point source

pollution, human population density and development, shoreline modification, and soils (Danz *et al*., 2005).

Although the GLEI data make up an extraordinarily comprehensive and valuable dataset, I was limited to studies that posed questions about biodiversity requiring correlation and regression since I could not apply sampling designs that specifically test hypotheses. Therefore, the results of my tests of various theories can only be judges as consistent or inconsistent with the predictions. My studies of biodiversity differ from those of community structure and dynamics, where the identity and functional role of each species is the focus of study.

Thesis Structure

Chapter 1 provides a general introduction and overview of the thesis.

In chapter 2, I tested two hypotheses related to invasion of communities using a case study. The first is a biotic interaction based theory, whereby biotic resistance to nonindigenous species establishment is thought to be greater in communities that have not been disturbed by human activities (communities not subject to urban or agricultural influences from the contributing watershed). The second is a neutral-interaction based hypothesis that predicts that invasion may occur wherever environmental conditions are appropriate for the colonist, regardless of the composition of the existing community and the level of disturbance. I tested these hypotheses by investigating the distribution of the nonindigenous amphipod, *Echinogammarus ischnus* Stebbing, 1899, in co-occurrence with a widespread amphipod, *Gammarus fasciatus* Say, 1818, at 97 Great Lakes coastal margin locations. The sampling sites were influenced by varying types and levels of anthropogenic stress. I examined the association between the occurrence of *E. ischnus* with i) disturbance gradients related to six anthropogenic disturbance variables that summarized overall nutrient input, nitrogen and phosphorus load carried from the adjacent coastal watershed, agricultural land area, human population density, overall pollution loading, and the site-specific dominant stressor; ii) the distribution of *G. fasciatus*, whose presence or absence at a location was used as an indicator of habitat suitability

for *E. ischnus;* and iii) the distribution of dreissenids with which both amphipod species have previously been found to co-occur in the Great Lakes (Griffiths 1993, Stewart and Haynes 1994, Dermott et al. 1998, Vanderploeg et al. 2002).

Chapter 3 tests the generality of findings from Chapter 2 by testing hypotheses relating community processes and invasibility using correlations of biodiversity data. I begin by reviewing hypotheses linking biotic interaction (i.e., richness, evenness, and dominance) and neutral-interaction (i.e., dispersal/propagule pressure) processes to invasibility. I tested hypotheses relating richness, evenness, and relative species dominance to invasibility and the distribution of nonindigenous species. I used regression and ANOVA to assess whether NIS richness or occurrence depended on the richness and evenness measures of native species. The data were compiled from 160 locations along the US coastline of the Great Lakes. I tested these hypotheses using biodiversity data of several taxonomic groups (birds, diatoms, fishes, and wetland vegetation) at various spatial scales and sample sizes (varying numbers of individuals) throughout the Great Lakes. I derived conclusions about the biotic interaction based and neutral-interaction based factors that influence the distribution and co-occurrence of native and nonindigenous species.

Chapter 4 assesses the relative accuracy of biodiversity data collected from synoptic surveys such as those used in chapters 2 and 3. Using amphibian, bird, and fish data, I compared biodiversity estimates based on datasets compiled from intensive (amphibian and bird: Bird Studies Canada; fish: US EPA) and synoptic (GLEI) sampling protocols. Estimating species richness through intensive surveys is time-consuming and costly. Since most biodiversity studies are based on surveys with limited sampling effort due to logistics, it is important to understand how well surveys represent the communities from which they are drawn. Although many statistical methods have been designed to estimate species richness from synoptic surveys, they may be inaccurate or unreliable when only limited sampling has been conducted. I investigated the potential for extrapolating biodiversity measures (richness and evenness) from a limited number of samples by testing Olszewski's (2004) proposal that the slope of the

rarefaction curve provides biodiversity information based on the relationship between the steepest segment of a community's rarefaction slope and a measure of evenness (probability of interspecific encounter, Δ_1; Hurlbert, 1971). The slope of the rarefaction curve can be determined from a minimum number of samples (at least 2 samples), and if these samples provide an accurate estimation of the slope, the samples can also provide an accurate estimation of biodiversity. I assessed the proposed relationship using sets of Great Lakes amphibian, bird, and fish data collected through relatively intensive sampling protocols. The findings from this chapter led me to question the accuracy and therefore the ultimate value of interpreting biodiversity surveys. In my concluding chapter, I suggest approaches to using information derived from biodiversity surveys that may provide more meaningful depictions of ecological processes.

The following gives a detailed breakdown of the main objectives of my thesis:

i) Evaluate the potential role of competition in NIS establishment (Chapter 2 and 3);

ii) Examine the importance of environmental factors, such as disturbance and habitat suitability, in regulating populations of a NIS (Chapter 2);

iii) Assess the biodiversity (i.e., richness and evenness) and dominance trends of native and nonindigenous species of Great Lakes taxonomic groups and relate them to biotic interaction and neutral-interaction processes (Chapter 3);

iv) Test hypotheses related to neutral-interaction and biotic interaction processes (Chapter 3);

v) Evaluate the usefulness of an evenness measure from synoptic surveys as a surrogate for estimates of richness derived from intensive sampling (Chapter 4);

vi) Assess the accuracy of estimation of biodiversity measures (i.e., richness and evenness) of synoptic and intensive sampling methods (Chapter 4);

vii) Evaluate general principles of diversity and invasion processes and relate them to community and ecosystem processes (Chapter 5)

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CHAPTER 2: THE INFLUENCE OF ANTHROPOGENIC DISTURBANCE AND ENVIRONMENTAL SUITABILITY ON THE DISTRIBUTION OF THE NONINDIGENOUS AMPHIPOD *ECHINOGAMMARUS ISCHNUS* AT LAURENTIAN GREAT LAKES COASTAL MARGINS

This chapter incorporates the outcome of a joint research undertaken in collaboration with Jan J.H. Ciborowski and Lucinda B. Johnson. In all cases, the key ideas, primary contributions, experimental designs, data analysis and interpretation, were performed by the author, and the contribution of co-authors was primarily through the provision of data.

INTRODUCTION

Records since the early 1800s document a dramatic sequence of invasions by nonindigenous species (NIS) originating from Europe, Asia, and the North American Atlantic coast into the Laurentian Great Lakes (Mills *et al.,* 1993, Grigorovich *et al.,* 2003). Ballast water exchange activities of transoceanic ships have been linked with NIS introductions that originate directly from native regions and indirectly by stepwise transport from recently colonized areas linked with the Great Lakes. Several NIS native to the Ponto-Caspian region of Eurasia (i.e., Black, Azov, and Caspian Sea basins) have expanded their range into the Great Lakes after becoming established in the Baltic Sea or lower Rhine River basins (MacIsaac *et al.,* 2001). Although many NIS never establish self-sustaining populations, the movement of organisms beyond their natural range can have consequences that are ecologically and sometimes economically devastating. Consequently, considerable research has been conducted to understand why some NIS are so successful at invading while others are unsuccessful (e.g., Baltz and Moyle, 1993; Simberloff and Von Holle, 1999; Keane and Crawley, 2002; Lockwood *et al*., 2005). Studies often examine the interaction between the NIS and its new habitat and attempt to elucidate habitat attributes that make ecosystems vulnerable to invasion (e.g., Mooney and Drake, 1986; Drake *et al*., 1989; Sax *et al.,* 2005).

Elton (1958) observed that invasions were often human-mediated and expanded this view with the concept of “biotic resistance.” He argued that the combined competitive abilities of species in undisturbed communities resist establishment of NIS, but communities disrupted or disturbed by human activities become more susceptible to invasion. Disturbance is widely regarded as a mechanism that permits NIS to avoid or reduce the intensity of biotic resistance usually manifested through interspecific competition or predation in the invaded community (e.g., Elton, 1958; Hobbs and Huenneke, 1992; D’Antonio, 1993; Burke and Grime, 1996). If disturbance is an important determinant of the success of biological invasions, it must modify species interactions or the nature of the environment in a manner that favours establishment of NIS. I use the term ”stressor” in this study as a reference to anthropogenic activities that cause disturbance, defined by White and Pickett (1985) as “any relatively discrete event in time that disrupts ecosystem, community, or population structure and changes resources, substrate availability, or the physical environment.”

Although a number of terrestrial studies corroborate the disturbance hypothesis (a demonstration of biotic resistance) (e.g., birds: Case, 1996; plants: Kotanen, 1997; Wiser *et al.,* 1998; Keeley *et al.,* 2003; Rose and Hermanutz, 2004), relatively few studies document the importance of disturbance for NIS establishment in aquatic habitats. In manipulative experiments of the Asian kelp, *Undaria pinnatifida*, in Tasmania, Valentine and Johnson (2003) found that disturbance that reduced native algal canopy cover was critical in the establishment of this NIS, whereas the presence of a stable native algal canopy inhibited invasion. Schreiber *et al.* (2003) found that invasion of the nonindigenous snail, *Potamopyrgus antipodarum*, was facilitated by flow-driven anthropogenic disturbance, and more likely to occur in areas with multiple land uses (e.g., grazing, forestry, urban development) at lowland sites in southern Victorian Australian streams. Cohen and Carlton (1998) highlighted the role of disturbance in facilitating the establishment of NIS of the highly invaded San Francisco Bay and delta. Except for these studies, the role of disturbance in invasion of aquatic environments has not been clearly elucidated, due to difficulty

in directly linking and assessing the contribution of disturbance to invasion success.

Contrasting the disturbance hypothesis, Moyle and Light (1996) studied the success of invading fishes in California streams and suggested that if environmental factors are appropriate for a NIS, successful invasion by that species is likely, regardless of the biota already present. They argued that failure of NIS to establish in new habitats is best attributed to their inability to adapt to environmental conditions (i.e., lack of environmental suitability) rather than to biotic resistance on the part of the recipient community (also see Baltz and Moyle, 1993; Harrison, 1999; Hood and Naiman, 2000; Fausch *et al*., 2001). Blackburn and Duncan (2001) used a global data set of historical bird introductions and showed that instances of successful introductions were not consistent with the biotic resistance hypothesis. Their model showed that the most species-rich regions of the Afrotropics and Central/South America were most invasible. Successful introductions appeared to depend on the combination of species and location (e.g., large range size, similarity of origin and introduction latitudes). Holway *et al.* (2002) compared the effects of interspecific interactions and abiotic factors on invasion success by the Argentine ant, *Linepithema humile* Mayr in scrub habitats of southern California. Their experimental data demonstrated that community-level vulnerability to invasion appears to depend primarily on the suitability of the physical environment from the perspective of *L. humile*. Similarly, Dethier and Hacker (2005) found that physical factors played a more important role than biotic resistance in field manipulations of the invasive marine grass, *Spartina anglica*.

The objective of this study was to elucidate the factors that regulate the distribution of the nonindigenous amphipod, *E. ischnus* Stebbing, 1899, in the Laurentian Great Lakes. I assessed the influence of land-based anthropogenic activities on the distribution of the established NIS in adjacent receiving waters, to test whether disturbance as a consequence of anthropogenic activity or environmental conditions better accounted for its local occurrence. I also studied the association between *E. ischnus* and *G. fasciatus* Say, 1818, whose

distribution was used as an indicator of habitat suitability for *E. ischnus* (see Study Organisms), and with dreissenids with which both amphipods have previously been found to co-occur in the Great Lakes (Griffiths, 1993; Stewart and Haynes, 1994; Dermott *et al*., 1998; Vanderploeg *et al.,* 2002).

Evidence that *E. ischnus* is limited to relatively disturbed locations, characterized by association with anthropogenic stressors, will support the disturbance hypothesis. Alternatively, a finding of *E. ischnus* at all sites with suitable habitat (those supporting *G. fasciatus*), independent of the spatial distribution of anthropogenic stressors, will better support the hypothesis that local environmental conditions determine establishment success.

These hypotheses were evaluated by examining a subset of zoobenthic samples collected at 149 locations across the US Great Lakes coastline, spanning gradients of stress, and a range of hydrogeomorphic characteristics. This study was part of the Great Lakes Environmental Indicators (GLEI) project (Danz *et al*., 2005), designed to develop and test indicators of condition along the coastal margins of the US Great Lakes.

Study Organisms

Witt *et al.* (1997) reported the first account of a breeding population of the nonindigenous amphipod, *E. ischnus,* in the Great Lakes basin in 1995 at a Detroit River site. However, van Overdijk *et al.* (2003) analyzed archived samples and postulated *E. ischnus'* entry into Lake Erie in 1994 and possibly as early as 1993 (although no specimens were found in samples collected in 1993 by Dahl *et al.*, 1995). By 1996, *E. ischnus* was widely distributed from southern Lake Huron downstream to the mouth of the Niagara River of Lake Ontario (Dermott *et al.,* 1998). *Echinogammarus ischnus* was reported from the nearshore rocky areas of the northern to southern ends of Lake Michigan in 1998 (Vanderploeg *et al*., 2002) and nearshore silty-sand areas adjacent to Thunder Bay, Ontario in Lake Superior in 2002 (Grigorovich *et al*., 2003).

Dermott *et al.* (1998) proposed that strong eastward longshore currents in Lakes Erie and Ontario (Csanady and Scott, 1974; Simons, 1976; Barton and Hynes, 1978) allowed *E. ischnus* to disperse from the west to the east end of

Lake Erie in two years and permitted rapid range expansion downstream to Lake Ontario. They predicted that *E. ischnus* would quickly move downstream in the St. Lawrence River to its estuary, and enter the Mississippi River and Hudson River basins via the interconnecting canals.

The first Detroit River population was found to occupy a habitat typical of *G. fasciatus*, suggesting the possibility of competitive displacement of the native species (Witt *et al*., 1997). As well, the proportion of *E. ischnus* increased while *G. fasciatus* decreased over a two-year study period (1996-1997) in Port Weller, Lake Ontario, suggesting the displacement of *G. fasciatus* (Dermott, *et al.,* 1998).

Dermott *et al.* (1998) predicted that *E. ischnus* would replace the widespread amphipod, *G. fasciatus,* primarily on rocky substrates (i.e., wave washed cobble beaches, rubble armored shorelines, breakwalls), especially in interconnecting rivers and larger tributaries of the Great Lakes, based on observations of the rarity of *G. fasciatus* and commonness of *E. ischnus* in rocky habitats, particularly where currents were moderate, such as in the St. Clair, Detroit, and Niagara rivers. Nalepa *et al.* (2001) reported the absence of *G. fasciatus* and the sole presence of *E. ischnus* along the eastern shoreline of Lake Michigan, supporting the prediction of competitive displacement by *E. ischnus* of *G. fasciatus* in rocky habitats (Dermott *et al.,* 1998).

Given that both *E. ischnus* and *G. fasciatus* are found in similar habitats in the Great Lakes, and are believed to use similar resources (and thus displacement of *G. fasciatus* by *E. ischnus* is predicted), habitat potentially suitable for *E. ischnus* was defined as those sites occupied by *G. fasciatus* to test the disturbance and environmental suitability hypotheses. All samples containing *G. fasciatus* were used in analyses. Sites at which other amphipods (such as *Hyalella azteca* Saussure, 1858) occurred, were not considered to be suitable habitat for *E. ischnus*, because these amphipods share fewer habitat requirements (Bousfield, 1958; Holsinger, 1976).

METHODS

Sampling Design and Site Selection

Zoobenthic sampling locations were originally selected for the GLEI project using a stratified random design from among the entire set of 762 second-order or higher drainage basins bordering the US Great Lakes coastline (Danz *et al.,* 2005). The coastline was divided into coastal segments whose endpoints were midway between adjacent second order or higher tributary streams. Digital elevation models were used to delineate the runoff areas (i.e., drainage basins) for each river basin and its adjacent shoreline. These units are referred to as "segment-sheds." The coasts of islands, the connecting channels, and Lake St. Clair were excluded from the final site selection.

A stratified-random design was used such that the total number of segments sampled encompassed the full range of intensity of each of six classes of stress ascertained from geospatially referenced measurements of 207 stressor variables in each drainage basin (Danz *et al.,* 2005). Principal components analysis was used to reduce the total number of stressor variables to a smaller suite representing six distinct classes of anthropogenic activities: agriculture (including rates of fertilizer and agricultural chemical applications), atmospheric deposition, land use and land cover, human population density and development, point and nonpoint source pollution, and shoreline modification. The subset of segment-sheds that was ultimately sampled encompassed the full range of each of the six classes of stress (Danz *et al.,* 2005). The segment-specific eigenvalue of each principal component provided a measure of the intensity of each class of stress to which the segment was subject (Danz *et al.,* 2005). My study used the five specific stressor variables that summarized most of the variability of each principal component: overall nutrient input, nitrogen and phosphorus load transported from the adjacent coastal watershed, agricultural land area, human population density, and overall pollution loading. The atmospheric deposition stressor was excluded as it stems from regional rather than local causes. An additional variable that summarized the site-specific dominant stress value (i.e.,

"Relmax"- the single highest principal component score of all stressor variables influencing a particular site) was also used in analyses.

Sampling locations were also classified and stratified on the basis of their hydrogeomorphologic connections with a Great Lake (following Keough *et al.,* 1999). These classifications are referred to as hydrogeomorphic types. Non-wetland areas were identified as being either high-energy shoreline, or low-energy shoreline/embayments. Three functional groups of wetlands were identified: coastal wetlands (i.e., wetlands occurring along open shorelines, unrestricted bays, or shallow, sloping beaches); river-influenced wetlands (i.e., river deltas, restricted riverine, and lake connected inland types); and protected wetlands (i.e., barrier beach systems that may be intermittently hydrologically connected to the main lake) (Keough *et al.,* 1999).

Invertebrates were sampled at a total of 149 sites distributed across the U.S. coastline of the Great Lakes between June and September, 2002 through 2004 (34 in Lake Superior, 42 in Lake Michigan, 28 in Lake Huron, 23 in Lake Erie, and 23 in Lake Ontario). This study uses data from 97 of these locations, and they are referred to as "basin" data. Samples from Lake Superior and protected wetlands were not included because it is unclear whether *E. ischnus* is able to persist in Lake Superior (Grigorovich *et al.,* 2003) or whether *E. ischnus* has had the opportunity to disperse into wetlands that are not permanently connected to the Great Lakes shoreline. In fact, no *E. ischnus* specimens were collected from any Lake Superior sites or from protected wetlands in the GLEI study.

Additional samples collected from Lake Erie in 2004 for the Lake Erie Comprehensive Collaborative Study (ECCS; Krieger *et al.,* 2007) supplemented the GLEI Lake Erie high-energy shoreline data. Amphipods were collected from 96 sampling locations along the U.S. coastline of Lake Erie between May and Sept 2004 using an airlift sampler (314 cm^2; stony substrates) or Ponar grab (506 cm^2; soft substrate sampler; see Krieger *et al.,* (2007) for a full description of their methods). Only those sites that were sampled along the U.S. coastline could be

used in my analyses because appropriate stressor scores were not available for segment-sheds on Canadian Great Lakes coastlines.

Amphipod Collection

Using a combination of 30-s D-net, 10-cm deep, 6.5-cm diameter cores, and Petite Ponar grabs (225 cm^2; or rock scrapes of equivalent top-face surface area in rocky habitats), we collected duplicate samples at two to four depth locations along each of two to six transects per site. Two to three transects were delineated extending from each of the two most common land use classes that made up at least 10% of the linear extent of the shoreline. High-energy and coastal wetland benthic samples were collected at four depth contours along each transect: 20-50 cm, 50-75 cm, 5 m (or 1 km from shore, whichever occurred first), and 10 m (or 2 km from shore, whichever occurred first). If depths were 5 m or less, only three locations were sampled along a transect at embayments, river-influenced wetlands, and protected wetlands (20-50 cm, 50-75 cm, deepest point encountered); a maximum of 24 points was sampled at each site.

All samples were preserved in 2.5:1 v/v ethanol: buffered formalin solution diluted 1:1 with lake water, and sorted in the laboratory.

In the laboratory, one randomly selected sample of each duplicate from each zone of each transect was sorted. Benthic samples were rinsed through a series of nested sieves (4 mm, 1 mm, 0.5 mm, 0.25 mm) following the procedures of Ciborowski (1991). Individual size fractions were subsampled as necessary to generate at least 100 invertebrates per fraction such that the total sorting time spent per sample did not exceed 3 hours. Similar methods were used for processing ECCS samples (see Krieger *et al., in press*). Amphipods were identified to the genus level using the key of Covich and Thorp (2001). *Gammarus* species were identified using keys of Holsinger (1976) and Bousfield (1958). *Echinogammarus ischnus* specimens were identified using the description outlined by Witt *et al*. (1997).

Statistical Analyses

The association between *E. ischnus and G. fasciatus* was examined to complement the tests of the disturbance hypothesis and environmental suitability

hypothesis of invader establishment at individual sites with suitable habitat. The associations were examined using frequency analyses (Yates corrected Chi-square analysis of presence/absence data, with one degree of freedom). Differences in degree of co-occurrence among lakes and hydrogeomorphic types were assessed using heterogeneity tests. A taxon was deemed present at a site if one or more individuals occurred in at least one sample. A significant positive association between two taxa was assumed to indicate that the taxa pair shared similar habitats (e.g., hydrogeomorphic types). A nonsignificant Chi-square outcome would imply that the broad distributions of the two taxa were independent of one another. Strongest support for the environmental suitability hypothesis would be achieved if *E. ischnus* was detected wherever *G. fasciatus* was encountered, and independently of the anthropogenic stressor scores.

Dreissena polymorpha Pallas, 1771, and *Dreissena bugensis* Andrusov, 1897, are two nonindigenous dreissenid species that occur in the Great Lakes. *Dreissena* spp. benefit some members of the benthic community, such as *Gammarus* spp. and *Echinogammarus ischnus*, in nearshore areas by providing substrate and food in the form of feces and pseudofeces (Vanderploeg *et al.*, 2002). Given that dreissenids are known to form mixed-species colonies (Bially and MacIsaac 2000) and have been shown to be associated with *E. ischnus* and *G. fasciatus* (Griffiths 1993, Stewart and Haynes 1994, Dermott *et al.,* 1998, Vanderploeg *et al.,* 2002), frequency analyses (Yates corrected Chi-square analysis of presence/absence data, with one degree of freedom) were also conducted to quantify the strength of association between dreissenids and each gammarid taxon. Dreissenids were collected using the same methods as for amphipod collection.

To test the disturbance hypothesis, simple and multiple logistic regression analyses were performed on occurrence records for *E. ischnus* data at sites from which *G. fasciatus* were also collected. *Echinogammarus ischnus* presence/absence (coded 1/0, respectively) site values were regressed against the principal component scores for each of the six stressor variables using simple logistic regression. Multiple logistic regression analysis evaluated the

simultaneous effect of the five single stressor measures. I anticipated that a logistic regression analysis approach would allow us to estimate theoretical critical/threshold stressor scores for *E. ischnus* occurrence (the stressor score at which *E. ischnus* is more than 50% likely to occur).

I used a hierarchical approach to test the hypotheses. Data were examined at the basin scale, lake-by-lake, by coastal hydrogeomorphic type, and finally, at the microhabitat (individual sample location) scale.

A modified Bonferroni correction (Holm 1979) was used to adjust the study-wide Type I error to 0.05. All analyses were performed using the Statistica® software package Version 6.0 (StatSoft, Inc. 2001).

RESULTS

Distribution and Associations among Taxa

Gammarus fasciatus was the predominant species of *Gammarus* collected, although *G. tigrinus* Sexton, 1939 (new records for the Great Lakes in Grigorovich *et al.,* 2005), and *G. pseudolimnaeus* Bousfield, 1958, were also found in samples. My power for detection of species weakened for analyses performed at smaller spatial scales for which there were smaller sample sizes (Lakes Erie and Ontario and specific hydrogeomorphic types). The sample sizes of the basinwide (n = 97 without Lake Superior and protected wetlands), Lakes Michigan (n = 39), Huron (n = 26), ECCS Lake Erie (n = 96), high-energy (n = 30), and coastal wetland (n = 28) scales provided suitable α-levels (0.75) for detection of rare species (as per McArdle 1990). The small sample sizes of Lakes Erie (n = 14), Ontario (n = 18), embayments (n = 15), and river-influenced wetlands (n = 24) resulted in analyses with low power to detect rare species. However, *E. ischnus* had its highest frequency of occurrence in Lakes Erie and Ontario (comprising 26% and 32%, respectively, of all Great Lakes sites at which *E. ischnus* occurred).

Based on its basinwide frequency of occurrence among sites, *E. ischnus* was under-represented in Lakes Michigan, Huron, coastal, and river-influenced

wetlands, and over-represented in Lakes Erie, Ontario, high-energy, and embayment sites (Table 2.1).

Gammarus fasciatus was collected more frequently in Lake Ontario, and river-influenced wetlands, and was more under-represented in high-energy and embayment sites than would be expected by chance if they were randomly distributed across the Great Lakes (Table 2.1).

Dreissena spp. mussels followed the same pattern of frequency as *E. ischnus* but were also over-represented in Lake Huron (Table 2.1).

E. ischnus-G. fasciatus Co-occurrence

Gammarus fasciatus was found at 54 of the 97 GLEI sites sampled (56%) (Figure 2.1). *Echinogammarus ischnus* was found at 19 of the 97 sites sampled (20%) (Fig. 2.1), and occupied 26% of the *G. fasciatus* sites. *Echinogammarus ischnus* was found without *G. fasciatus* at only five locations: one embayment in Lake Huron, and at two high-energy sites in each of Lakes Michigan and Erie. Although the number of sites with co-occurrence was higher than would be expected by chance (132%), the association between *E. ischnus* and *G. fasciatus* at the basin level was not statistically significant ($\chi^2 = 2.27$, d. f. = 1, $p>0.05$; Table 2.2). Tests for association at the scales of individual lakes, and hydrogeomorphic types, were also nonsignificant (Table 2.2). There was also no significant among-lake heterogeneity in the degree of association between *E. ischnus* and *G. fasciatus* ($p>0.05$). However, there was significant heterogeneity in the degree of co-occurrence among the hydrogeomorphic types ($p<0.001$). The distributions of *E. ischnus* and *G. fasciatus* deviated significantly from expectation of independence at high-energy and river-influenced sites ($p<0.005$ and $p<0.001$, respectively) due to their respective over-representation in these types of sites.

There was a highly significant association between the two gammarid species at the microhabitat (individual sample location) scale ($\chi^2 = 27.32$, $p<0.0005$, n = 925; Table 2.2). The number of samples in which *E. ischnus* and *G. fasciatus* co-occurred was much higher than what would be expected by chance.

Analyses of the ECCS data failed to show significant association between *E. ischnus* and *G. fasciatus* distributions for Lake Erie ($\chi^2 = 0.38$, $p>0.05$, $n = 96$; Table 2.2). *Echinogammarus ischnus* was found at 19 of the 96 sites sampled (20%) (Table 2.2), and overlapped at 5% of the *G. fasciatus* sites. Thirteen sampling locations occupied by *E. ischnus* were not occupied by *G. fasciatus*.

Distribution of *E. ischnus* across Stressor Gradients

The geographic extent and range of stress covered by the 97 GLEI sites that I sampled is suitable to test the disturbance and the environmental suitability hypotheses (Figure 2.2). *Echinogammarus ischnus* sites spanned the complete range of most stressor variable PC scores and were not concentrated at specific levels for any of the stressor variables (Fig. 2.2), as was corroborated by visual examination of scatterplots derived from the logistic regression analyses.

The distribution of *E. ischnus* at GLEI sites that supported *G. fasciatus* was independent of the degree of stress for all variables evaluated at the basin, individual lake, and hydrogeomorphic type scales ($p>0.05$ experiment-wise adjusted for multiple tests). A marginally significant relationship was detected for the human population density stressor variable at Lake Erie sites ($\chi^2 = 12.10$, $p < 0.05$ nominal, $n = 7$). However, the sample size for this analysis was so small that the ordering of *E. ischnus* absences and presences on the stressor axis could have arisen by chance. Analyses of ECCS data, which consisted of more sampling locations. did not corroborate the GLEI Lake Erie results ($p > 0.05$, $n = 19$).

Amphipod-*Dreissena* spp. Co-occurrence

Dreissena spp. were found at 32 of the 97 GLEI sites sampled (33%) (Fig. 2.1). *Echinogammarus ischnus* occurred at 56% of the *Dreissena* spp. sites. *Echinogammarus ischnus* was found without *Dreissena* spp. at only one river-influenced wetland site, in Lake Ontario.

Echinogammarus ischnus and *Dreissena* spp. co-occurrence was highly significant across many scales (basin: $\chi^2 = 37.35$, $p < 0.001$, $n = 97$; Lake Michigan: $\chi^2 = 10.42$, $p < 0.05$, $n = 39$; Lake Erie: $\chi^2 = 9.98$, $p < 0.05$, $n = 14$;

high-energy: $\chi^2 = 13.13$, $p < 0.0005$, $n = 30$; Table 2.3). None of the 18 ECCS locations at which *Echinogammarus* was found lacked *Dreissena* spp. ($\chi^2 = 89.55$, $p < 0.00005$, $n = 96$) (Table 2.3).

This association was also significant at the microhabitat scale ($\chi^2 = 169.17$, $p < 0.0005$, $n = 925$; Table 2.3). *Echinogammarus ischnus* and *Dreissena* spp. co-occurred in 34 samples collected (2% of all samples), and neither were collected from 787 samples (85% of all samples) out of a total of 925 samples collected. *Echinogammarus ischnus* was collected in a total of 39 samples (4% of all samples), while *Dreissena* spp. were collected in a total of 114 samples (12% of all samples). *Echinogammarus ischnus* was not associated with *Dreissena* spp. in five samples collected from a single river-influenced wetland site in eastern Lake Ontario, which did not score highly for any stressor variable. Otherwise, every GLEI D-net, core, and Petite Ponar sample containing *E. ischnus* also contained *Dreissena* spp.

Gammarus fasciatus and *Dreissena* spp. co-occurred at 27% of all sampled sites (Table 2.4). The association between *G. fasciatus* and *Dreissena* spp. was significant at the basin ($\chi^2 = 11.16$, $p < 0.05$, $n = 97$) and microhabitat ($\chi^2 = 41.60$, $p < 0.0005$, $n = 925$) scales (Table 2.4). ECCS data showed that *G. fasciatus* and *Dreissena* spp. co-occurrence was highly significant ($\chi^2 = 89.80$, $p < 0.00005$, $n = 96$).

DISCUSSION

At the hydrogeomorphic type scale, *G. fasciatus* appeared to be more widespread among river-influenced wetlands than among high energy shorelines or in embayments. In contrast, *Echinogammarus* was twice as frequently encountered at the high-energy and embayment sites than in the wetlands. However, this may be more a reflection of the relative distribution of hydrogeomorphic types among Great Lakes, which were sampled with equal effort rather than by actual habitat occurrence. For example, *Echinogammarus* was most prevalent in Lake Erie, where there were a disproportionately large number of high-energy sites and relatively few river-influenced wetland sites

sampled. The highly significant association between the two amphipod species at the sample scale suggests that microhabitat preferences are similar. Although the small sample size of *E. ischnus* sites does not provide conclusive evidence for a difference in habitat (hydrogeomorphic) preferences, this study and others (Palmer and Ricciardi 2004, Palmer and Ricciardi 2005, Limen *et al.,* 2005) suggest that *E. ischnus* is not systematically replacing *G. fasciatus* in the Great Lakes. Differential resource use (Limen *et al.,* 2005), and differential responses to substrate characteristics, water chemistry variables, and current velocity (Palmer and Ricciardi 2004, Palmer and Ricciardi 2005) are evidence that *E. ischnus* can utilize different microhabitat from *G. fasciatus*. Alternatively, although *E. ischnus* has been reported from all of the Great Lakes, the patchiness in occurrences among lakes and hydrogeomorphic types may reflect its limited dispersal capabilities and relatively recent introduction, resulting in insufficient time to disperse throughout the lakes.

Overall, the presence or absence of *E. ischnus* at *G. fasciatus* sites was independent of the degree of anthropogenic stress. The Holm (1979) correction used to adjust the detection level for significance to correct for inflated Type I Error from the many simple logistic regression analyses, rendered several of what would have been nominally significant ($p<0.05$) relationships nonsignificant. Ultimately, the only simple logistic regression analysis of *E. ischnus* presence/absence found to be marginally significant at the experiment-wise corrected probability level was for the human population density stressor variable at GLEI Lake Erie *G. fasciatus* sites. Since this analysis was based on a small sample size ($n = 7$) with a marginally significant likelihood of getting the observed significant results by chance ($p<0.03$), it imparts weak support at best for the disturbance hypothesis. The ECCS Lake Erie data, for which more records of *E. ischnus* were observed, did not corroborate the GLEI Lake Erie results.

The distribution of dreissenids, which co-occurred with *E. ischnus* at numerous scales, appeared to determine the distribution of the nonindigenous amphipod more consistently than stressors or the distribution of *G. fasciatus*. This finding across such a broad geographic range suggests that dreissenids may

regulate the distribution of *E. ischnus* from broad to microhabitat scales, illustrating the importance of facilitative interactions for NIS success. If this is the case, *E. ischnus* may eventually inhabit protected wetland sites if it is able to disperse to those areas where *Dreissena* spp. also occur. The NIS occupy the same native habitat of the Ponto-Caspian region, and it is speculated that co-evolution with dreissenids has assisted *E. ischnus* establishment in the Great Lakes (Dermott *et al.,* 1998, van Overdijk *et al.,* 2003). *Dreissena* spp. provides *E. ischnus* with substrate and shelter from predators with its druses, as well as food in the form of feces and pseudofeces (Vanderploeg *et al.*, 2002). Studies have predicted (Witt *et al.,* 1997) or demonstrated (Dermott *et al.,* 1998, Stewart *et al.,* 1998, Burkart 1999) replacement of *G. fasciatus* by *E. ischnus* on *Dreissena* substrata in the Great Lakes. This replacement of *G. fasciatus* by *E. ischnus* may be related to the stronger affinity of the latter for substrata fouled by *Dreissena*. Conversely, increases in *G. fasciatus* abundances have also been predicted as a consequence of the *Dreissena* spp. invasion (Griffiths 1993, Stewart and Haynes 1994). Field and laboratory studies revealed that *E. ischnus* preferred *Dreissena*-encrusted rocks more than *Cladophora*-encrusted rocks, whereas *G. fasciatus* used both substrata (van Overdijk *et al.,* 2003).

The distribution of *G. fasciatus* was also significantly associated with that of dreissenids but not as strongly as the association between *E. ischnus* and *Dreissena* spp. Forty-eight percent of the sites at which *G. fasciatus* were collected did not support dreissenids. Thus, although they often co-occur across the basin, *G. fasciatus* are not regulated by dreissenids (Table 2.4). Furthermore, *G. fasciatus* were well established in the Great Lakes decades before the arrival of dreissenids (Mills *et al.,* 1993).

Because of its relatively recent arrival in North America, the distribution of *E. ischnus* across the Great Lakes would be expected to reflect the propagule pressure imparted from ballasting activities of transoceanic ships and recreational boating (Ricciardi and MacIsaac 2000). However, this seems not to be the case for *E. ischnus.* The results of my heterogeneity tests and comparisons with expected frequencies show a higher proportion of *E. ischnus* and *Dreissena* spp.

occurrences at Lakes Erie and Ontario sites than for the other lakes (Table 2.1). In contrast, *E. ischnus* did not appear in Lake Superior samples, even though Duluth and Thunder Bay harbours (Lake Superior) receive a disproportionate number of visits by transoceanic ballasted and NOBOB vessels (ships with no-ballast-on-board status) compared to other ports of the Great Lakes (Colautti 2001). In general, Duluth and Thunder Bay support few NIS in their vicinity (Grigorovich *et al.,* 2003). Lakes Erie and Ontario may provide better environmental conditions for mesothermic NIS entering the basin than the other Great Lakes (Vanderploeg *et al.,* 2002, Grigorovich *et al.,* 2003).

Results from this study do not support the disturbance hypothesis (increased likelihood of establishment at location in which stress has disrupted normal interaction among species comprising the natural community), and are more consistent with the environmental suitability hypothesis (NIS become established wherever conditions are adequate). Anthropogenic stressors at Great Lakes coastal margins do not appear to facilitate *E. ischnus*. My results and those of others (Levine and D'Antonio 1999, Blackburn and Duncan 2001, Holway, *et al.,* 2002, Dethier and Hacker 2005) suggest that the same environmental properties that provide suitable habitat for native species are also invasible for NIS.

Relatively sessile benthic macroinvertebrates are the closest animal equivalent to terrestrial plant communities, where disturbance often does increase invasibility. However, this study suggests that disturbance does not factor into invasion by *E. ischnus* as has been shown with terrestrial plants. Aquatic habitats are thought to be highly vulnerable to invasions (Mills *et al.,* 1993) due to their generally low level of native species diversity and frequent invasion opportunities. However, few studies test this assertion due to the difficulty in directly linking and assessing the contribution of disturbance to NIS success. Movement into potential habitats and dispersal limitations may be the primary obstacles for aquatic invasions (Levine 2000), but this does not explain why relatively few of the aquatic NIS that arrive in a new habitat establish viable populations. Factors such as habitat match (Kolar and Lodge 2001, Moyle and

Light 1996), phenotypic plasticity (Crawley 1987), propagule pressure (Levine 2000, Lockwood *et al.,* 2005, Von Holle and Simberloff 2005), facilitative interactions (Simberloff and Von Holle 1999, Ricciardi 2001, Bruno 2003), and life history requirements of NIS that inhibit establishment success (Fausch *et al.,* 2001) are almost certainly involved. Further studies attempting to elucidate the disparity between the dependence of plant and animal NIS on disturbance for establishment would be helpful in understanding the dynamics of invasion biology, particularly for aquatic environments.

CONCLUSIONS

I did not find any consistent association between *E. ischnus* distribution in the Great Lakes and degree of stress contributed from the land to drainage basin-scale habitats. My results do not support the hypothesis that invasion is more likely to occur in locations influenced by the types of stressors examined in this study. The presence of *Echinogammarus ischnus* at sites that are subject to varying intensities and types of stressors across the Great Lakes basin suggests that this NIS occurs wherever environmental conditions are suitable and that are concurrently occupied by *Dreissena* spp. This finding gives precedence to the environmental suitability hypothesis over the disturbance hypothesis as an explanation for the distribution of *Echinogammarus* at Great Lakes coastal margins.

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Table 2.1: Representation of sites with presence of *E. ischnus* (E), *G. fasciatus* (G), and *Dreissena* spp. (D). Arrows indicate whether a taxon was collected more frequently (↑) or less frequently (↓) than expected if distribution was random across all sites at a given scale. Numbers given show relative percentage of expected frequency.

Scale	E (%)	G (%)	D (%)
Michigan	↓52.4	↓96.7	↓69.9
Huron	↓78.6	↓89.8	↑116.6
Erie	↑182.5	↓89.8	↑108.2
Ontario	↑170.0	↑129.7	↑134.7
Coastal wetland	↓72.9	↑109.1	↓97.4
Embayment	↑136.1	↓71.9	↑121.2
High-energy	↑136.1	↓53.9	↑121.2
River-influenced wetland	↓63.8	↑164.7	↓63.1

Table 2.2: Number of sites with presence (G only or E only), co-occurrence (E and G), and absence (None) of *E. ischnus* (E) and *G. fasciatus* (G) from GLEI and ECCS data. Significant Yates corrected p-values and nonsignificant (ns) associations are indicated.

Scale	E and G	G only	E only	None	Total (n)	p
Basin*	14	40	5	38	97	ns
Michigan*	2	19	2	16	39	ns
Huron*	3	10	1	12	26	ns
Erie	3	4	2	5	14	ns
Ontario	6	7	0	5	18	ns
Coastal wetland*	4	13	0	11	28	ns
Embayment	3	3	1	8	15	ns
High-energy*	4	5	4	17	30	ns
River-influenced	3	19	0	2	24	ns
Microhabitat*	26	237	13	649	925	<0.0005
ECCS*	5	14	13	64	96	ns

*Scales at which numbers of sites sampled provide suitable α-levels (0.75) for detection of rare species (as per McArdle 1990).

Table 2.3: Number of sites with presence (D only or E only), co-occurrence (E and D), and absence (None) of *E. ischnus* (E) and *Dreissena* spp. (D) from GLEI and ECCS data. Significant Yates corrected p-values, and nonsignificant (ns) associations are indicated.

Scale	E and D	D only	E only	None	Total (n)	p
Basin*	18	14	1	64	97	<0.0005
Michigan*	4	5	0	30	39	<0.05
Huron*	4	6	0	16	26	ns
Erie	5	0	0	9	14	<0.05
Ontario	5	3	1	9	18	ns
Coastal wetland*	4	5	0	19	28	ns
Embayment	4	2	0	9	15	ns
High-energy*	8	4	0	18	30	<0.0005
River-influenced	2	3	1	18	24	ns
Microhabitat	34	99	5	787	925	<0.0005
ECCS*	18	0	0	78	96	<0.00005

*Scales at which numbers of sites sampled provide suitable α-levels (0.75) for detection of rare species (as per McArdle 1990).

Table 2.4: Number of sites with presence (D only or G only), co-occurrence (G and D), and absence (None) of *G. fasciatus* (G) and *Dreissena spp*. (D) from GLEI and ECCS data. Significant Yates corrected p-values, and nonsignificant (ns) associations are indicated.

Scale	G and D	D only	G only	None	Total (n)	p
Basin*	26	6	28	37	97	<0.05
Michigan*	7	2	14	16	39	ns
Huron*	9	1	4	12	26	ns
Erie	5	0	2	7	14	ns
Ontario	5	3	8	2	18	ns
Coastal wetland*	9	0	8	11	28	ns
Embayment	5	1	1	8	15	ns
High-energy*	7	5	2	16	30	ns
River-influenced	5	0	17	2	24	ns
Protected wetland	2	0	2	15	19	ns
Microhabitat	62	52	201	610	925	<0.0005
ECCS*	19	0	0	77	96	<0.00005

*Scales at which numbers of sites sampled provide suitable α-levels (0.75) for detection of rare species (as per McArdle, 1990).

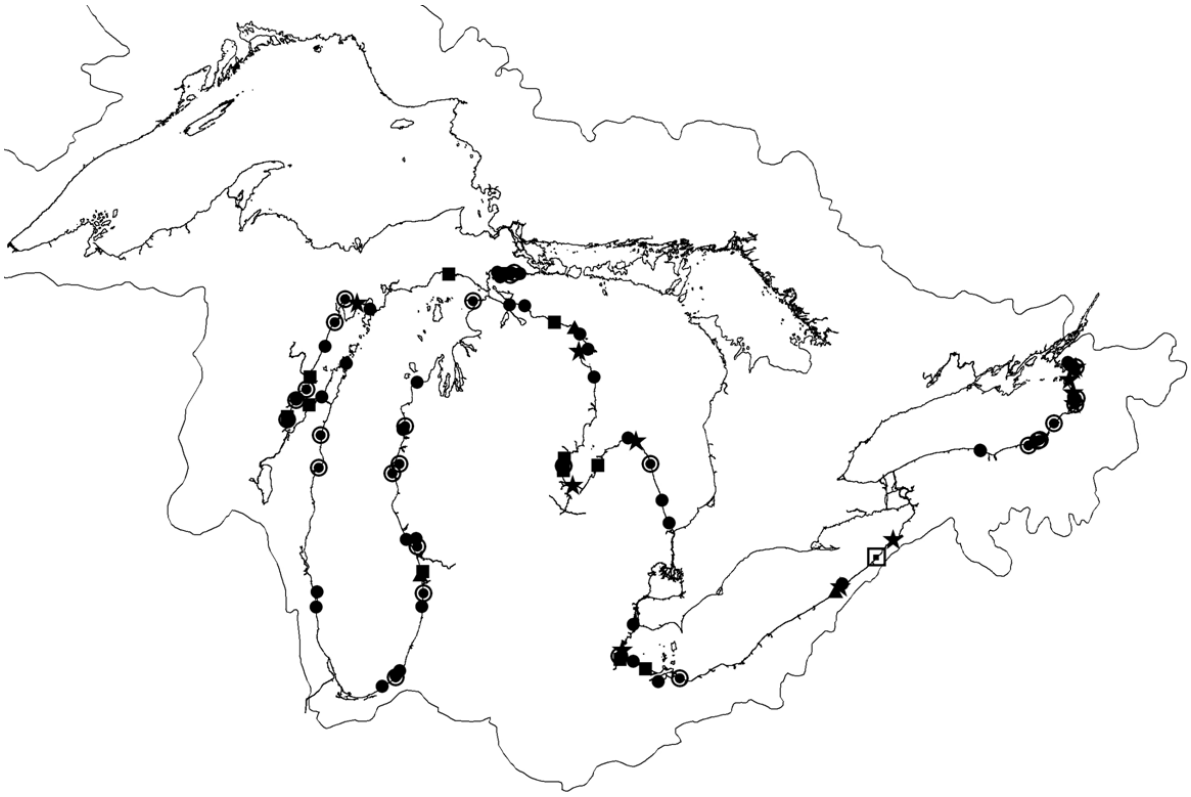

Figure 2.1: Distribution of *E. ischnus* (E), *G. fasciatus* (G), and *Dreissena* spp. (D), across the U.S. Great Lakes basin for GLEI and ECCS (inset) sites. Symbols indicate occurrences of E+G+D (★), E+D (▲), E+G (♦), D+G (■), D (⊙), G (⊡), and none of the taxa (●) at sampled sites.

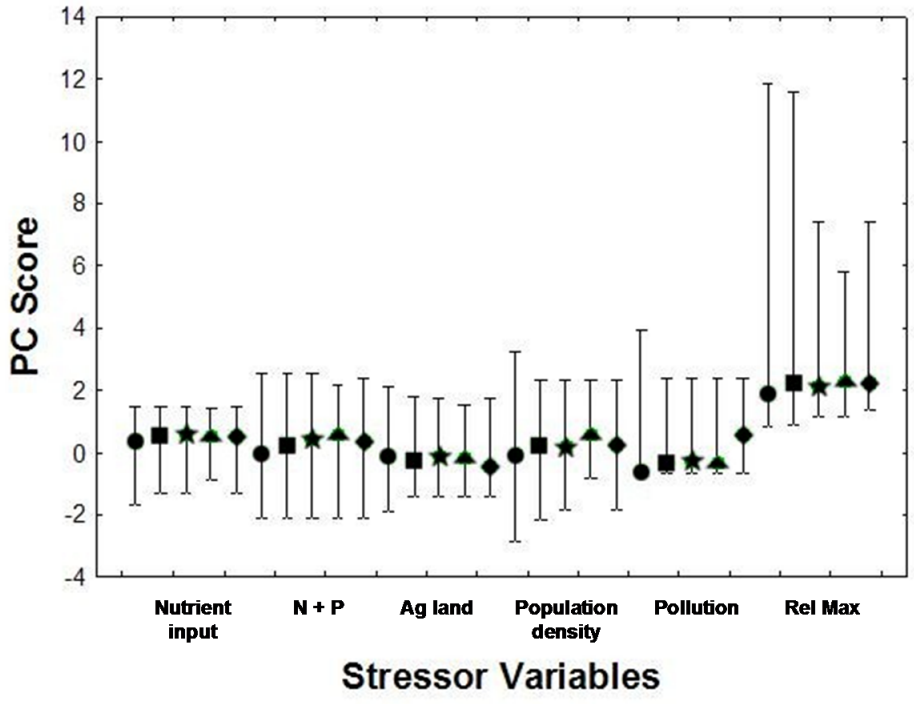

Figure 2.2: Ranges of overall nutrient input, N and P load, agricultural land area, human population density, overall pollution loading, and relative maximum stressor variables for all GLEI sites (●), Basin (■), *Echinogammarus* (★), *Gammarus* (▲), and *Dreissena* (◆) sites. Symbols denote median PC Score.

CHAPTER 3: NATIVE-NONINDIGENOUS SPECIES BIODIVERSITY RELATIONSHIPS, AND DOMINANCE TRENDS OF TAXONOMIC GROUPS AT LAURENTIAN GREAT LAKES COASTAL MARGINS – INTERACTION VERSUS NEUTRAL-INTERACTION PROCESSES

INTRODUCTION

Species richness has often been proposed to be an important variable associated with the invasibility of systems. Species-poor communities have been argued to be invasible due to the presence of empty niches and the lack of biotic resistance, whereas species-rich communities are said to have filled niches and repel invaders (Elton, 1958; MacArthur, 1970; Fox and Fox, 1986; Pimm, 1991; Rejmanek, 1996; Lonsdale, 1999). However, others argue that diverse communities are invasible due to greater resource availability and weak interspecific interactions (Huston, 1994; McCann *et al.,* 1998), or because nonindigenous species (NIS) benefit from facilitation by residents, either directly or indirectly (Levine 1976; Case, 1991; Simberloff and Von Holle, 1999; Ricciardi, 2001; Kang *et al.*, 2007).

Other aspects of biodiversity and biotic interactions may also have important impacts on invasions, such as species evenness and individual species dominance in communities (Crawley *et al.,* 1999; Smith and Knapp, 1999; Wilsey and Polley, 2002; Callaway *et al.,* 2003; van Ruijven *et al.,* 2003; O'Connor and Crowe, 2005; Wilsey *et al.,* 2005; Smith *et al.,* 2004).

Unlike biotic interaction based theories that emphasize interactions among species, neutral theory assumes that all species are competitively equivalent and that regional abundances are determined by dispersal driven by demographic stochasticity (Hubbell, 2001). Due to the development of transportation routes around the world, many species have overcome geographic barriers that previously prevented their dispersal. Nonindigenous species disperse to areas such as the Laurentian Great Lakes due to both intentional and unintentional human-mediated introductions (Mills, 1993), but particularly from ballasting activities of transoceanic ships (Carlton and Geller, 1993) and recreational boating (Carlton, 1993). Successful invasion has been attributed to high propagule pressure of NIS, either through human activities or natural dispersal

processes, and is thought to be the most important factor in establishment success (i.e., population grows to become self-sustaining) of NIS of various taxa in a variety of ecosystems worldwide (Lonsdale, 1999; Fine, 2004), more important than the influence of biotic resistance (Levine, 2000). A “propagule” is an individual released in the non-native environment (Lockwood *et al*., 2007) and “propagule pressure” is the combined effects of propagule size (i.e., the number of propagules), propagule number (i.e., the number of release events of a set of propagules), and the physiological condition of propagules (Lockwood *et al*, 2007). Few studies have documented the influence of propagule pressure and/or dispersal on invasion events given the difficulty in finding accurate information on propagule size and/or propagule number. Those that do provide reliable information on propagule pressure come from biocontrol studies and intentional release of vertebrate game (Beirne, 1975; Veltman *et al*., 1996; Duncan, 1997; Green, 1997; Memmott *et al*., 2005). Beirne (1975) reviewed Canadian insect release efforts for biological control and found that the higher the propagule size and propagule number, the greater the probability of establishment success. Cassey *et al.,* (2005) conducted a meta-analysis of bird introductions to quantitatively assess the results of multiple studies and the influence of predictor variables identified to explain the variation in establishment success. They found that variables describing characteristics specific to the individual introduction event (i.e. event-level variables), such as propagule pressure, were consistently better predictors of establishment success than characteristics of the location where the species was introduced (i.e., location-level variables) or characteristics of the species introduced (i.e., species-level variables). Although these studies illustrate the importance of propagule pressure, the taxa chosen for deliberate introductions were likely physiologically matched with habitats and thus the role of climate in determining success or failure of establishment was de-emphasized.

The various hypotheses that have been proposed to describe NIS/native species relationships have invoked differences primarily in richness (R), evenness (E), dominance (D) or intensity of introduction (i.e., propagule pressure). Depending on the scale and the underlying processes, the

relationships are proposed to be either positive (+), negative (-), or nonsignificant (N) (discussion follows). Consequently, one can organize the hypotheses proposed to explain invasion success into 9 classes as related to richness (R+/R-/RN classes), evenness (E+/E-/EN classes), NIS dominance (D+/D-/DN classes) (Table 3.1). The RN/EN/DN classes represent neutral response (Table 3.1) and may be consistent with regulation by propagule pressure. The independent variable for bivariate richness, evenness, and dominance relationships with invasion success is native species richness/NIS presence or absence, NIS presence or absence/NIS richness, and NIS or native species status, respectively. The dependent variable for richness, evenness, and dominance relationships are NIS species richness/total richness, evenness, and relative abundance/frequency among sites, respectively. Below, I outline expectations that would corroborate the hypothesis "classes". Hypothesis classes are proposed to aid readers in reviewing relationships.

Relationship between Richness and Invasibility (R+/R-)

Depending on the study, the relationship between invasion success and community diversity has been found to be negative (R-), positive (R+), or nonexistent (= 'neutral'; RN) (reviewed by Levine and D'Antonio, 1999). This inconsistency has been referred to as the "invasion paradox" (Fridley *et al*., 2007). In contrast to theoretical studies, some empirical studies found that diverse (native species-rich) communities tend to be the most invasible (Levine and D'Antonio, 1999). Spatial correlation studies indicated that negative richness-invasibility relationships (R-) tend to occur when the unit of spatial resolution is fine (e.g., ~1 m^2 or less), whereas positive relationships (R+) tend to be found at regional scales of evaluation (thousands of square meters) (see Levine and D'Antonio, 1999; Table 3.1). This discrepancy has been suggested to be an artifact of methodology - environmental variables are held constant while native species number are manipulated in small-scale experimental studies (Byers and Noonburg, 2003); and variation in resource availability, intensities of propagule pressure, and facilitative interactions covary with biodiversity in large-scale studies (Levine and D'Antonio, 1999; Levine, 2000; Richardson *et al.,* 2000;

Bruno *et al.,* 2003; Shea and Chesson, 2002; Brown and Peet, 2003). These results suggest that the same environmental properties that support a rich diversity of native species may also support a rich diversity of introduced species (both R+ and E+; Levine and D'Antonio, 1999). Clearly, the scale of investigation in invasion studies has an important influence on the perceived outcome (Byers and Noonburg, 2003).

The assertion that community richness influences invasibility (R+/R-; Table 3.1) is controversial, and many studies attribute processes other than biotic interactions to invasion events. Gido *et al.,* (2004) found that total abundance and community structure of native fish assemblages changed at several of their Oklahoma and Kansas sites over an 18-y study period. However, they reasoned that these changes arose from factors other than interactions with introduced fishes given that similar changes were observed in assemblages with few or no NIS (RN). Dunstan and Johnson (2004) showed that invasion of sessile marine invertebrate community patches in Tasmania increased with richness of the patch (R+). They inferred that these patterns were the result of particular properties of individual species and local species dynamics, and that reduced risk of invasion is not necessarily an intrinsic property of species-rich communities. Stohlgren *et al.,* (2006) found that both native and nonindigenous plant, bird, and fish densities of the US were positively cross-correlated at various scales (R+) and suggested that multiple biological groups may track each other in predictable ways (Currie, 1991). They also found evidence that relatively diverse areas tend to become more diverse over time ('the rich get richer'; Stohlgren *et al.,* 2006; both R+ and E+). Their findings suggest that biotic resistance (i.e., competition, which should produce R-) is a weak force in the establishment of NIS at relatively large scales (Stohlgren *et al.,* 1999, 2002, 2003, 2006). Thus, my study would support this assertion if areas that have a rich diversity of one group also have a rich diversity of other groups and that they are controlled largely by environmental factors (both R+ and E+).

Relationship between Relative Abundance and Invasibility: Evenness (E+/E-) and Dominance (D+/D-)

Few experiments have been performed in which evenness is varied while richness is held constant (Wilsey & Potvin 2000), even though evenness contributes to a larger proportion of the variance (53%) in diversity (H') of plant communities than does species richness (6%) (Stirling and Wilsey, 2001). Communities with high evenness could be viewed as similar to communities with high species richness, with both components increasing the functional diversity of a community (R+ and E+; Wilsey and Polley 2002, Mulder *et al.,* 2004). However, some theory suggests that communities with low evenness may be a result of complete use of a limiting resource by the dominant species (Tilman 1982, Robinson *et al.,*1995), thus leading to low invasibility (E-; Table 3.1) while others show that although evenness enhances community productivity, it confers no resistance to invasion in otherwise functionally diverse communities (Mattingly *et al*., 2007). Few studies have explicitly examined the relationship between evenness and invasibility (Wilsey and Polley, 2002; Tracy and Sanderson, 2004). Wilsey and Polley (2002) manipulated the evenness of four plant species in a field experiment and found number of dicot invaders from natural sources was lower in plots with high evenness (E-; Table 3.1). Similarly, Tracy and Sanderson (2004) found that natural weed invasion (density of all invading species) decreased in forage plots planted with an even mixture of forage species (E-). They also found that weed abundance varied depending on the identity of the most common species. Low evenness in invaded sites might indicate that NIS may be lowering evenness by dominating the communities of sites at which they establish (in terms of relative abundance), hence influencing subsequent invasion) (D+). Nonindigneous species are often characterized as invasive because of their strong potential for dispersal and dominance. In an observational study of intact communities, Robinson *et al.* (1995) found that invasion success did not depend on species richness but was a function of the level of dominance exerted by a resident grass species. Although they did not specifically examine the influence of evenness, the findings of Robinson *et al.,* (1995) showed that invasion success (i.e., the total number of invader plants germinating, producing seeds, or perennating) decreased with increasing species evenness (E-; Table

3.1). The dominant invader outcompeted resident species and prevented new invaders from establishing (D+; Table 3.1).

Other studies have suggested that invasibility may be contingent upon the identity of the dominant native species within low-evenness communities (Crawley *et al.,* 1999; Smith and Knapp 1999; van Ruijven *et al.,* 2003; Smith *et al.,* 2004). Experiments manipulating density through seed addition or plant removal have also shown that dominance by a particular native species may be more important than species richness in determining invasibility (D+; Emery and Gross, 2007; Smith *et al.,* 2004). Conceptually, the relationships between invasibility and evenness and between invasibility and dominance cannot be mutually exclusive since any community that contains a dominant (whether a native species or NIS) must be uneven. I distinguish between the influence of evenness and dominance on invasion in this study to differentiate between the influence of the competitive ability of the NIS (D+) and the influence of potential resource availability of the community (E-) on invasion. A community may be uneven and invaded by a non-dominant due to availability of an unused resource.

Neutral Theory/Propagule Pressure and Invasion (RN/EN/DN)

Neutral models used to simulate the biodiversity-invasibility relationship have produced patterns that seemingly match those of theoretical predictions that diverse communities are less invasible than species poor communities. Thus, patterns that have been attributed to the consequences of species interactions (i.e., competition) or other ecological processes (Connor and Simberloff, 1983; Gotelli and Graves, 1996; Fridley *et al.,* 2004; Herben *et al.,* 2004) may actually be a product of statistical or sampling artifacts (Strong 1980). Negative relationships between native and NIS richness that result from small-scale studies may be due to spurious correlations with low overall density that constrain native-NIS richness values but are interpreted as manifestations of competitive interactions (i.e., biotic resistance) (Fridley *et al.,* 2004; Herben *et al.,* 2004). Positive native-NIS relationships may be the result of the chance inclusion of more native species and NIS given that larger areas tend to have higher total richness, and the likelihood of species occurrences may be unassociated with

interactions or environmental variables (Fridley *et al.,* 2004; Herben *et al.,* 2004). Fridley *et al.,* (2004) demonstrated that artifactual negative relationships at small scales and positive relationships at large scales emerge even when there is no interaction between native species and NIS. Herben *et al.* (2004) also showed that statistical artifacts could explain the small-scale negative and large-scale positive relationships that resulted from a neutral model composed of identical native and NIS where the number of individuals was allowed to vary.

Von Holle and Simberloff (2005) manipulated flood regimes (physical environment) and the number of established resident species to study their influence on invasibility of plots. They found that the effects of a highly variable flooding regime among plots and significant reduction in resident richness had negligible impact on net native species and NIS invasion success as compared to propagule pressure (richness nonsignificant/neutral = RN).

Data required to specifically examine the influence of propagule pressure on invasions (i.e., propagule size and propagule number) were not available for my study. However, evaluations of the influence of biotic interactions as manifested through richness and evenness of the invaded community, and relative dominance of the NIS were performed for various taxonomic groups, spatial scales, and sample sizes. Richness, evenness, and dominance trends consistent with regulation by availability of suitable habitat and propagule pressure (neutral-interaction processes) would be demonstrated by the null relationships of richness (RN), evenness (EN), and dominance (DN).

The objectives of this study were to i) evaluate the relationships between native species (NS) richness and nonindigenous species (NIS) richness at various spatial scales and sample sizes to assess the hypotheses that NS richness influences NIS richness (R+ and R-; Table 3.1); ii) compare evenness of invaded and uninvaded communities to determine the influence of evenness on invasibility (E+ and E-; Table 3.1); iii) examine dominance trends in terms of distribution and proportion of total individuals collected at a site and determine whether widespread and/or abundant (i.e., dominant) species tend to be of nonindigenous identity and hence influenced evenness (D+; Table 3.1) or

whether NIS were able to invade due to processes unrelated to competitive ability (D-; Table 3.1); and iv) evaluate the influence of propagule pressure and habitat suitability for NIS distributions (RN/EN/DN). Results from this study will provide insight to community and invasion processes, as well as general biodiversity trends across taxonomic groups.

These hypotheses were evaluated by examining bird, diatom, fish, and wetland emergent vegetation samples collected at locations across the US Great Lakes coastline, spanning 2 ecoprovinces and a range of hydrogeomorphic characteristics. This study was part of the Great Lakes Environmental Indicators (GLEI) project, designed to develop and test indicators of condition along the coastal margins of the US Great Lakes(Danz *et al.,* 2005; Niemi *et al.,* 2007). I examined relationships at both fine-scale (i.e., within-sampling site, small spatial scales, supporting relatively small numbers of individuals) and broad scale (i.e., among sampling sites across the Great Lakes basin, larger spatial scales, involving relatively large numbers of individuals) levels of resolution to evaluate distribution trends of taxonomic groups and prevent anomalies related to statistical or sampling artifacts. Spatial scales examined varied depending on the taxonomic group investigated, and reflected conventional sampling methods.

METHODS

A list of abbreviations used throughout the thesis and their definitions are given in Appendix 3.1.

Data Sources and Survey Methods

Bird, diatom, fish, and wetland vegetation samples for the GLEI project were collected using standard methods from stratified randomly selected subsets of coastline of the 762 second-order or higher US watersheds that drain into the Laurentian Great Lakes (Hollenhorst *et al*., 2007). Sampling locations were spread across the 5 Great Lakes and approximately evenly apportioned among 2 ecoprovinces (Laurentian Mixed Forest in the northern lakes (ECO-N), and Eastern Broadleaf Forest in the southern lakes (ECO-S); Keys *et al.,* 1995), 5 wetland types classified by hydrogeomorphic (HGM) connections to a Great Lake

(coastal (CW), embayment (EB), high-energy (HE), river-influenced (RW), and protected (PW); Keough *et al.,* 1999), and range of anthropogenic disturbance gradients selected using a stratified random sampling design (Danz *et al.,* 2005).

Benthic and sedimented diatoms were sampled from 113 wetlands from June - September 2002 and May - August 2003 on natural substrates at 0.5 - 3 m depth using a 6.5-cm diameter push corer and core tube and processed as described by Reavie *et al.* (2007). Data on diatoms found on surface sediments in unconsolidated bottom substrates were analysed in this study.

Vegetation was sampled in 40 wetlands from 1-m^2 quadrats randomly established within 20-m segments of randomly placed transects within emergent and wet meadow areas (Bourdaghs *et al.,* 2006; Johnston *et al*., 2007). Transect length and target number of sample plots were determined in proportion to the size of the wetland to be sampled (20 plots/60 ha, minimum transect length = 40 m, minimum of 8 plots/site mean number of plots/site = 21). Plants were identified to the lowest taxonomic division possible (Bourdaghs *et al.,* 2006; Johnston *et al*., 2007). Cover was estimated visually for each taxon using modified Braun-Blanquet cover classes (ASTM, 1997). No vegetation was collected at HE or EB locations.

Bird surveys were conducted by trained observers (Howe *et al*., 2007) at 227 wetlands during June and early July in 2000, 2001, and 2002 using the Marsh Monitoring Workshop wetland breeding bird survey protocol (Ribic *et al.,* 1999; Weeber and Vallianatos, 2000). No bird surveys were conducted at HE or EB locations.

Fishes were sampled in separate, independent surveys by two methods. Boat-mounted electrofishing surveys (electro-fish) and fyke-net sampling (fyke-fish) were undertaken using the methods described by Trebitz *et al.* (2007) and Bhagat *et al*. (2007), respectively. The two methods were used by separate field crews that overlapped at 35 sites. Fyke-nets were fished at 139 locations, whereas electrofishing was completed at 58 sites. No electrofishing surveys were conducted at HE or EB locations. Analyses of electro- and fyke-fishes were performed separately for schooling and nonschooling taxa where appropriate

(i.e., analyses examining richness and abundance trends) to avoid possible misrepresentation of trends.

Nonindigenous species were identified as those species that are introduced to the Great Lakes region according to classifications of the American Ornithologist's Union (1998) for birds, Ricciardi (2006) for diatoms and fishes, and the United States Department for Agriculture (USDA) Plants Database for vegetation (USDA NRCS, 2004). Analyses that included hybrid vegetation NIS primarily showed no difference between results of analyses excluding hybrid NIS. Given that analyses of other taxonomic groups could not include hybrids because of difficulty in hybrid identification, vegetation hybrid analyses are not presented in this study unless relationships differed from those that included hybrids. An invaded site was considered to be any site that supported at least a single NIS individual.

Statistical Analyses

Richness

To evaluate the relationship between NS richness and NIS richness, linear regression was performed on data for each taxonomic group. These analyses were conducted at the basin, ecoprovince, lake, and HGM scales to detect distribution trends of taxonomic groups (i.e., areas with differing biodiversity) and the higher propensity of invasion in certain habitats (i.e., areas subject to higher propagule pressure and/or those locations that provide suitable habitat). Analyses were also performed at various spatial scales of sites (size ha) and total number of individuals (total number of observations for vegetation) collected in samples to prevent possible sampling artifacts of different scales and sample sizes (see Fridley *et al*., 2004; Herben *et al.,* 2004). Spatial and sample size increments were based on taxonomic group and comparable to similar studies in the literature. Differences in total and native richness (dependent variables) between invaded and uninvaded sites (factor) for each taxonomic group at each scale were also assessed using multiple one-way ANOVAs to determine whether invaded sites were characterized as having higher richness (supporting the idea

that habitats suitable for NS are also suitable for NIS; R+) or lower richness (supporting the idea that NIS invade areas where they are likely to encounter less competition; R-). Nonsignificant results would suggest that propagule pressure and suitable habitat determine invasion.

Multiple one-way ANOVAs were used to test for differences in NIS richness (dependent variable) between ecoprovinces (k=2), and among lakes (k=5), and HGM ($k_{electro\text{-}fish}$=2; $k_{diatom,\ veg}$=3; $k_{diatom,\ fyke\text{-}fish}$=5) scales (factors) to determine geographic differences in NIS distributions for each taxonomic group.

These analyses were performed both with and without the inclusion of Lake Superior data since some NIS may not be able to persist in Lake Superior (Grigorovich *et al*., 2003).

Evenness

Evenness at each site was calculated using Simpson's evenness measure, ($1/\mathrm{E}p_i^2$*$1/S$), where p is the proportion of a species i relative to the total number of individuals collected in a sample (number of observations was used for vegetation) and S is the total richness of a sample (Simpson, 1949). Differences in evenness between invaded and uninvaded sites, characterized by the presence or absence of an NIS, respectively, were assessed using one-way ANOVA for each taxonomic group. The same suite of ANOVAs performed to evaluate trends in richness (above) was conducted using evenness as a dependent variable. Evenness of sites was recalculated after excluding NIS to see if NIS dominated sites and hence affected site evenness after invasion. A finding that invaded sites have significantly lower evenness than uninvaded sites would demonstrate that invasion is determined by the relative dominance of NIS relative to NS and availability of resources (E-) while a finding that evenness is significantly higher at invaded sites than uninvaded sites would support the hypothesis that resident species facilitate NIS or that there is incomplete resource use among NIS and NS (E+).

Given that richness and number of individuals are properties of Simpson's evenness, the relationships between evenness and richness and between evenness and number of individuals (properties related to total, NS, and NIS

were differentiated) were examined to see if trends followed expected trends of Simpson's evenness. I expected to find that evenness would decrease as richness and/or numbers of individuals increased given the definition of the measure. Thus, if NIS dominate sites, a strong negative relationship between evenness and NIS richness and between evenness and number of NIS individuals would be expected (de Benedictis 1973; Hill 1973; Ma *et al*., 2005; Wilsey *et al*., 2005; E- and D+). A positive relationship between NIS richness and NS richness, along with a positive relationship between NIS richness and evenness at a site would lend support for the 'rich get richer' hypothesis (both R+ and E+; Stohlgren *et al.,* 2006).

Dominance

Mean relative abundance curves across sampling units were plotted for each taxononomic group to assess species dominance in terms of proportion of total individuals collected at a site, and abundant NIS and NS were identified. Abundant species were identified as the top 5% with the highest proportion of total individuals collected at a site. Multiple one-way ANOVAs were performed on relative abundance data (dependent variable) to determine whether there was a significant difference in relative abundance between NS and NIS (factor=invader status) for each taxononomic group. The abundance of NIS was further assessed by ranking each species in terms of their relative abundance and evaluating the probability using the binomial theorem that each NIS would be given its rank by chance. Probabilities for each invaded site were combined to test the overall probability that the most abundant NIS could be ranked disproportionately higher than it should be (Fisher, 1954). Site frequency curves were plotted for each taxonomic group to assess species dominance in terms of distribution, and widespread NIS and NS were identified. Widespread species were identified as the top 5% of taxa with the highest frequency of occurrence among sites. Dominant species were identified as those species that were both abundant and widespread. The prevalence of abundant and/or widespread taxa was assessed to determine whether dominant species tend to be nonindigenous. Analyses were performed to assess whether NIS are able to invade due to competitive abilities

(D+) or due to processes unrelated to competitive ability (D-). A finding that NIS dominance is not significantly different from NS dominance would support the hypothesis that NIS distributions are determined by propagule pressure and suitable habitat.

A modified Bonferroni correction (Holm 1979) was used to adjust the study-wide Type I error to 0.05. All analyses were performed using the Statistica® software package Version 6.0 (StatSoft, Inc. 2001).

RESULTS

Figure 3.1 shows the proportion of invaded and uninvaded sites for taxonomic groups at various scales, as well as their respective richness and evenness measures.

A low proportion of sites (less than 25%) were invaded by bird NIS at all scales examined. This may reflect the low number of established bird NIS (total = 5). ECO-S and Lake Ontario had the highest proportion of invaded bird sites (21 and 24%, respectively), whereas Lake Superior had the lowest proportion of invaded bird sites (4%).

Only a small proportion of diatom sites supported NIS at all scales examined (<40% of sites were invaded for each scale; median proportion of invaded sites was 21% across all scales), except for Lake Erie (70% of sites were invaded). However, there are few established diatom NIS in the Great Lakes (total = 4). ECO-N, Lake Superior, Lake Huron, and protected wetland sites had the lowest proportion of invaded diatom sites (9, 5, 8, and 9% of sites were invaded, respectively).

A high proportion of electro-fish and nonschooling electro-fish sites were invaded at all scales examined (>65% of sites were invaded at all scales). All sites from ECO-S and lakes Huron, Erie, and Ontario were invaded whereas Lake Superior had the lowest proportion of invaded electro-fish and nonschooling electro-fish sites.

Similarly, a high proportion of fyke-fish and nonschooling fyke-fish sites were invaded at all scales examined (>50% of sites were invaded at each scale,

except for Lake Ontario (43 and 38% of sites were invaded for fyke-fishes and nonschooling fyke-fishes) and nonschooling Lake Michigan sites (49% of sites were invaded). All sites in Lake Erie were invaded. Lake Ontario, river-influenced and protected wetlands had the lowest proportion of sites at which invading fish species were captured.

A high proportion of vegetation sites was occupied by NIS at all scales examined (>50% of sites were invaded at each scale), except for Lake Superior. ECO-S had a higher proportion of invaded vegetation sites than ECO-N. All vegetation sites from lakes Huron, Erie, Ontario, and coastal wetlands were invaded. Lake Superior had the lowest proportion of invaded sites for both analyses with and without hybrids (45 and 36% of sites, respectively). All uninvaded river-influenced and ECO-N sites were located in Lake Superior.

i) Relationship between native and nonindigenous species richness

Table 3.2 summarizes analyses of the native-nonindigenous species richness relationship at various scales for the various taxonomic groups investigated. The only relationships that were found to be significant at the Holm-corrected level were for diatoms in ECO-S and for fyke-fishes at the Basin, protected wetland and 100-999 ha scales (all R+). The Holm (1979) correction used to adjust the detection level for significance to correct for inflated Type I Error from the many simple regression analyses, rendered nonsignificant the nominally significant ($p<0.05$) relationships between NS and NIS at the scale of ECO-N, Lake Huron, and coastal wetland for birds, at the scale of 0-50 hectares and for Lake Michigan and Lake Ontario for electro-fishes, at the scale of 50-99 individuals and for ECO-S, lakes Michigan, Huron, high-energy, and coastal wetland for fyke-fishes, at the scale of the basin (with the exclusion of Lake Superior), 100-200 individuals (without hybrids) for vegetation (a total of 14 tests out of 121 regressions performed). These non-Holm level relationships were all positive (R+), except for electro-fishes (those scales mentioned in previous sentence) and hybrid-included vegetation at the scale of 100-200 individuals, which were consistent with R- hypotheses.

There was significantly higher total richness at invaded sites than at uninvaded sites (R+) at the Holm-corrected level for fyke-fish (schooling: $p<0.0005$, nonschooling: $p<0.00005$) basin scale sites, diatom ($p<0.005$) and fyke-fish (schooling: $p<0.005$, nonschooling: $p<0.0005$) ECO-S sites, fyke-fish (schooling: $p<0.001$) coastal wetland sites, and fyke-fish (schooling: $p<0.005$, nonschooling: $p<0.005$) high-energy sites. However, NS richness did not differ significantly between invaded and uninvaded sites for any taxonomic group or scale at the Holm-corrected level. Given that **total** richness of some taxonomic groups was significantly different between invaded and uninvaded sites (see above), the NIS of these taxonomic groups must contribute to total richness without affecting NS richness.

Table 3.3 shows trends in NS and NIS richness across taxonomic groups and scales. Lake Ontario had significantly fewer bird NS than any of the other Great Lakes (pairwise comparisons all $p<0.05$) while Lake Superior had significantly lower bird NS richness than Lake Michigan ($p<0.05$). Protected wetlands had significantly higher bird NS richness than the 2 other HGMs (both $p<0.05$). Unlike the other taxonomic groups examined, bird NIS richness was not constrained by ecoprovince, lake, or HGM.

Diatoms had significantly higher NS richness in ECO-N and Lake Superior than ECO-S and lakes Michigan, Huron, and Erie, respectively (Table 3.3). High-energy sites had significantly lower NS richness than embayments, coastal, and river-influenced wetlands (all $p<0.05$; Table 3.3). Diatom NIS richness was better explained by lake ($p<0.00005$; Table 3.3) than by NS richness since certain lakes have more NIS than others. ECO-S and Lake Erie have significantly higher diatom NIS richness than ECO-N ($p<0.005$; Table 3.3) and the other lakes (all $p<0.001$; Table 3.3), respectively.

Both electro-fish and nonschooling electro-fish protected wetland sites had significantly lower NS richness than river-influenced wetlands (all $p<0.05$; Table 3.3). Electro-fish and nonschooling electro-fish NIS richness was better explained by Lake and HGM (all $p<0.05$; Table 3.3) than by NS richness since certain lakes and HGMs had more NIS than others. Nonindigenous species richness of ECO-S

and Lake Erie was significantly higher than NIS richness of ECO-N (both $p<0.005$; Table 3.3) and the other lakes (all $p<0.05$; Table 3.3), respectively.

Lake Michigan fyke-net fish samples had significantly lower NS richness than Lakes Erie or Lake Ontario samples (both $p<0.05$; Table 3.3). Lake Michigan nonschooling fyke-fishes had significantly lower NS richness than Lake Erie ($p<0.05$; Table 3.3). High-energy fyke-fish sites of both types had significantly fewer NS than the other HGMs (all $p<0.005$; Table 3.3), except for nonschooling fyke-fishes at coastal wetland sites. Variation in fyke-fish and nonschooling NIS richness was better explained by differences in ecoprovince, lake, and HGM ($p<0.05$; Table 3.3) than by NS richness since certain localities had more NIS than others. ECO-S has significantly higher NIS richness than 212 ($p<0.05$; Table 3.3). Lake Erie had significantly higher NIS richness than the other lakes (all $p<0.05$; Table 3.3). Surprisingly, Lake Ontario had lower NIS richness than any of the other Great Lakes (all $p<0.05$; Table 3.3). This may be a reflection of the HGMs representing Lake Ontario sites – 24% of Lake Ontario sites were protected wetlands. Coastal wetlands had higher NIS richness than high-energy, protected, and river-influenced wetland sites ($p<0.05$; Table 3.3). Similar trends were found for nonschooling fyke-fish data, although coastal wetlands did not have significantly higher NIS richness than protected wetland sites.

Vegetation in ECO-N sites had significantly higher NS richness than ECO-S sites ($p<0.01$; Table 3.3). Vegetation NIS richness was better explained by lake ($p<0.05$; Table 3.3) than by NS richness since certain lakes have more NIS than others. Lake Superior had significantly lower NIS richness than the other lakes ($p<0.05$; Table 3.3) and Lake Erie had significantly lower NIS richness than Lake Ontario ($p<0.05$; Table 3.3). Protected wetland sites had significantly lower NIS richness than river-influenced sites ($p<0.05$; Table 3.3) and coastal wetland sites when Lake Superior sites were included in the analysis ($p<0.05$; Table 3.3).

ii) Comparison of evenness at invaded and uninvaded sites

There was no significant difference in evenness between invaded and uninvaded sites at the Holm corrected level at any scale, for any taxonomic group. Evenness of invaded sites was nominally lower than uninvaded ECO-N

bird sites ($p<0.05$), high-energy diatom sites ($p<0.05$), basin fyke-fish sites ($p<0.01$), and ECO-S ($p<0.01$), Lake Michigan ($p<0.05$), and protected wetland ($p<0.05$) vegetation sites when the Holm correction was not considered (all nominally E-). No significant differences in evenness were detected across taxonomic groups when comparisons of evenness measures calculated with and without NIS were made to assess the relative contribution of NIS to site evenness.

ECO-N bird sites as a group were significantly more even than ECO-S bird sites ($p<0.05$), and Lake Huron electro-fish sites had significantly higher evenness than Lake Erie electro-fish sites ($p<0.05$) (Fig. 3.1). There was no significant difference in mean evenness across scales of sampling for other taxonomic groups (Fig. 3.1).

Table 3.4 shows the relationships between evenness and richness and between evenness and numbers of individuals for the various taxonomic groups examined. All significant relationships are negative, as is the expected trend of Simpson's evenness measure with respect to richness. There were highly significant negative relationships between evenness and total richness (except for diatoms), between evenness and total number of individuals, between evenness and NS richness (except for diatoms and nonschooling electro-fishes), and between evenness and numbers of NS individuals across taxonomic groups (all $p<0.005$, except nonschooling electro-fish NS individuals $p<0.01$). There were significant relationships between evenness and NIS richness (E-) and between evenness and number of NIS individuals (E-) for vegetation (both $p<0.05$). Birds and diatoms did not exhibit either of the expected negative relationships between evenness and NIS richness and between evenness and numbers of NIS individuals, while at least one of the relationships was significant for electro-fishes and fyke-fishes (with and without inclusion of schooling fishes) (E-; all $p<0.05$).

Overall, fishes and vegetation were the only taxonomic groups that exhibited the expected significant negative trend between evenness and NIS richness (E- for fyke fishes including schooling taxa, vegetation) and between evenness and number of NIS individuals (E- for nonschooling fyke-fishes, all

electro-fishes, vegetation). Differences in the relationships were shown when considering sampling technique and whether schooling taxa were included or excluded for fishes. Relationships were weaker for electro-fish analyses as compared to fyke-fish analyses and when schooling taxa were excluded from fish analyses. Diatoms, the most species-rich taxonomic group, did not show the expected negative trends between evenness and total richness and between evenness and NS richness. In fact, this taxonomic group exhibited positive (although nonsignificant) relationships between the variables likely due to the high number of species and individuals collected for this group.

iii) Comparison of native and nonindigenous species dominance

Table 3.5 lists the proportions of the most dominant NS and NIS in terms of relative abundance and frequency of occurrence at sites. Across taxonomic groups, ANOVA results showed that NIS generally do not dominate sites either in terms of frequency among sites or relative abundance within sites as compared to NS. *Typha angustifolia* L. was the only NIS that was found to be dominant (both abundant and widespread).

Only a single NIS electro-fish and 2 NIS vegetation taxa were identified as abundant (top 5% of species with the highest proportion of total individuals collected at a site) at invaded sites (*Carassius auratus,* goldfish; *Typha angustifolia* L., *Urtica dioica* L.). No NIS from the other taxonomic groups were abundant. Mean relative abundance curves (not shown) showed that a number of species are abundant at invaded sites that are not NIS: 4 bird NS (of a total of 67 species) had higher relative abundances than *Passer domesticus* (the most abundant bird NIS); 60 diatom NS (of a total of 383 species) were more abundant than *Cyclotella atomus* (the most abundant diatom NIS); 2 electro-fish NS (of a total of 75 species) are more abundant than *Carassius auratus* (the most abundant electro-fish NIS); 15 NS (of a total of 95 species) have higher relative abundances than *C. auratus* (the most abundant fyke-fish NIS); 8 NS (of a total of 303 species) have higher relative abundances than *Typha. angustifolia* L. (the most abundant vegetation NIS). When schooling taxa were excluded from analyses, *C. auratus* (an NIS), was the most abundant species (of a total of 71

species) in electro-fish samples and 11 fyke-fish NS (of a total of 92 species) were more abundant than *C. auratus* (the most abundant NIS). Specific diatom and vegetation species did not tend to dominate invaded sites – no species made up more than 15% of all the individuals (diatoms) or number of observations (vegetation) at a site. A number of diatom and vegetation NS are more abundant at invaded sites than NIS. In contrast, electro-fish and fyke-fish mean relative abundance curves showed that a number of species were abundant at invaded sites, and many fyke-fish NS were more abundant at invaded sites than fyke-fish NIS.

Assessment of probabilities of NIS relative abundances showed that no NIS from any taxonomic group was ranked disproportionately higher than it should be. The probability that the most abundant NIS was given its rank or a higher rank by chance was low.

Only 1 NIS electro-fish and 1 NIS vegetation were identified as widespread (top 5% of species with the highest frequency of occurrence among sites) at invaded sites (*Cyprinus carpio*, common carp; *Typha angustifolia* L.). Site frequency curves for taxonomic groups (not shown) showed that a number of NS were more widespread across the Great Lakes than NIS: 32 bird NS (of a total of 117 species) had higher site frequency than *Sternus vulgaris* (the most widespread bird NIS); 49 diatom NS (of a total of 747 species) had higher site frequency than *C. atomus* (the most widespread diatom NIS); 3 electro-fishes NS (of a total of 75 species) had higher site frequency than *Cyprinus carpio* (the most dominant electro-fish NIS with and without schooling taxa); 11 fyke-fishes NS (of a total of 102 species) had higher site frequency than *C. carpio* (the most dominant fyke-fish NIS with and without schooling taxa); 9 vegetation NS (of a total of 303 species) had higher site frequency than *T. angustifolia* (the most widespread vegetation NIS). These trends may be a function of time since invasion.

DISCUSSION

Overall, trends in distribution of NS and NIS were specific to each Great Lakes taxonomic group in terms of proportion of invaded and uninvaded sites, richness, and evenness at the various scales examined in this study (Fig. 3.1). Fishes and vegetation have invaded the greatest proportions of sites compared to other taxonomic groups. This is likely due to their higher dispersal potential and/or mobility, although birds, arguably the most mobile taxonomic group, did not follow these trends. Birds had low NIS richness and less opportunity for human-mediated introductions compared to fishes and vegetation. Diatoms and vegetation were the richest taxonomic groups and this may reflect a higher sensitivity to environmental gradients of these immobile taxa. These differences in trends among taxonomic groups illustrate that biota of the Great Lakes coastal margin are each regulated by different factors. Further studies that investigate these differences are necessary for understanding biodiversity trends and potential impacts that anthropogenic activities will have on these trends.

Table 3.6 summarizes the possible hypotheses that characterize invaded sites in terms of richness, evenness, and dominance of NIS described in Table 3.1, and support for hypotheses from this study.

Community richness and invasibility (R+ and R-)

There was no significant relationship between NS and NIS richness at any of the spatial scales across taxonomic groups except for positive relationships detected for diatom ECO-S sites and fyke-fish sites at the Basin, protected wetland, and 100-999 ha scales (all R+). This likely reflects the higher proportion of Lake Erie and Lake Ontario sites in diatom ECO-S sites and fyke-fish protected wetland sites. Lakes Erie and Ontario are subject to high propagule pressure of NIS due to shipping and recreational boating activities and may provide better environmental conditions for incoming mesothermic NIS than the other Great Lakes (Vanderploeg *et al.,* 2002, Grigorovich *et al.,* 2003). Fyke-fish sites that covered 100-999 ha made up 53% of all sites sampled. Expectations that support either R+ or R- hypotheses were not met even when various spatial scales (i.e., area and numbers of individuals) were considered, suggesting that biotic interactions (R-), facilitation (R+), and/or the presence of generally suitable

habitat with high resource availability (R+) are not strong regulatory factors in the distribution of Great Lakes NIS (Table 3.6). Bird, diatom, and fyke-fish NIS contributed materially to total richness, since ANOVA results indicated that there was significantly higher total richness at invaded sites than uninvaded sites, while there were no significant differences in bird, diatom, and fyke-fish NS richness between invaded and uninvaded sites at the Holm corrected level. This lends further support for the hypothesis that there is no relationship between NS richness and NIS richness (RN; Table 3.6).

Native species distribution was constrained by Lake and HGM. Richness trends for NS were specific to the taxonomic group and likely reflect differing dispersal histories, mobility, and habitat suitability. NIS richness was best predicted by Lake across taxonomic groups, except for birds. Birds did not show any significant biogeographic differences in NIS richness at any scale. These findings support the idea that apparent trends between NS and NIS richness are more likely due to higher propagule pressure and/or better environmental suitability at ECO-S, Lake Erie, and Lake Ontario sites. However, Lake Superior receives a disproportionate number of visits by transoceanic ballasted and NOBOB vessels (ships with no-ballast-on-board status) compared to other ports of the Great Lakes (Colautti 2001). In general, Lake Superior supports few NIS (Grigorovich *et al.,* 2003). Lakes Erie and Ontario may provide better environmental conditions for mesothermic NIS entering the basin than the other Great Lakes (Vanderploeg *et al.,* 2002, Grigorovich *et al.,* 2003), giving precedence to environmental suitability as the main regulating factor in NS and NIS richness trends of the lower Great Lakes. The patterns that I observed are not consistent with studies that have proposed that species-rich communities either offer fewer vacant niches (niche complementarity effect of NS richness; R-) or a greater probability that an invader will be competitively excluded by a superior competitor (sampling effect of NS richness; R-) (Tilman, 1999; Wardle, 2001, Fargione and Tilman, 2005).

ECO-N and Lake Superior had the lowest proportion of invaded sites across taxonomic groups, except for fyke-fishes and nonschooling fyke-fishes, for

which the proportion of invaded sites was lowest in Lake Ontario. As discussed, this is likely due to the high proportion of Lake Ontario sites being made up of protected-wetland sites. Lake Erie had the highest proportion of invaded sites for all taxonomic groups, except for birds. Overall, few sites were invaded by birds across scales (less than 25% of sites were invaded at all scales), likely reflecting the low NIS richness and absence of human-mediated propagule pressure of this group.

Community evenness and invasibility (E+ and E-)

Low community evenness did not characterize invaded sites in my study. There was no significant difference in evenness between invaded and uninvaded sites at any scale, for any taxonomic group. Results did not support either hypothesis of high or low evenness at invaded sites (EN; Table 3.6), and this suggests that NIS as a general rule do not tend to dominate and influence the evenness of communities (Wilsey and Polley, 2002; Tracy and Sanderson, 2004. Instead, invasion is more likely due to incomplete use of resources by NS (Wilsey and Polley, 2002; Tracy and Sanderson, 2004) or facilitation among established species (Levine 1976; Case, 1991; Simberloff and Von Holle, 1999; Ricciardi, 2001). My results do not corroborate the E- findings from plant studies that have shown negative relationships between community evenness and invasibility (Wilsey and Polley, 2002; Tracy and Sanderson, 2004; Tracy *et al.,* 2004), which was thought to be due to more efficient use of available resources by resident plants in even communities. Wilsey and Polley (2002) found a negative relationship between evenness and number of invading dicot species, but decreasing evenness had a negligible effect on number of invading monocot species. They associated these different responses to differences in frequency of invasion events (dicots invaded continuously while monocots invaded in pulses), by some functional difference between grasses and dicots, or because of insufficient statistical power in the grass analyses.

Although studies have shown variable influences of community evenness on susceptibility of a site to invasibility during the pre-establishment phase, my study found that NIS did not influence the evenness of a community after

successful invasion events given that there is no difference between community evenness of invaded and uninvaded sites. This is further supported by the finding that there were no significant differences between evenness measures that included only NS and those that included both NS and NIS, for any taxonomic group. Conditions faced by the presently established NIS when first entering new habitats are likely similar to conditions faced by new propagules (of either NS or NIS identity) entering habitats, unless they are part of a successional series. Site evenness is not likely to be a determinant of invasion success for a new propagule. Following their findings that event-level variables, such as propagule pressure, were better predictors of introduced bird establishment success than location-level or species-level variables, Cassey *et al*. (2005) suggested that features of the environment and species interact to determine establishment success. This environment interaction may explain the distribution of NS and NIS of the Great Lakes and warrants further study, pending availability of pertinent data.

The finding that NS and NIS richness trends do not mirror each other among taxonomic groups fails to support the idea that species-rich sites get richer (R+ and E+; Stohlgren *et al.,* 2006). A closer examination of sites that were surveyed for more than one taxonomic group indicated that a site that had the highest richness for one group did not have especially high richness of other taxonomic groups (data not shown).

Bird sites across the Great Lakes tended to be relatively even (mean E = 0.67) when compared to the evenness of communities of other taxonomic groups (all < 0.60). There was no significant difference in mean evenness across scales of sampling (i.e., ecoprovince, lake, HGM) for any taxonomic group, except that higher evenness occurred at ECO-N than at ECO-S bird sites, and higher evenness was observed at Lake Huron than at Lake Erie electro-fish sites. There were significant negative relationships between evenness and NS richness and numbers of native individuals across most taxonomic groups, as expected, although these trends were not mirrored by total richness of diatoms and native richness of diatoms and nonschooling electro-fishes. The nonschooling electro-

fish result showed a slightly negative trend, following expectations, but diatom results showed positive trends. Diatoms were the most diverse group in this study (total species=117; Table 3.1) and also occurred at the highest abundances. Richness and abundance data fell within a narrow range, likely reflecting the passive dispersal of diatoms, which may explain the positive trends with evenness.

Species dominance/identity and invasibility (D+ and D-)

Although some species have a higher propensity to dominate sites than others, no single species made up more than 50% of the total number of individuals recorded at a site. Species collected that occurred at >50% of all sites sampled were made up by only 4, 3, 15, 10, and 2% of the all bird, diatom, electro-fish, fyke-fish, and vegetation species, respectively (none of these taxa were NIS). Across all taxonomic groups, *Typha angustifolia* L. was the only NIS that dominated sites both in terms of frequency among sites and relative abundance within sites. As a general rule, dominance of NIS did not explain their distribution. My study provides evidence that NS remain abundant in the presence of NIS, and this trend is corroborated by community evenness data, suggesting that biotic interactions possibly play only a limited role in determining community composition in Great Lakes biota at the scales examined. My findings contradict studies that suggest that invasibility is regulated by the identity of the dominant NS within low-evenness communities (Crawley *et al.,* 1999, Smith and Knapp 1999, van Ruijven *et al.,* 2003, Smith *et al.,* 2004) given that evenness of invaded sites did not differ from evenness at uninvaded sites, NIS were not constrained to uneven communities (E- hypotheses were not supported; Table 3.6), and NIS did not tend to be site dominants (D+ hypotheses were not supported; Table 3.6) at Great Lakes coastal margins. Limiting similarity theory predicts that successful invaders should differ functionally from species already present in the community, and studies that specifically test whether successful invaders are functionally dissimilar from community dominants have shown mixed results (e.g. Naeem *et al.,* 2000; Dukes, 2001; Dukes, 2002; Prieur-Richard *et al.,* 2002; Pokorny *et al.,* 2005; Emery, 2007). If NIS dominance is a major regulatory

factor that explains NIS distributions, more Great Lakes communities would be dominated by NIS. Alternatively, invaded sites may be in a transition where the competitive dominance of NIS has not had time to be expressed because it has not reached its density threshold.

Given that evenness measures are not influenced by the incorporation of NIS data and are influenced primarily by NS richness and individuals, changes in evenness are likely due to changes in dominance of NS rather than NIS. These results are corroborated by dominance trends of NS and NIS.

Aside from the single example of high dominance by a vegetation NIS, *Typha angustifolia* L., results overwhelmingly do not support the hypothesis that biotic interaction based processes explain the distribution of Great Lakes NIS. This study does not specifically examine the influence of propagule pressure and dispersal on invasion events since the data needed to explicitly assess levels of propagule pressure and dispersal rates are beyond the scope of this study. However, my evaluation of Great Lakes NS and NIS richness, eveness, and dominance trends demonstrated null relationships, suggesting propagule pressure and suitable habitat may be factors that regulate their distributions. Memmott *et al*. (2005) conducted field experiments in New Zealand that manipulated the propagule size (i.e., the number of propagules) of a psyllid phloem feeder, *Arytainilla spartiophila*, native to Europe and followed the released individuals for six years after the initial release. The probability of establishment was significantly and positively related to propagule size during the first year; however, populations surviving after the initial year were not significantly related to the initial propagule size. They also found that some populations with small propagule sizes established successfully, although they were less likely to survive initially. Small propagule sizes may have a higher probability of establishment than assumed so invasion events with small propagule sizes and high propagule number (i.e., repeated invasion events) may have a high probability of success as compared to single large introduction events (Lockwood *et al*., 2007). It is clear from my study and others (Beirne, 1975; Veltman *et al.*, 1996; Duncan, 1997; Green, 1997; Cassey *et al.,* 2005;

Memmott *et al*., 2005) that propagule pressure has a significant and positive effect on establishment success in many systems.

In general, trends in NIS distributions were unrelated to NS distributions, de-emphasizing the role biotic interactions play in determining community composition in Great Lakes biota at the scales examined. Trends demonstrate null relationships with richness, evenness, and NIS dominance (RN, EN, DN; Table 3.6). These findings do not demonstrate neutral-interaction processes, manifested through availability of adequate propagule pressure (Simberloff, 1989; Williamson; 1996; Hubbell, 2001Lockwood, 2005; VonHolle and Simberloff, 2005) and suitable habitats (Baltz and Moyle, 1993; Moyle and Light, 1996), but are consistent with expectations of regulation by these processes. This assertion is tentative since data on failed invasions and propagule pressure are absent, aside from those resulting from biocontrol and game introductions.

Davis *et al.* (2005) proposed that invasibility is a dynamic property of communities and that invasibility of a community, along with regional processes, determines its diversity (not *vice versa* as has been the customary focus). Invasibility is a composite of local biological and physical processes that is measurable and is influenced by availability of resources (Davis *et al.,* 2005). This view is different from other approaches that have examined competition, facilitation, environmental variables, predation, and propagule pressure independently of one another and warrants further study. Examination of the requirements of a potential invader/disperser and the characteristics of the recipient community and resources that allow species-specific invasion are required.

CONCLUSIONS

Overall, I found that in Great Lakes coastal margin habitats, NS richness is statistically independent of, and thus apparently does not influence, NIS richness, even when potential sampling artifacts are taken into account by examining the relationship at various spatial scales of spatial area and with various numbers of

individuals collected. Richness trends for NS and NIS differ by spatial scale, and initially might suggest that different processes influence NS and NIS distributions. The distribution of NIS is lake-specific, likely reflecting habitat suitability and/or propagule pressure, while NS distribution varies among classes of HGM and reflects dispersal history and habitat suitability. However, both dispersal history and propagule pressure can be regarded as similar processes in that they both determine the arrival of an individual into a new habitat and the likelihood that it will encounter the conspecifics necessary for successful reproduction. The findings that NIS do not influence the evenness of invaded sites, are not constrained to uneven sites, and do not tend to be the dominant species at sites, either in terms of relative abundance within sites or frequency among sites, corroborate the claim that similar factors regulate NS and NIS distributions.

My study demonstrated null relationships of NS and NIS richness, evenness, and dominance. This finding suggests that suitable conditions, comprised of sufficient dispersal/propagule pressure and suitable habitat, that allow an individual of a species to persist and contribute to the establishment of a population, may be determinants of invasion success. Regulation of successful invasions by interaction-neutral processes cannot be tested given that data on failed introductions, dispersal and/or propagule pressure, and distributions of species specific suitable habitat, are unavailable and largely nonexistent. This is a general problem for invasion studies.

Geographic distributions of NS and NIS suggest that the same conditions of necessity pertain to both NS and NIS. Constraints to NIS establishment and dispersal are not unlike the conditions that are needed for the dispersal of NS, although constraints to NIS are often considered different from those of NS. The utility of various taxonomic groups for use as environmental indicators has been demonstrated by GLEI collaborators (Brazner *et al.,* 2007; Howe *et al.,* 2007; Johnston *et al.,* 2007; Reavie *et al.,* 2007). This illustrates the strong influence of environmental factors in regulating the distribution of biota. Further work examining long-term dispersal and distribution trends of NIS and parallels with

NS would be valuable for further elucidating the applicability of universally suitable environmental conditions.

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Table 3.1: Predicted characteristics of invaded sites and NIS in terms of richness, evenness, and dominance; Hypothesis classes relate to richness (R), evenness (E), and relative dominance (D); NIS relationships with R, E, and D may be negative (-), positive (+), or nonsignificant (N); independent (ind) and dependent (dep) variables are identified under expectations for each relationship.

Hypothesis Class	Parameter	Hypothesis	Expectation
R-	Richness (Low)	Biotic interactions (e.g., competition, predation, mutualisms) structure communities and determine success of NIS[1]	NS richness (ind) is negatively associated with NIS richness(dep); invaded sites (ind) have significantly lower richness (dep) than uninvaded sites (ind)
R+	Richness (High)	'The rich get richer'[2]: biotic interactions are a weak force in invasions[2,3]; generally suitable environmental conditions present with high resource availability[3]; facilitation by resident species[4]	NS richness (ind) positively associated with NIS richness (dep); invaded sites (ind) have significantly higher richness (dep) than uninvaded sites (ind)

Hypothesis Class	Parameter	Hypothesis	Expectation
RN	Richness (Neutral)	Suitable habitat and propagule pressure determines invasion[5]	No relationship between NIS (dep) and NS (ind) richness; no difference between richness (dep) at invaded and uninvaded sites (ind)
E-	Evenness (Low)	Invasion determined by dominance (i.e., ability to become widespread and/or abundant) of NIS relative to dominant NS[6]; unused resources available to NIS	Invaded sites (ind) have significantly lower evenness (dep) than uninvaded sites (ind); negative relationship between NIS richness (ind) and evenness (dep)
E+	Evenness (High)	Facilitation by resident species[4] and/or incomplete resource use among NIS and NS and suitable habitat[6]	Invaded sites (ind) have significantly higher evenness (dep) than uninvaded sites (ind)
EN	Evenness (Neutral)	Dominance not related to invasion; suitable habitat and propagule pressure determines invasion[5]	No difference between evenness (dep) at invaded and invaded sites (ind)

Hypothesis Class	Parameter	Hypothesis	Expectation
D-	NIS Dominance (Low)	NIS able to invade due to processes unrelated to competitive ability	NIS (ind) are not more widespread and/or abundant (dep) than NS (ind)
D+	NIS Dominance (High)	NIS able to invade due to high competitive ability and complete use of resources[7]	NIS (ind) are widespread and/or abundant (dep) than NS (ind)
DN	NIS Dominance (Neutral)	Suitable habitat and propagule pressure determines invasion[5]	NIS (ind) abundance (dep) and frequency among sites (dep) nonsignificant

[1] Elton, 1958; MacArthur, 1970; Fox and Fox, 1986; Pimm, 1991; Rejmanek, 1996; Lonsdale, 1999

[2] Stohlgren *et al.,* 2006

[3] Huston, 1994; McCann *et al.,* 1998

[4]Levine 1976; Case, 1991; Simberloff and Von Holle, 1999; Ricciardi, 2001

[5]Simberloff, 1989; Williamson, 1996; Hubbell, 2001; Lockwood, 2005; VonHolle and Simberloff, 2005

[6]Wilsey and Polley, 2002; Tracy and Sanderson, 2004

[7]Tilman 1982; Crawley *et al.,* 1999; Smith and Knapp 1999; Robinson *et al.,* 1995; van Ruijven *et al.,* 2003; Smith *et al.,* 2004; Emery and Gross, 2007

Table 3.2: Summary of significance of regression analyses of the relationship between native species (NS) and nonindigenous species (NIS) of various taxonomic groups of the Great Lakes across spatial scales and sample sizes. Scale at which the relationship is positively significant is specified and the corresponding p value is given; nonsignificant differences are designated with 'ns'.

Taxonomic group	n	#NIS	#NS	Basin	Ecoprovince	Lake	HGM	Area (ha)	# Individuals
Bird	227	5	112	ns (n=227)	ns (n_{212}=129, n_{222}=98)	ns (n_S=45, n_M=74, n_H=47, n_E=23, n_O=38)	ns (n_{CW}=69, n_{RW}=73, n_{PW}=85)	ns	ns
Diatom	113	4	743	ns (n=113)	222, p<0.005 (n_{212}=57, n_{222}=56)	ns (n_S=20, n_M=33, n_H=25, n_E=20, n_O=15)	ns (n_{CW}=27, n_{RW}=30, n_{PW}=22, n_{HE}=19, n_{EB}=15)	ns	ns
Electrofish	58	9	66	ns (n=58)	ns (n_{212}=32, n_{222}=26)	ns (n_S=17, n_M=17, n_H=6, n_E=6, n_O=12)	ns (n_{RW}=29, n_{PW}=29)	ns	ns

Taxonomic group	n	#NIS	#NS	Basin	Ecoprovince	Lake	HGM	Area (ha)	# Individuals
Fyke fish	139	14	88	$p<0.005$ (n=139)	ns (n_{212}=80, n_{222}=59)	ns (n_S=32, n_M=39, n_H=27, n_E=20, n_O=21)	PW $p<0.005$ (n_{CW}=27, n_{RW}=30, n_{PW}=24, n_{HE}=39, n_{EB}=19)	100-999 $p<0.05$ n=42	ns
Vegetation	40	24	279	ns (n=40)	ns (n_{212}=25, n_{222}=15)	ns (n_S=11, n_M=12, n_H=7, n_E=4, n_O=6)	ns (n_{CW}=12, n_{RW}=15, n_{PW}=13)	ns	ns

Table 3.3: Native species (NS) and nonindigenous species (NIS) richness trends across taxonomic groups and geographic scales. Significant differences in NS and NIS richness for a particular taxonomic group at a particular scale are given by p-values; nonsignificant differences are designated with 'ns'.

Taxonomic group	NS			NIS		
	Ecoprovince	Lake	HGM	Ecoprovince	Lake	HGM
Bird	ns	$p_{OvsS}<0.005$, $p_{OvsM}<0.00005$, $p_{OvsH}<0.005$, $p_{OvsE}<0.0001$, $p_{SvsM}<0.05$	$p_{PWvsCW}<0.05$, $p_{PWvsRW}<0.05$	ns	ns	ns
Diatom	$p<0.001$	$p_{SvsM}<0.05$, $p_{SvsH}<0.005$, $p_{SvsE}<0.05$	$p_{HEvsRW}<0.005$, $p_{HEvsCW}<0.01$, $p_{HEvsEB}<0.005$	$p<0.00005$	$p_{EvsS}<0.00005$, $p_{EvsM}<0.00005$, $p_{EvsH}<0.000005$, $p_{EvsO}<0.001$	ns
Electro-fish	ns	ns	$p_{PWvsRW}<0.05$	$p<0.005$	$p_{EvsS}<0.00005$, $p_{EvsM}<0.0005$, $p_{EvsH}<0.05$, $p_{EvsO}<0.005$	ns
Nonschooling Electro-fish	ns	ns	$p_{PWvsRW}<0.05$	$p<0.005$	$p_{EvsS}<0.000005$, $p_{EvsM}<0.00005$, $p_{EvsH}<0.005$, $p_{EvsO}<0.0005$	ns

Taxonomic grou	NS			NIS		
	Ecoprovince	Lake	HGM	Ecoprovince	Lake	HGM
Fyke-fish	ns	$p_{MvsE}<0.05$, $p_{MvsO}<0.05$	$p_{HEvsPW}<0.0001$, $p_{HEvsRW}<0.000005$, $p_{HEvsCW}<0.000005$, $p_{HEvsEB}<0.005$, $p_{EBvsCW}<0.05$	$p<0.05$	$p_{EvsS}<0.00005$, $p_{EvsM}<0.05$, $p_{EvsH}<0.05$, $p_{EvsO}<0.000005$, $p_{OvsS}<0.05$, $p_{OvsM}<0.005$, $p_{OvsH}<0.005$	$p_{CWvsHE}<0.05$ $p_{CWvsPW}<0.05$ $p_{CWvsRW}<0.005$
Nonschooling Fyke-fish	ns	$p_{MvsE}<0.05$	$p_{HEvsPW}<0.00005$, $p_{HEvsRW}<0.000005$, $p_{HEvsCW}<0.000005$, $p_{HEvsEB}<0.005$	$p<0.05$	$p_{EvsS}<0.0005$, $p_{EvsM}<0.0005$, $p_{EvsH}<0.05$, $p_{EvsO}<0.000005$ $p_{OvsS}<0.05$, $p_{OvsM}<0.05$, $p_{OvsH}<0.005$	$p_{CWvsHE}<0.05$ $p_{CWvsRW}<0.05$
Vegetation	$p<0.01$	ns	ns	ns	$p_{SvsM}<0.005$, $p_{SvsH}<0.001$, $p_{SvsE}<0.05$, $p_{SvsO}<0.00005$ $p_{EvsO}<0.05$	$p_{PWvsRW}<0.05$, $p_{PWvsCW}<0.05$ (incl. Lake Superior sites)

Table 3.4: Summary of significance of regression analyses of the relationships between evenness and measures of richness (R) and between evenness and numbers of individuals. The p-value (p), coefficient of determination (r^2), slope (m), and standard error of estimation (SE) significant relationships are given; nonsignificant relationships are denoted with 'ns'.

Taxonomic group	Total R	Total #Individuals	Native R	Native #Individuals	NIS R	NIS #Individuals
Bird n=227	p<0.005, r^2=0.04 m=-0.01 SE=0.18	p<0.005, r^2=0.51 m=-0.01 SE=0.13	p<0.005, r^2=0.04 m=-0.01 SE=0.18	p<0.005, r^2=0.51 m=-0.01 SE=0.12	ns	ns
Diatom n=113	ns	p<0.00005, r^2=0.15 m=-0.0006 SE=0.08	ns	p<0.00005, r^2=0.15 m=-0.0005 SE=0.08	ns	ns
Electro-fish n=58	p<0.005, r^2=0.17 m=-0.02 SE=0.12	p<0.0005, r^2=0.20 m=-0.001 SE=0.12	p<0.005, r^2=0.14 m=-0.01 SE=0.12	p<0.005, r^2=0.15 m=-0.002 SE=0.12	ns	p<0.05 (outlier excluded), r^2=0.07 m=-0.01 SE=0.12
Nonschooling Electro-fish n=58	p<0.05, r^2=0.08 m=-0.01 SE=0.14	p<0.001, r^2=0.18 m=-0.006 SE=0.13	ns	p<0.01, r^2=0.12 m=-0.01 SE=0.13	ns	p<0.05, r^2=0.08 m=-0.004 SE=0.14
Fyke-fish n=139	p<0.0000005, r^2=0.17 m=-0.01 SE=0.13	p<0.001, r^2=0.08 m=-0.0001 SE=0.14	p<0.000005, r^2=0.15 m=-0.01 SE=0.13	p<0.005, r^2=0.07 m=-0.0001 SE=0.14	p<0.01, r^2=0.05 m=-0.02 SE=0.14	ns
Nonschooling Fyke-fish n=139	p<0.000005, r^2=0.15 m=-0.01 SE=0.13	p<0.005, r^2=0.08 m=-0.0001 SE=0.14	p<0.000005, r^2=0.16 m=-0.01 SE=0.13	p<0.005, r^2=0.07 m=-0.0001 SE=0.14	ns	p<0.05 (outlier excluded), r^2=0.04 m=-0.001 SE=0.14
Vegetation n=40	p<0.05, r^2=0.15 m=-0.0031 SE=0.10	p<0.0005, r^2=0.31 m=-0.0006 SE=0.09	p<0.05, r^2=0.11 m=-0.003 SE=0.11	p<0.001, r^2=0.27 m=-0.0006 SE=0.10	p<0.05, r^2=0.15 m=-0.02 SE=0.10	p<0.05, r^2=0.10 m=-0.003 SE=0.11

Table 3.5: Proportions of the 3 most dominant NS and NIS in terms of relative abundance (at invaded sites) and site frequency. Superscripts highlight top 3 most abundant and widespread taxa.				
Taxonomic group	Abundant NS (% of individuals)	Abundant NIS (% of individuals)	Widespread NS (% of sites)	Widespread NIS (% of sites)
Bird	[1]*Agelaius phoeniceus,* red-winged blackbird (29), [2]*Larus argentatus,* herring gull (22), [3]*Cistothorus platensis,* sedge wren (19)	*Passer domesticus,* house sparrow (16), *Sturnus vulgaris,* European starling (16), *Cygnus olor,* Mute swan (14)	[1]*Agelaius phoeniceus*, red-winged blackbird (90), [2]*Geothlypis trichas*, common yellowthroat (80), [3]*Melospiza melodia*, song sparrow(76)	*Sturnus vulgaris*, European starling (8), *Carpodacus mexicanus*, house finch (3), *Cygnus olor*, Mute swan (3)

Diatom	[1]*Hippodonta smalla* (10), [2]*Hippodonta costulata* (9) [3]*Geissleria decussis* (9)	*Cyclotella atomus* (2), *Skeletonema potamos* (1), *Cyclotella cryptica* (1)	[1]*Staurosirella pinnata* (98), [2]*Amphora pediculus* (93), [3]*Achnanthidium minutissimum* (92)	*Cyclotella atomus* (27), *Thalassiosira pseudonana* (6), *Cyclotella cryptica* (4), *Skeletonema potamos* (4)
Electro-fish	[1]*Dorosoma cepedianum*, gizzard shad (26), [2]*Perca flavescens*, yellow perch (19), *Notropis spilopterus*, spotfin shiner (14)	[3]*Carassius auratus*, goldfish (17) *Alosa pseudoharengus*, alewife (11), *Cyprinus carpio*, common carp (7)	[1]*Perca flavescens*, yellow perch (85), [2]*Lepomis gibbosus*, pumpkinseed sunfish (79), [3]*Notemigonus crysoleucas*, golden shiner (72)	*Cyprinus carpio*, common carp (71), *Alosa pseudoharengus*, alewife (26), *Carassius auratus*, goldfish (16)

Nonschooling Electro-fish	[2]*Perca flavescens*, yellow perch (21), [3]*Notropis spilopterus*, spotfin shiner (14), *Pimephales notatus*, bluntnose minnow (13)	[1]*Carassius auratus*, goldfish (22), *Cyprinus carpio*, common carp (12), *Lepomis microlophus*, redear sunfish (5)	[1]*Perca flavescens*, yellow perch (84), [2]*Lepomis gibbosus*, pumpkinseed sunfish (79), [3]*Notemigonus crysoleucas*, golden shiner (72)	*Cyprinus carpio*, common carp (71), *Carassius auratus*, goldfish (16), *Neogobius melanostomus,* round goby (12)

Fyke-fish	[1]*Semotilus atromaculatus*, creek chub (38), [2]*Notropis heterodon*, blackchin shiner (32) [3]*Notropis hudsonius*, spottail shiner (26)	*Carassius auratus*, goldfish (10), *Neogobius melanostomus*, round goby (9), *Alosa pseudoharengus*, alewife (5)	[1]*Ambloplites rupestris*, Northern rock bass (69), [2]*Lepomis gibbosus*, pumpkinseed sunfish (63), [3]*Perca flavescens*, yellow perch (56)	*Cyprinus carpio*, common carp (30), *Alosa pseudoharengus*, alewife (24), *Morone americana*, white perch (18)
Nonschooling Fyke-Fish	[1]*Semotilus atromaculatus*, creek chub (38), [2]*Notropis heterodon*, blackchin shiner (32) [3]*Notropis hudsonius*, spottail shiner (22)	*Carassius auratus*, goldfish (13), *Neogobius melanostomus*, round goby (10), *Morone americana*, white perch (8)	[1]*Ambloplites rupestris*, Northern rock bass (69), [2]*Lepomis gibbosus*, pumpkinseed sunfish (63), [3]*Perca flavescens*, yellow perch (56)	*Cyprinus carpio*, common carp (30), *Morone americana*, white perch (19), *Neogobius melanostomus,* round goby (18)

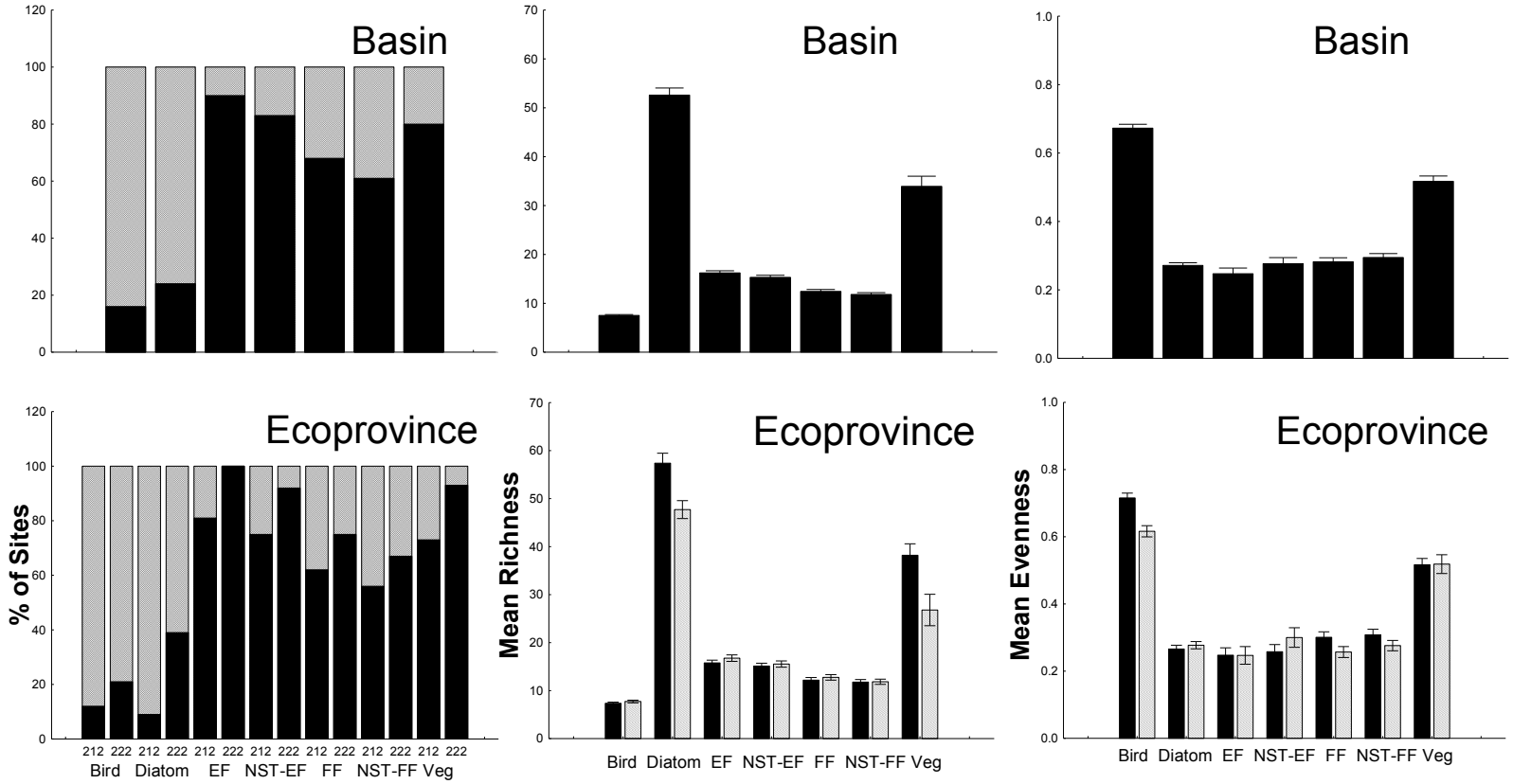
Vegetation	[1]*Brasenia schreberi J.F. Gmel.* (16), [2]*Schoenoplectus pungens* var. *pungens* (Vahl) Palla (11), [3]*Sagittaria latifolia* Willd. (8)	*Typha angustifolia* L. (6), *Urtica dioica* L. (6), *Hydrocharis morsus-ranae* L. (5)	[1]*Cicuta bulbifera* L. (68), [2]*Calamagrostis canadensis* (Michx.) Beauv. (63), [3]*Schoenoplectus tabernaemontani* (K.C. Gmel.) Palla (63)	*Typha angustifolia* L. (48), *Lythrum salicaria L.* (38), *Cirsium arvense (L.) Scop.* (28)

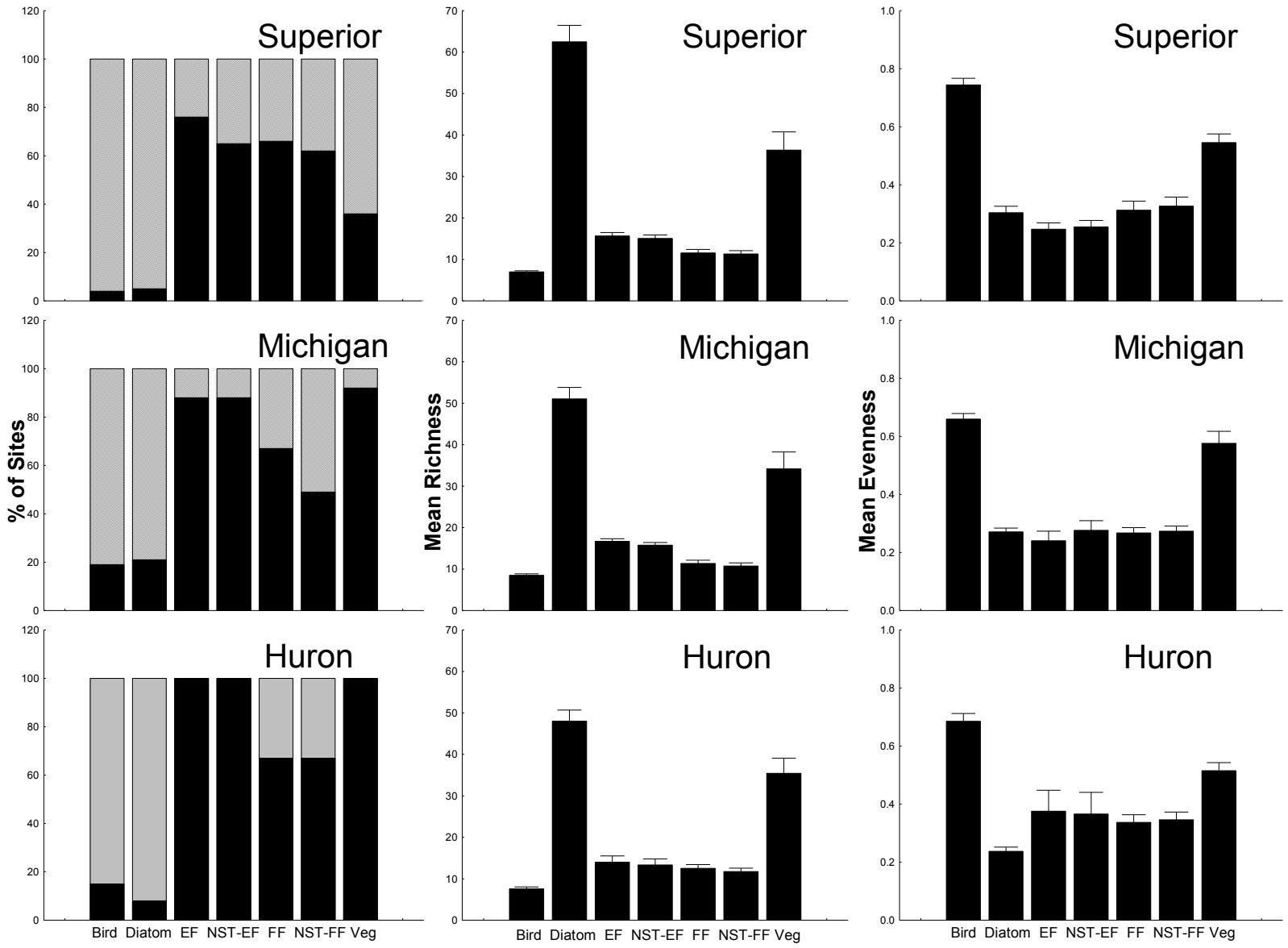
Table 3.6: Summary of support and alternative explanations for predicted characteristics of invaded sites and NIS in terms of richness, evenness, and dominance. Hypothesis classes relate to Richness (R), Evenness (E), and relative Dominance (D); NIS relationships with R, E, and D may be negative (-), positive (+), or nonsignificant (N).

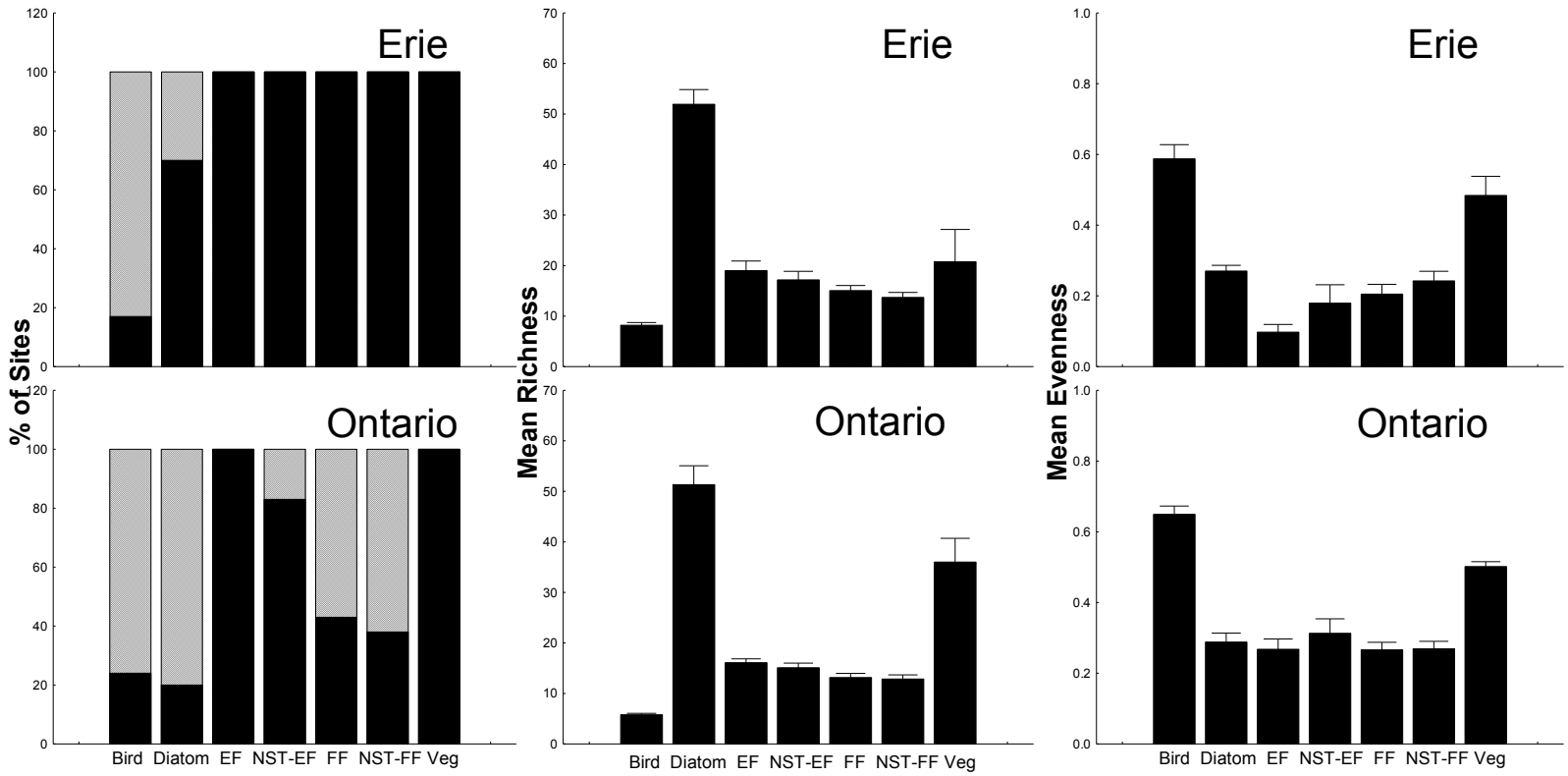
Hypothesis Class	Parameter	Hypothesis	Expectation	Supported?
R-	Richness (Low)	Biotic interactions (e.g., competition, predation, mutualisms) structure communities and determine success of NIS[1]	NS richness is negatively associated with NIS richness; invaded sites have significantly lower richness than uninvaded sites	No
R+	Richness (High)	'The rich get richer'[2]: biotic interactions are a weak force in invasions[2,3]; generally suitable environmental conditions present with high resource availability[3]; facilitation by resident species[4]	NS richness positively associated with NIS richness; invaded sites have significantly higher richness than uninvaded sites	No

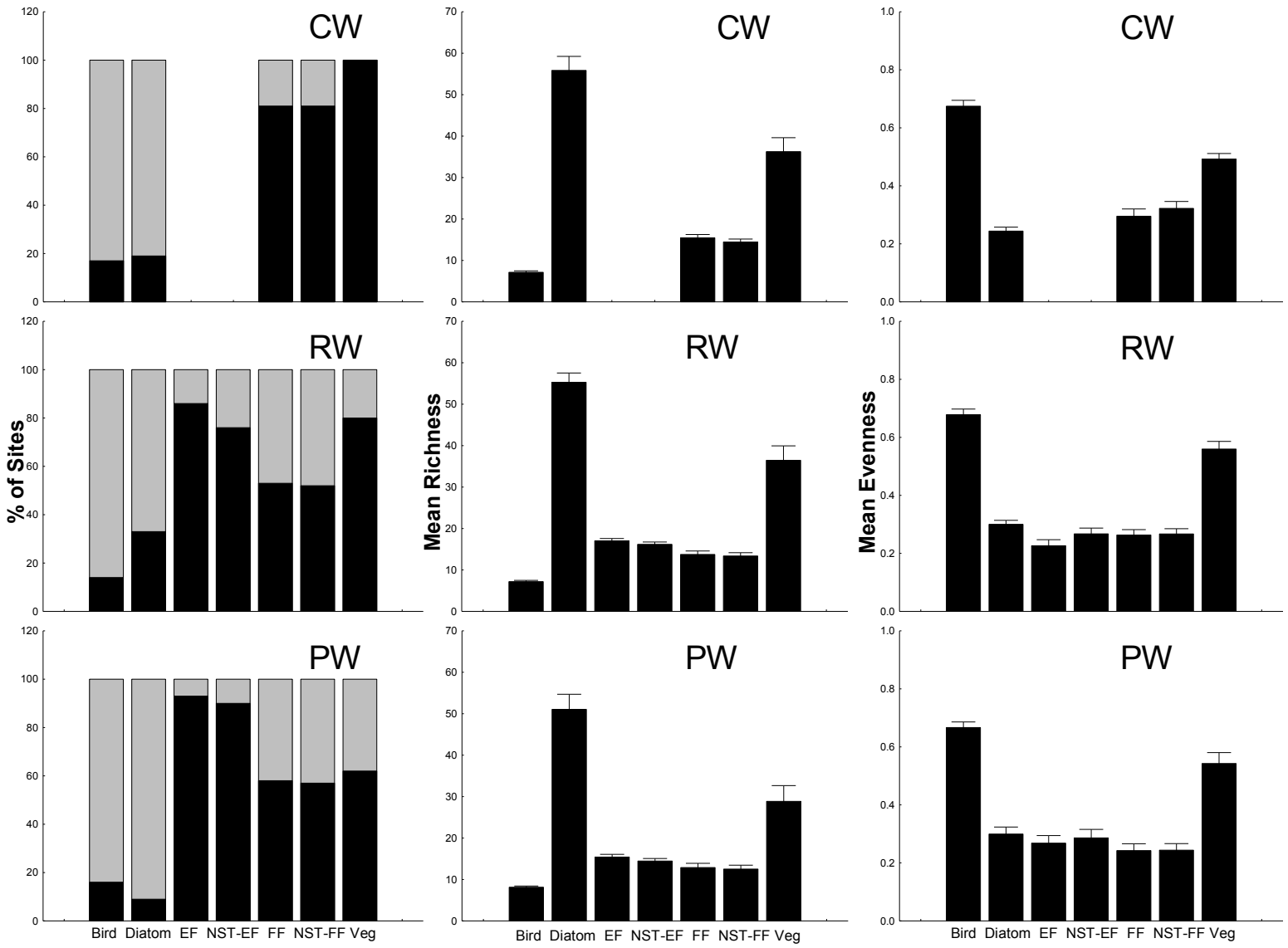
RN	Richness (Neutral)	Suitable habitat and propagule pressure determines invasion[5]	No relationship between NIS and NS richness; no difference between richness at invaded and uninvaded sites	Findings consistent with expectations
E-	Evenness (Low)	Invasion determined by dominance (i.e., ability to become widespread and/or abundant) of NIS relative to dominant NS[6]; unused resources available to NIS	Invaded sites have significantly lower evenness than uninvaded sites; negative relationship between NIS richness and evenness	No
E+	Evenness (High)	Facilitation by resident species[4] and/or incomplete resource use among NIS and NS and suitable habitat[6]	Invaded sites have significantly higher evenness than uninvaded sites	No
EN	Evenness (Neutral)	Dominance not related to invasion; suitable habitat and propagule pressure determines invasion[5]	No difference between evenness at invaded and invaded sites	Findings consistent with expectations

D-	NIS Dominance (Low)	NIS able to invade due to processes unrelated to competitive ability	NIS are not more widespread and/or abundant	No
D+	NIS Dominance (High)	NIS able to invade due to high competitive ability and complete use of resources[7]	NIS are widespread and/or abundant	Yes (for vegetation)
DN	NIS Dominance (Neutral)	Suitable habitat and propagule pressure determines invasion[5]	NIS abundance and frequency among sites nonsignificant	Findings consistent with expectations


Basin
Basin
Basin
Ecoprovince
Ecoprovince
Ecoprovince
% of Sites
Mean Richness
Mean Evenness
212 222 212 222 212 222 212 222 212 222 212 222 212 222
Bird Diatom EF NST-EF FF NST-FF Veg
Bird Diatom EF NST-EF FF NST-FF Veg
Bird Diatom EF NST-EF FF NST-FF Veg


Superior
Michigan
Huron
% of Sites
Mean Richness
Mean Evenness
Bird Diatom EF NST-EF FF NST-FF Veg


Erie
Ontario
% of Sites
Mean Richness
Mean Evenness
Bird Diatom EF NST-EF FF NST-FF Veg


CW
RW
PW
% of Sites
Mean Richness
Mean Evenness
Bird Diatom EF NST-EF FF NST-FF Veg

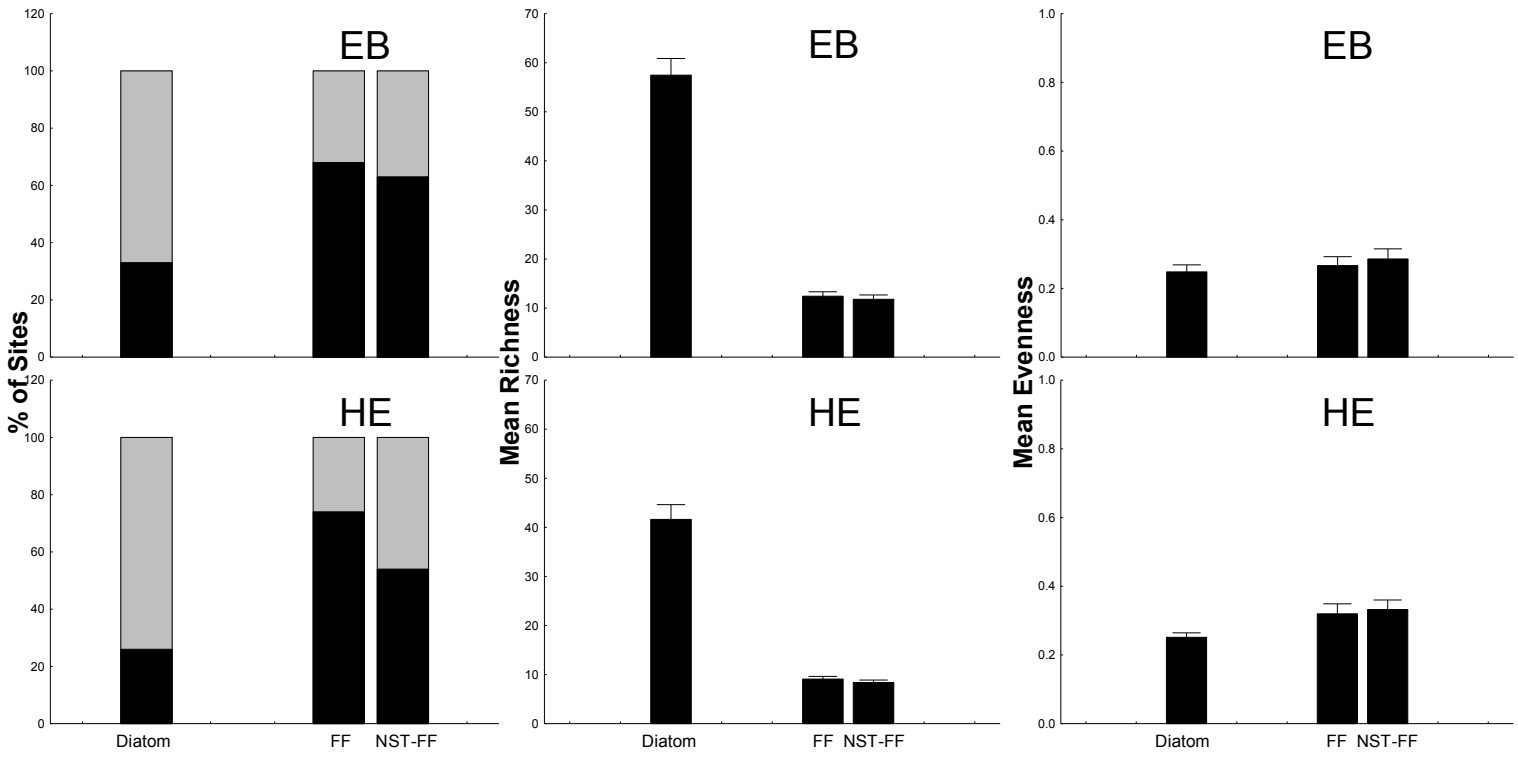


Figure 3.1: Proportion of invaded (dark portion of bar) and uninvaded (hatched portion of bar) sites, mean total richness, and mean evenness at various spatial scales for birds, diatoms, electro-fish (EF), nonschooling electro-fish (NST-EF), fyke-fish (FF), nonschooling fyke-fish (NST-FF), and vegetation (Veg). Ecoprovince comparisons of richness and evenness show ECO-N with dark bars and ECO-S with hatched bars.

Appendix 3.1: List of abbreviations used throughout thesis and their definitions	
Abbreviation	Definition
GLEI	Great Lakes Environmental Indicators
NIS	Nonindigenous species
NS	Native species
ECO-N	Laurentian Mixed Forest (Ecoprovince)
ECO-S	Eastern Broadleaf Forest (Ecoprovince)
S	Lake Superior
M	Lake Michigan
H	Lake Huron
E	Lake Erie
O	Lake Ontario
HGM	Hydrogeomorphic type of site
HE	High-energy
EB	Embayment
CW	Coastal wetland
RW	River-influenced wetland
PW	Protected wetland
R	Richness
E	Evenness
D	Dominance
b_1	Asymptotic species richness
b_2	Growth coefficient
b_1b_2	Rarefaction curve slope
Δ_1	Evenness measure, probability of interspecific encounter (Hurlbert, 1971; equation given in Chapter 4)
SME	Scaled mean error
CV	Coefficient of variation
SMSE	Scaled mean square error

CHAPTER 4: APPLICATION OF AN EVENNESS MEASURE AS AN ESTIMATE OF RICHNESS FROM SYNOPTIC SAMPLES

INTRODUCTION

Impending global climate change and human-mediated habitat alterations require accurate extrapolative and forecasting techniques, and this highlights the importance and urgency of the task of evaluating biodiversity (Colwell and Coddington, 1994). Species richness (the number of species in a community), its variation over time and space, and testing hypotheses about factors that are potentially associated with species richness variation, are a focus of biodiversity research (Ricklefs and Schluter, 1993; Huston, 1994; MacArthur, 1965, 1972). Substantial effort has been devoted to estimating species richness at different times and locations for monitoring environmental change, determination of species extinction, colonization, and turnover rates (Karr, 1991; Nichols *et al.,* 1998; Williams *et al.,* 2002). Conventional methods used in biodiversity studies have predominantly focused on determination of total species richness of a study area. This focus, on an often unquantifiable measure (depending on the study area and its habitat), has set precedence to rare species and their detection (Gaston, 2008) and much effort has been devoted to field and statistical methods for species richness estimation.

Determining total species richness from field collected data requires intensive sampling (Palmer, 1990; Colwell and Coddington, 1994; Patton, 1990). Yet, it is difficult to demonstrate that a biological community or population has been completely and representatively sampled. Sampling sufficiency is a critical aspect of community surveys, that is, whether sampling effort adequately describes the community (Cao *et al.,* 2001). Regional species richness is usually estimated by compiling species data across multiple surveys and species sightings when the data are available (Miller and White, 1986; Buzas and Culver, 1999; White *et al.,* 1999; Dupre, 2000) but it is difficult to statistically determine the completeness of species inventories (Stohlgren *et al.,* 1995, 1997), and these methods do not allow for description of latest status and trends of regional

biodiversity since regional estimates are accumulated over many years (Cao *et al.,* 2004).

Most studies comprise of surveys using a limited number of samples, hence use a synoptic approach (Leibowitz *et al.,* 1992; Abbruzzese and Leibowitz, 1997) in the context that they are often short-term investigations of specific ecological characteristics within all or part of a study area with sampling occurring simultaneously in many locations of a study area. A limitation of synoptic data is that they do not constitute a comprehensive survey of species present at a study area but rather provide a broad perspective (Leibowitz *et al.,* 1992; Abbruzzese and Leibowitz, 1997). Although they may provide a good summary of the most common habitats and associated species, rare and incidental species are likely to be missed, especially those that are strongly tied to uncommon microhabitats. Given that richness estimates are heavily weighted by rare rather than common species, a more appropriate measure of diversity derived from synoptic surveys may be the evenness component (the relative abundances of species in a community), especially given that detection probabilities of all species are likely not equal. This idea will be explored in more depth later in this study and a method is proposed to estimate species biodiversity (i.e., richness and evenness) based on a mathematical relationship between evenness (represented by Hurlbert's probability of interspecific encounter measure, 1971) and the slope of a study area's rarefaction curve (the curve is a commonly used method for determining species richness and sampling sufficiency) (Olszewski, 2004). This method is also tested in this study using datasets compiled for various Great Lakes taxonomic groups resulting from relatively intensive sampling protocols. The following section explores methods used in the literature to estimate species richness.

Species Richness Estimation

Species accumulation curves can indicate whether a community has been sampled intensively enough to provide an estimate of species richness. Species accumulation curves record the total number of species encountered as additional individuals or sample units are added to the pool of all previously

observed or collected individuals or samples. As sampling effort increases, the number of singletons (i.e., species represented by only one individual in a sample; Colwell and Coddington, 1994) typically decreases once enough species have been found. The total species richness is believed to be reached when the species accumulation curve reaches an asymptote. The persistence of singletons in the data, implies that total species richness has not been inventoried (Walther and Moore, 2005). The probability of finding a new species in an additional observation is approximately the proportion of singletons remaining to be observed (see Good, 1953 and Chao and Lee, 1992 for details). Raw species richness counts can be validly compared only when species accumulation curves have reached a clear asymptote (Gotelli and Colwell, 2001). Asymptotes are rarely reached in most real data collections (e.g. Novotny and Basset, 2000; Mao and Colwell 2005), but some studies have provided examples of adequate sampling (Walther and Morand, 1998; Walther and Martin 2001). It is often impractical to add sampling stations until species accumulation reaches an asymptote, and limitations in species detectability may prevent the detection of all species despite intensive sampling effort. The greater the number of rare species in a data set, the more likely it is that other species are present that were not represented in the data set (Gotelli and Colwell 2001). Consequently, Gotelli and Colwell (2001) speculate that observed asymptotic species richness is more likely the lower bound of species richness, and species richness estimation methods should be used to explore the upper bound on species richness.

Sampling effort sufficiency can also be estimated by plotting rarefaction curves. In contrast to species accumulation curves, rarefaction curves are produced by randomly re-sampling the pool of individuals or samples repeatedly (generally without replacement) from the large pool of individuals or samples and plotting the average number of species represented by each successive individual or sample (Simberloff, 1978; Gotelli and Colwell, 2001). Rarefaction (either individual- or sample-based) allows interpolation to smaller sample sizes and estimating species richness in the rising part of the sampling curve (Gotelli

and Colwell, 2001) but cannot be used for extrapolation - it does not provide an estimate of asymptotic richness (Tipper, 1979).

An ideal method to determine species richness is through statistical estimation of species richness using a limited number of survey units, especially if well-sampled real datasets are not available. Estimators attempt to estimate the total species richness of a community from an incomplete sample of the community (Walther and Moore, 2005). Many species richness estimators have been developed, and the best performers are nonparametric estimators based on mark recapture statistics (Colwell and Coddington, 1994). Nonparametric estimators use information on the distribution of rare species in the assemblage (i.e., singletons, doubletons, or a few individuals). The greater the number of rare species in a dataset, the more likely it is that other, undetected species exist. The asymptotic richness (or non-asymptotic richness) can be estimated by curve fitting extrapolation methods (e.g., Palmer, 1990; Lamas *et al.,* 1991; Soberon and Llorente, 1993; Mawdsley, 1996; Keating and Quinn, 1998; Fisher, 1999). Nonparametric estimators based on the distribution of individuals among species are defined as abundance based estimators, whereas those based on the distribution of species among samples are defined as incidence-based estimators (Colwell and Coddington, 1994). Estimator comparison studies identify no single best method for estimating species richness, but an understanding of the key factors influencing estimator performance has emerged. Key factors found to influence estimator performance include species evenness or heterogeneity (He and Legendre, 2002; Foggo *et al.,* 2003), sampling intensity (Smith and van Belle, 1984; Hellmann and Fowler, 1999; Cao *et al.,* 2001; Brose *et al.,* 2003; Foggo *et al.,* 2003; Brose and Martinez, 2004), true species richness (Hellmann and Fowler, 1999; Brose *et al.,* 2003; Brose and Martinez, 2004), rare species (Heltshe and Forrester, 1983; Smithand van Belle, 1984; Longino *et al.,* 2002), and species mobility (Brose and Martinez, 2004). As mentioned previously, species have unequal detection probabilities and can therefore cause systematic underestimations of true species richness by species accumulation curves and nonparametric estimators (Brose and Martinez, 2004). Differential mobility of

species further affects species detectabilities and accuracy of species richness estimation. Brose and Martinez (2004) compared dependence of species richness estimator performance on species movement heterogeneity and found that increased movement heterogeneity between the species reduced estimator performance by reducing the sample coverage, which systematically determined which estimator was most accurate.

Biodiversity Estimation Using Rarefaction

Olszewski (2004) showed that using rarefaction curves (relating number of individuals/sample to total species richness) to compare the diversity of two samples provides information on both richness and evenness. Rarefaction curves based on the hypergeometric distribution assume subsampling of a collection without replacement. The equation,

$$E(s_m) = S - \frac{\Sigma_{i=1}^{S}\binom{N - n_i}{m}}{\binom{N}{m}} = \Sigma_{i=1}^{S}\left[1 - \frac{\binom{N - n_i}{m}}{\binom{N}{m}}\right]$$

gives the probability that a sub-sample of size m (number of individuals) will not contain species i ($E(s_m)$), where S is species richness, N is the total number of sub-samples, and n_i is the number of sub-samples with species i. The numerator $\binom{N - n_i}{m}$ represents the number of possible sub-samples of size m that do not include an individual of species i, where N is the total number of sub-samples and n_i is the number of sub-samples with species i. The denominator $\binom{N}{m}$ is the total number of different possible sub-samples of size m from a collection of size N, regardless of species composition. The complement of this equation is the probability that species i will occur in the sub-sample. This is equivalent to the expected contribution of species i to the richness of the sub-sample, which when summed over all species, is the expected richness of the sub-sample (Olszewski, 2004).

The results of rarefaction are typically depicted as species accumulation curves. The incremental increase in richness from a sub-sample of size m to a sub-sample of size m+1 (i.e., $E(s_{m+1}) - E(s_m)$) is the probability that the additional individual in the larger sub-sample represents a previously unsampled species.

Rarefaction can be directly related to a commonly used measure of evenness, Hurlbert's (1971) probability of interspecific encounter (Δ_1). This metric is based on Simpson's (1949) dominance index,

$$\lambda = \Sigma_{i=1}^{S} p_i^2 = \Sigma_{i=1}^{S} \left(\frac{n_i}{N}\right)^2$$

which is the probability that two specimens picked at random (with replacement) from a sample are of the same species. An evenness index Δ_2 can be derived by taking its complement (Heck *et al*., 1975),

$$\Delta_2 = 1 - \Sigma_{i=1}^{S} p_i^2 = 1 - \lambda$$

Accounting for finite collection size leads to Δ_1 (Simpson, 1949; Hurlbert, 1971; Olszewski, 2004):

$$\Delta_1 = 1 - \Sigma_{i=1}^{S} \left(\frac{n_i}{N}\right)\left(\frac{n_i - 1}{N - 1}\right) = \frac{N}{N - 1}\left(1 - \Sigma_{i=1}^{S} p_i^2\right)$$

Δ_1 can be readily interpreted as the probability that the second specimen randomly picked from a sample (without replacement of the first specimen) will be of the same species as the first specimen. Δ_1 can be directly related to rarefaction ($\Delta_1 = E(s_2) - E(s_1) = E(s_2) - 1$), as derived by Olszewski (2004) (see Appendix 1), and is depicted by the steepness of the initial slope since a rarefaction curve grows by adding the probability that each consecutively larger sub-sample will include a new species. A sub-sample of m=1 will necessarily have $E(s_1)=1$. The expected richness of a sub-sample of m=2 is the richness of $E(s_1)=1$ plus the probability that the second specimen will be a different species than the first, i.e., Δ_1. The difference is simply the slope of the steepest segment of the rarefaction curve and can never exceed a value of 1. Thus, the curve that initially rises more

steeply is the more even of the two collections no matter what the total richness of the samples (Olszewski, 2004).

If one can acquire an accurate estimate of the slope of the rarefaction curve by analyzing data from a limited number of sites, then exhaustive sampling of study areas may not be necessary to assess biodiversity, providing that evenness is an unbiased measure of overall biodiversity. Estimation of the asymptote of rarefaction curves can hence provide an accurate estimate of richness. In such cases, synoptic sampling may provide an unbiased and accurate relative estimate of the true biodiversity of an area. This will have great relevance to ecological studies that rely on exhaustive sampling to assess biodiversity both in terms of the interpretation of data collected and costs associated with research and conservation programs. Survey data may provide reliable estimates of biodiversity and may not require intensive and expensive sampling protocols.

I conducted a simulation study to produce rarefaction curves for datasets generated from locations that were intensively sampled for amphibians, birds, and fishes to evaluate the application of the use of the steepest tangent to the slope of the rarefaction curve as an estimate of evenness (Hurlbert's probability of interspecific encounter, Δ_1). The objectives of the study were to i) estimate species richness using rarefaction and statistical species richness estimators; ii) test the relationship between the slope of rarefaction curves and Hurlbert's probability of interspecific encounter (Δ_1) and determine if rarefaction curve slopes are a good estimator of Δ_1. Results that show that slopes perform well as an estimator of evenness (Δ_1) will indicate that information from synoptic samples can be used as a reliable surrogate for total richness estimated from more intensive surveying procedures for biodiversity studies and management, when biodiversity estimates are required.

METHODS

I used datasets of intensively sampled study areas for birds (data provided by Bird Studies Canada), amphibians (data provided by Bird Studies Canada),

and fishes (data provided by US EPA) collected across the Great Lakes to construct species accumulation and rarefaction curves. These datasets were used for analyses of this study because their sampling protocols comprised of collections of numerous sample replicates over the course of a sampling season, and hence provide relatively accurate biodiversity information. Assessment of the relationship between the slope of rarefaction curves and Hurlbert's probability of interspecific encounter (Δ_1) required accurate estimates of richness and evenness that may be provided by datasets of intensively sampled locations. Data resulting from synoptic sampling, such as the GLEI dataset, would not be appropriate for analysis of the slope-evenness relationship since data may not represent the true biodiversity of the study site. The terms 'study area' and 'site' are used interchangeably in this study and refer to particular areas of interest that have been sampled intensively for biodiversity data of the taxonomic group of interest, following the protocols outlined in the following sections.

Amphibian and Bird Survey Site and Station Delineation

Amphibian and bird data were compiled between 1995 and 2007 by the Marsh Monitoring Program (MMP), a bi-national, long-term program that coordinates volunteers in monitoring birds and calling amphibians of coastal and inland marshes of the Great Lakes basin (The Marsh Monitoring Program, 2003). Survey sites (termed 'routes' by MMP) were established in marshes at least 1 ha in size and consisted of one to eight monitoring stations located at least 250 metres (275 yards) apart for bird sites, and 500 metres (550 yards) apart for amphibian sites to minimize duplicate counts of individuals. MMP survey stations were defined as a 100 m radius semicircle with emergent marsh vegetation covering at least 50% of the semicircle area. Marsh habitat was defined as habitat regularly or periodically wet or flooded to a depth of up to two metres where non-woody vegetation was predominant. Counts were conducted from the midpoint of the 200-metre (220 yard) base of the semi-circle towards the arc of the station perimeter. A replicate sample was represented by a survey conducted at a station for each site.

Bird Sampling

Marsh bird survey visits were conducted twice annually between May 20 and July 5, beginning after 18:00 h under appropriate survey conditions (i.e., 16 ºC or warmer, no precipitation and wind with a maximum score of three on the Beaufort scale) with at least 10 days separation between visits. A 5-minute broadcast tape was played at each station during the first half of each 10-minute survey visit to help elicit calls from several elusive bird species (i.e., Virginia Rail, Sora, Least Bittern, Common Moorhen, American Coot and Pied-billed Grebe). Surveyors recorded all birds heard and/or seen within the survey station area during the call playback period and during a five minute silent period following call playback.

Amphibian Sampling

Amphibian sites were surveyed three times each year between April and the end of July, with at least 15 days between visits. Given that peak amphibian calling periods are closely associated with temperature and precipitation rather than date, visits were scheduled to occur three separate evenings according to night air temperatures of 5°C (41° F), 10° C (50° F), and 17° C (63° F), respectively. Amphibian surveys were executed for three minutes at each station and began one-half hour after sunset and ended before midnight on evenings with little wind.

Fish Sampling

Fish data were collected for a 1995 study that examined fyke net position, wing configuration, and duration of set in the inner and outer marsh of Allouez Bay, a barrier-beach wetland of western Lake Superior (See Brazner *et al.,* 1998; Tanner *et al.,* 2004; Tanner *et al.,* in press for additional details). Fyke net orientation and the effect of wings on net catch were examined by comparing catches from 2 arrays set parallel to shore in the outer marsh to 2 separated arrays set with a lead running from and perpendicular to the shoreline in the inner marsh. Each array consisted of one large and one small mesh net (either 13 mm or 4 mm bar mesh 5 m length, 0.9 m x 1.2 m front opening), set at 0.6 to 1.2 m depths (depending on seiche activity) in a lead-to-lead orientation (15 m length x 0.9 m high, 4 mm bar mesh connecting lead) in the outer marsh. Similarly, four

nets were set separately in a perpendicular-to-shore configuration in the inner marsh, two each of 13 mm or 4 mm bar mesh, (0.9 m x 1.2 m front opening) with a 15 m long x 0.9 m high, 4 mm bar mesh with the lead running from shore to the opening of each net. The effect of wings on net catch was tested at the same time by attaching wings to one parallel-set array and two perpendicular-set nets, one of each mesh size. Wings were 0.9 m high, 3.0 m long, with 4 mm bar mesh. They were attached to the sides of the front opening and set at a 60 degree angle from the front of the net. Data comparisons were made using 96 h catch data by combining data from four sequential 24 h sets.

The effectiveness of fyke net sampling over 24, 48, 72, and 96 h was tested using the parallel oriented outer marsh arrays (with blocking wings) as described above. These nets were set for four consecutive nights and tended daily during June 5-8, June 26-29, July 31-August 3, September 4-7, and October 2-5. All captured fishes were identified to species, weighed (0.1 g), and measured (0.1 cm) in the field. A replicate sample was represented by a 24 h collection from all fyke nets of both sizes set for each marsh.

The inner marsh site was typified by dense emergent and submergent vegetation and low wave energy. The outer marsh site had dense emergent vegetation only along its inner perimeter, moderate cover of submergent vegetation, and greater wave energy. Dominant emergents were burreed (*Sparganium eurycarpum*), and softstem bulrush (*Schoenoplectus validus*). Dominant submerged and floating species were *Potamogeton richardsonii*, *Ceratophyllum demersum*, *Utricularia vulgaris*, and *Nuphar variegatum*.

Biodiversity Estimation Using Rarefaction and Estimators

Ten randomly chosen (determined by using a random number generator) sites from each of the amphibian (of a total of 610 sites) and bird (of a total of 493 sites) datasets were used for analyses. Fish data were available from 2 sites.

Species accumulation curves were plotted using observed data for each site and taxonomic group. Rarefaction curves were produced by repeatedly re-sampling all samples from each replicate and determining the average number of species computed with increasing effort (measured as number of individuals

collected in each sample) for each site and taxonomic group. The re-sampling procedure drew randomly, without replacement, 1,000 different sets for each site and was performed using the software, EstimateS version 8 (Colwell, 2005). A rarefaction curve can be viewed as the statistical expectation of the corresponding accumulation curve (Gotelli and Colwell, 2001). Rarefaction curves were constructed using richness data generated by a variety of estimators available in EstimateS software (Colwell, 2005): ACE, ICE, Chao-1, Chao-2, Jack-1, Jack-2, Bootstrap (Burnham & Overton, 1978, 1979; Heltshe & Forrester, 1983; Chao, 1984, 1987; Smith & van Belle, 1984; Palmer, 1991; Chazdon *et al.,*1998; Chao *et al.,* 2000; Appendix 2 gives definitions of each estimator). Incidence-based estimators require less information (single sampling events) than abundance-based equivalents, which require numerous replication of sampling of a system using multiple sample locations. Incidence-based estimators are not affected by spatially heterogeneous species distributions in simulated landscapes (Brose *et al.,* (2003) but abundance-based estimators may be biased by such spatial heterogeneity (Chazdon *et al.,* 1998). I defined sufficient sampling effort as the number of replicate samples required to detect 80% of the total number of observed species. Asymptotic richness was deemed to be attained when subsequent samples did not add species richness to the preceding sample.

Richness data generated by the best estimator (i.e., provided the highest coefficient of determination, R^2, value for the relationship between species richness and sampling effort) were used to test Olszewski's evenness-slope hypothesis (2004). Slopes of rarefaction curves were estimated by computing parameters of the equation generated by a variation of MacArthur and Wilson's equilibrium model of species diversity on islands (Preston, 1962; MacArthur and Wilson, 1963, 1967; Sheldon, 1977): $N_t=(k/m)(1-e^{-mt})$, where N_t is the number of individuals present at time t, k/m is the asymptotic number of individuals after infinite time, and e is the base of the natural logarithms. This equation models richness as a function of numbers of individuals collected in a sample to give the rarefaction equation: $S = b_1*(1-(e^{-b}{}_2{}^{*n}))$, where S is species richness, b_1 is mean

asymptotic species richness, b_2 is the emigration/extinction coefficient constant, and n is number of individuals in a sample. The b_1 and b_2 variables were estimated from data generated by the best estimator for each site and taxonomic group by least squares nonlinear estimation. The slope of the steepest segment of the rarefaction curve from the origin is the product of b_1 and b_2. Estimates of the slope (b_1b_2) were regressed against measures of Hurlbert's probability of interspecific encounter (Δ_1): $\Delta_1 = (n/n\text{-}1)*(1\text{-}Ep_i^2)$, where n is the total number of individuals in a sample and p is the proportion of species i relative to the total number of individuals collected in a sample. Linear regression was performed to evaluate the relationship between b_1b_2 and Δ_1 and between b_1b_2 and rarefaction parameter variables (b_1 and b_2). If analyses demonstrated that there was a significant relationship between slope and evenness, then synoptic samples may characterize the true biodiversity of a study area given that they are able to provide an unbiased estimate of the rarefaction slope. A minimum number of samples are required to give the rarefaction slope (i.e., the number of samples required to estimate the ascending portion of the curve before the asymptote is reached) and this minimum must be attained in synoptic sampling for true biodiversity estimates to be made. The parameter, b_2, is the 'emigration' or loss of individuals in the equilibrum model and can be interpreted as rare species that are undetected. Hence, when b_2 is small, there are many rare species, and the sample sizes needed to reach an asymptote are large, suggesting that evenness would be low (i.e., there are many uncommon species whose probability of encounter would be low). This relationship was evaluated with linear regression of b_2 and Δ_1.

Estimation Assessment

Species accumulation curves of observed data were assessed for species richness estimation performance using three commonly used criteria: bias (i.e., how close an estimate is to the true value), precision (i.e., the variability among replicates), and accuracy (i.e., the combined effects of bias and precision) (Palmer, 1990; Hellmann and Fowler, 1999; Walther and Moore, 2005). Performance measures used for bias, precision, and accuracy calculations were

scaled mean error (SME), coefficient of variation (CV), and scaled mean square error (SMSE), respectively (as per Walther and Moore, 2005). A perfectly performing estimator should have SME and SMSE values of zero and low CV values (Palmer, 1990; Walther and Morand, 1998).

The accuracy of richness and evenness information contained in each replicate was assessed by comparing replicate residual richness and evenness estimates with mean values for each site and taxonomic group. This method allows for detection of any bias (i.e., under-, over-estimation) and changes with sampling effort. Comparisons were made using all replicates and means, as well as for each year of collection to account for year-to-year variation in richness and evenness.

To determine the adequacy of theoretical sampling from the datasets for determining the total richness in a community (and hence adequacy of theoretical sampling from the datasets for identifying rare species), the persistence of singletons, doubletons (i.e., species represented by two individuals in a sample), uniques (i.e., species that occurred in only one sample), and duplicates (i.e., species that occurred in only two samples) (collectively referred to as 'rare species') with increased sampling effort (represented by number of individuals collected in each sample) were assessed. If rare species were not detected with increased sampling effort, sampling effort was deemed to have been sufficient to capture all species at the site.

Comparisons were made between synoptic sampling (datasets compiled for the GLEI project – see Chapters 2 and 3) and intensive sampling (datasets used in this study) methods to assess similarities in identification of common species (i.e., species with high relative abundance and site frequency).

All analyses were performed using the Statistica® software package Version 6.0 (StatSoft, Inc. 2001).

RESULTS

Species Richness Estimation

Table 4.1 summarizes sampling effort, observed total richness, and scaled performance measures (bias, precision, and accuracy) of observed replicate data for study areas. Mean bias measures were 0.663, 0.732, and 0.646 for amphibians, birds, and fishes, respectively. Mean precision measures were 37.819, 32.737, and 26.531 for amphibians, birds, and fishes, respectively. Mean accuracy measures were 0.464, 0.551, and 0.428 for amphibians, birds, and fishes, respectively. Richness estimation using observed data did not perform well given that bias and accuracy measures were well above zero and precision values were high, except for amphibian site MI122, where only a single species was collected in each replicate.

Species accumulation curves of observed data (Figure 4.1) failed to reach an asymptote, indicating that richness could not be adequately measured from observed data due to lack of sampling intensity. Hence, rarefaction of data was necessary to permit accurate estimation of asymptotic richness for birds and fishes. Figure 4.2 gives an example of a rarefaction curve that reached asymptotic richness and hence gave an accurate estimate of species richness (for amphibian site NY021 by Cole estimator; Fig. 4.2a) and one that did not reach asymptotic richness and hence gave an inaccurate species richness estimate (for bird site NY024 by Jack-1 estimator; Fig. 4.2b).

Figure 4.3 shows scatterplots relating residual species richness and evenness (Δ_1) with sampling effort (number of individuals collected in a sample) based on all replicates and on yearly replicates (residuals based on yearly species richness). Trends based on all replicates and those based on yearly replicates are similar but yearly trends generally estimate observed total species richness better than those based on all replicates. All amphibian replicates underestimate the observed total species richness except for site NY021 (yearly replicates estimate richness well). Bird replicates are generally able to estimate observed species richness with maximum sampling effort (i.e., replicates from a sampling event that collected the maximum number of individuals represent the

observed total species richness). Fish replicates (only based on sampling during a single year, 1995) underestimate observed species richness. Richness estimates generally improved with increasing sampling effort for all taxonomic groups. Residual evenness-sampling effort trends generally show random scatters of points, suggesting that evenness estimates do not improve with sampling effort. In fact, residual evenness is lower with increased sampling effort for birds and fishes. This may be due to the presence of dominant species.

Rarefaction curves failed to reach an asymptote with most species richness estimators (Figure 4.4). However, in decreasing order of performance, Chao-1, Bootstrap, Jack-1, and Jack-2 estimators performed better than other estimators (i.e., had lowest bias and highest precision and accuracy; Walther and Moore, 2005). Chao-1, an abundance-based estimator, performed best for amphibian richness estimation, while Bootstrap, an incidence-based estimator, performed best for bird richness estimation. Fish richness estimation of the two sites were performed best by Jack-2, an incidence-based estimator, and Bootstrap. Overall, these trends appear to reflect sampling sufficiency of the taxonomic groups. Estimators were better able to estimate total species richness overall for certain study areas than others – asymptotes were reached by estimators for amphibian sites IL005 and NY021, bird sites MI107, NY017, and WI033 (Fig. 4.4a, b). Estimators failed to reach asymptotes at the 2 fish sites (Fig. 4.4c).

Table 4.2 summarizes evenness values (Hurlbert's probability of interspecific encounter, Δ_1) and rarefaction curve parameters (mean asymptotic species richness, b_1, and the growth coefficient, b_2) based on the best species richness estimator for amphibian, bird, and fish data. Simulated total number of individuals per sample and simulated total number of samples collected at each site for each taxonomic group are also listed, as well as the observed total species richness and proportion of asymptotic richness. Generally, observed species richness underestimated asymptotic richness, except for amphibian site NY033, bird site OH010, and fish site Outer Allouez Bay. Most sites estimated at least 80% of asymptotic richness, except for amphibian site MI129, bird sites

MI024, MI100, NY024, NY073, and fish site Inner Allouez Bay, hence overall, sampling was sufficient enough to estimate true species richness.

Adequacy of sampling effort to determine total asymptotic species richness of communities differed among taxonomic groups and none showed that rare species disappeared with increased sampling effort (Figure 4.5). Amphibian sampling curves showed that rare species (i.e., singletons, doubletons, uniques, duplicates) usually ranged between 1-2 species with maximum sampling effort (12.8-65.6% of total asymptotic richness in the location), except for MI030, which had a sampling curve that increased to 4 duplicates species with the maximum number of individuals/sample (Fig. 4.5). Increased sampling effort did not adequately eliminate rare species from bird communities. In fact, most sites showed either an increase in rare species occurrence, particularly of singletons and uniques, or no decrease in singletons or uniques with increased sampling effort (Fig. 4.5). Fish sampling curve trends were similar to bird sampling curves although the sampling effort for the Outer site was better for doubletons and duplicates than for the Inner site (Fig. 4.5).

Rarefaction Slope-Evenness Relationship

There was no significant relationship between slope of the steepest part of the rising limb of a rarefaction curve (b_1b_2) and mean Δ_1 (Table 4.3; Figure 4.6). However, the trend was negative, which contradicts expectations of Olszewski's hypothesis (Table 4.3; Fig. 4.6). This relationship was also not significant when analyses were performed for each taxonomic group. There was no significant relationship between mean Δ_1 and b_2 for either birds or amphibians (both $p>0.05$). The relationship was positive for birds but negative for amphibians. Fish data could not be analyzed since the data were based on only two sampling sites.

Common Species Identification

Comparisons of datasets resulting from synoptic sampling and intensive sampling showed similarities in the identities of common species in terms of relative abundance and site frequency (Table 4.4). Fish data for both sampling methods were local for Allouez Bay and the abundance information from the two intensively sampled locations (Allouez Bay Inner and Allouez Bay Outer) were

pooled together. Amphibian and bird datasets gave regional species information of the Great Lakes. Table 4.4 lists the 3 most abundant and widespread amphibian, bird, and fish species identified by both sampling methods. *Rana sylvatica* (wood frog) and *Rana clamitans melanota* (green frog) were identified as abundant amphibian species by both synoptic and intensive sampling methods, while *Rana clamitans melanota* (green frog) and *Pseudacris crucifer* (spring peeper) were identified as widespread by both sampling regimes; *Agelaius phoeniceus* (red-winged blackbird) and *Melospiza melodia* (song sparrow) were identified as widespread by both synoptic and intensive sampling protocols; *Notropis atherinoides* (emerald shiner), and *Perca flavescens* (yellow perch) were identified by both synoptic and intensive sampling as abundant fish species.

DISCUSSION

Although most sample collections depicted at least 80% of rarefaction asymptotic species richness at sites, species accumulation curves plotted with bird and fish data indicated that sampling effort was not sufficient for species richness estimation since asymptotes were not reached, despite intensive sampling protocols. This variability in sampling sufficiency may be related to biological and habitat heterogeneity, and sampling efficiency (Bayley *et al.,* 1989; Lyons, 1992; Angermeier and Smogor, 1995). Amphibian sites were adequately sampled for species richness estimation since this taxonomic group has few species and all species can be collected at sampling locations. The amphibian dataset contained the entire Great Lakes regional species pool (15 species; Hecnar, 2004), while the records of birds represented approximately 70% (286 species reported in Ontario, including the Hudson Bay Lowlands, an area outside the reach of the Great Lakes; Cadman *et al.,* 2007) and fishes represented approximately 40% (86 species reported in Lake Superior; Cudmore-Vokey and Crossman, 2000) of all known species of the respective region.

The Chao and Jackknife estimators performed better than the other estimators examined in this study, and this corroborates findings of other studies

(see Walther and Moore, 2005 for evidence and a review of other study findings). Walther and Moore (2005) caution that, although Chao and jackknife estimators have been shown to perform well, there is no overall best estimator that performs well in all situations or for all taxonomic groups. Estimator performance depends on variables that change the size of the species-sample data matrix (i.e., total species richness and sample size) and the distribution of individuals within samples (i.e., the species-abundance distribution and the sampling protocol) (Walther and Moore, 2005). This substantiates my reasoning for choosing the best fitting estimator out of the range of estimators used in this study for estimating rarefaction parameters.

An abundance-based estimator (Chao-1) performed best for amphibian richness estimation, while incidence-based estimators performed best for bird and fish richness estimation (Jack-2 for fishes and Bootstrap for both taxonomic groups). Differences in estimator performance among taxonomic groups may be due to differences in mobility and/or detectability. Movement and abundance heterogeneities yield unequal detection probabilities (i.e., more mobile and/or abundant species are more likely to be detected). Unequal detection probabilities reduce the proportion of the true richness that is sampled, especially at low sampling intensities, and consequently produce less accurate estimates (Brose *et al.,* 2003; Brose and Martinez, 2004). Predominance of species with low abundance (i.e., rare species) also influences the behaviour of abundance-based estimators. The asymptotic richness of communities that support many species whose numbers are low is likely to be more strongly underestimated than for communities with fewer low abundant species. Accuracy of estimators changes with the proportion of the true richness that is sampled and do so unequally between abundance- and incidence-based estimators (Brose *et al.,* 2003; Brose and Martinez, 2004). However, with increased sampling intensity, the number of rare species become more similar and, therefore, the difference between abundance- and incidence based estimators vanishes (Chazdon *et al.,* 1998).

The slope of the steepest segment of the rarefaction curve from the origin (b_1b_2) was not a good estimator of Hurlbert's probability of interspecific encounter

(Δ_1) (i.e., evenness). Although most sites were sampled sufficiently to attain 80% of rarefaction asymptotic richness, sampling effort was inadequate to estimate total species richness from species accumulation curves of observed bird and fish data, and may not have been adequate for determining species evenness (Δ_1). Drake (2007) estimated the sampling effort required to adequately determine the species richness and composition of nearshore fish communities of central Minnesota lakes and found that the effort needed to describe species richness was most sensitive to the evenness of fish species among sampling stations. Fewer sampling stations were needed to estimate species richness in lakes with high species evenness among stations, whereas more sampling stations were required for lakes with low species evenness. However, species evenness was not related to indices of whole-lake habitat diversity or evenness (Drake, 2007).

Estimating species richness for communities examined in my study may have required more intensive sampling in communities that were less even, to account for rare species. Olszewski's hypothesis (2004) implies that rarefaction slopes should increase with increasing evenness, indicating that most species are taken into account in the initial phase of the sampling effort. This should mean that greater sampling effort is required to account for the less-abundant species in less-even communities. However, given that amphibians were adequately sampled for species richness estimation and the finding that there was no relationship between (b_1b_2) and (Δ_1), species-habitat interactions, rather than insufficient sampling effort, may have influenced results. Otherwise, a significant relationship between (b_1b_2) and (Δ_1) would have been detected. Rarefaction does not take into account habitat complexity (i.e., the abundance of distinct physical elements) or habitat heterogeneity (i.e., the spatial arrangement of qualitatively different physical elements) of communities and habitats (Gorman and Karr, 1978; Ricklefs and Schluter, 1993; Rosensweig 1995; Pickett *et al.,* 1997). However, Collins and Simberloff (In press) argue that rarefaction is not sensitive to nonrandom spatial dispersion patterns, such as clumping within a species and segregation among species since rarefaction selects individuals randomly from a whole collection. Habitat structure variables of amphibian, bird,

and fish sites examined in this study were not available, and their incorporation into analyses may have eliminated possible confounding by species-habitat associations. If replicate samples did not cover all available microhabitats of the study area or if there was high seasonal variation, datasets may not have provided a good representation of the biodiversity and thus, prevented rigourous testing of Olszewski's hypothesis. Although datasets may not have accurately depicted biodiversity of sampling locations, they were the result of intensive sampling methods and provided the most accurate data as one might have applied for Olszewski's method. Tests of the method using other comparable datasets will likely produce similar results with the finding that data cannot allow rigourous testing of Olszewski's hypothesis.

As well as overlooking the effects habitat interactions, species richness estimation using species accumulation curves and rarefaction also disregard how well samples represent communities. These procedures do not describe how well the sample represents the taxonomic composition and relative abundances of species of a study location or of the communities being surveyed and consequently can introduce biases into community comparisons (Cao *et al.,* 2002). Randomization of samples does not permit one to determine the similarity of a sample to the community from which it is drawn (i.e., does not provide an indication of sample representativeness). Accurate estimation of species richness is not possible unless, on average, all species are equally detectable, that is, there is equal mean species detectability (MSD) (Kery and Schmid, 2006). Cao *et al.,* (2002) proposed a method for estimating species richness by measuring the average similarity among replicate samples randomly drawn from a community (referred to as autosimilarity; Cao *et al.,* 2002) using the Jaccard coefficient. The Jaccard coefficient is the ratio of the number of shared species by two samples (S_{12}) to the total number of species recorded in the first (S_1) and second (S_2) samples: $(S_{12})/(S_1+S_2- S_{12})$. When most or all species are present in all replicate samples (i.e., high autosimilarity), the observed species richness should approach total species richness. If many species are present in only a single replicate sample (i.e., low autosimilarity), the observed species richness

underestimates total species richness and gives a low percentage of total species richness. Cao *et al.,* (2002) found that the proportion of total species richness was positively and almost linearly correlated with autosimilarity, suggesting autosimilarity is a good predictor of total species richness. They also found that relative differences in species richness among sites were independent of sample size, overcoming the problem of variation of sample representativeness faced by richness estimation using samples of equal size (Cao *et al.,* 2002). The average Jaccard coefficient calculated among multiple pairs of replicate samples estimates MSD. Estimates of MSD across multiple pairs of replicate samples is referred to as mean replicate similarity (MRS). The accuracy of true species richness estimates depends on how well estimates of MRS and MSD agree with one another and the MRS-MSD relationship has been shown to be highly consistent across different assemblages using several datasets (Cao *et al.,* 2002, 2004) and estimating true species richness using standardization on MRS performed better than rarefaction or statistical estimators (Cao *et al.,* 2007). Sample standardization on mean species detectabilities may be more efficient and accurate that standardizing on sampling effort to estimate species richness and also eliminates dependence on the occurrence of rare species in samples. Further examination of the applicability of sample standardization on MRS for estimating species richness will be useful for biodiversity studies and conservation efforts where estimates of biodiversity are needed.

Study Implications

The aim of this study was to determine whether a representative measure of evenness of Great Lakes amphibian, bird, and fish communities could be estimated from a limited number of samples following Olszewski's hypothesis (2004). This hypothesis proves mathematically that the evenness of a community can be estimated from a minimum number of samples (requiring at least two for a depiction of the slope) but my study shows that the information portrayed in collections resulting from intensive sampling protocols was insufficient to provide an accurate estimate. Although the representative amphibian and bird sites were chosen randomly and may not have depicted the full range of Great Lakes

biodiversity, the inability of the method to demonstrate a relationship between evenness and slope indicates that, in general, surveys used for biodiversity studies do not accurately represent the communities studied since most surveys are the result of substantially less effort than the ones used in this study. The information provided in a single sample should theoretically reliably depict the community being studied, as expected by Olszewski's model. However, different behavioural and habitat complexities prevent the full spectrum of species from occurring in a single or limited number of sample areas. Sampling designs are not capable of covering all of these complexities under manageable sampling effort. Rarefaction curves showed that asymptotic richness was not approached even when sampling effort comprised of over 100 individuals at most bird sites (e.g., IN001, MI024, MN001, NY024, NY073, and OH010; Fig. 4.4b) and over 1000 individuals at fish sites (Fig. 4.4c). Given that accurate predictions of behavioural and habitat complexities cannot be made, mathematical estimators cannot accurately model these complexities. The existence of these stochastic factors renders it inappropriate to try to characterize biodiversity through surveys. In other words, it is important to recognize that the estimates of biodiversity components are inherently unreliable, which is why it may be difficult to find patterns or explanations.

Given the inaccuracy of biodiversity characterization through intensive sampling protocols, findings from Chapters 2 and 3 of this dissertation, as well as all other comparable biodiversity studies, may also be inaccurate given that studies were based on data from synoptic samples. This is further complicated by the fact that the nonindigenous species examined in studies may not have dispersed to the furthest extent of their possible habitat ranges in the Great Lakes due to insufficient time for dispersal to suitable communities and/or lack of detection in surveys. However, findings from these studies do provide clear insights to trends related to common and/or detectable species, which are arguably the community members that have the greatest influence on species interactions, resource allocation, and community function, aside from any rare keystone species (see Recommendations section).

Synoptic sampling and intensive sampling methods identified similar common species for all taxonomic groups examined. These findings indicate that synoptic sampling was sufficient to identify the numerically dominant species of communities even though sampling locations were not identical for both sampling methods (i.e., synoptic sampling and intensive sampling sites did not overlap one another). This reinforces the accuracy of identification of dominant/common native and nonindigenous species in Chapter 3.

In general, studies based on datasets produced by surveys, especially those without habitat structure data, may prevent rigorous testing of biotic interaction based and neutral-interaction based hypotheses given inaccuracy of species richness and evenness estimation and thus, prevent clear-cut elucidation of factors that regulate communities.

Recommendations

Much of ecological research has been preoccupied with species richness estimation, due to the conceptualization of biodiversity, its basis on richness and evenness measures, and interest in causes of biodiversity, although the role of biodiversity has not been carefully studied (Raffaelli *et al.,* 2005). Historically, biodiversity measures have been considered as response/dependent variables of ecosystem function rather than explanatory/independent variables, likely influenced by global change, human activities, and interest in biodiversity loss (Gamfeldt and Hillebrand, 2008). Many research dollars have been invested in investigations and collections to compile species lists (and chiefly to unveil rare species) and to determine the biodiversity of a location of interest. The limitations of these attempts are realized when considering that total species richness cannot be accurately determined, as exemplified in this study, and the fact that many regions of the world go unstudied, lessening the importance of these "complete" lists when comparisons among regions are made. Although the biodiversity paradigm is slowly changing (see review by Gamfeldt and Hillebrand, 2008), many research programs continue to set richness estimation as a goal, with rare species taking precedence over common species (Gaston, 2008). Their vulnerability to extinction due to their low abundances has made rare species a

priority in conservation efforts, particularly when their persistence is threatened by anthropogenic activities. However, ecological research would benefit, both economically and scientifically, from complementary studies designed to use the information provided by common species, given that common species are detectable. Studies of the factors that regulate the distributions and relative abundance of common species provide valuable insights to the major factors that regulate communities and ecosystems in general. Commonness is unusual since most species tend to be rare. Hence determining the conditions that allow a species to become common addresses the exception rather than the norm (just as it is essential to understand why some nonindigenous species are able to establish and become common enough to significantly influence the pre-invasion community). There are many accounts of declines in abundance of common species – determining the underlying principles that cause their declines will likely also elucidate causes for rare species decline and provide insights to successful design and methods for applications for conservation. Understanding why common species are common does not necessarily explain why rare species are rare. However, developing an understanding of the major factors regulating common species provides insights to the regulatory factors for the majority of individuals.

Gaston (2008) advocates studying the importance of common species in his review of the influence of common species on biodiversity patterns and macroecology. His research on bird assemblages gives evidence for the dominance of common species in terms of their relative abundance, regional and global occurrences, and of the total biomass. The most abundant wild breeding bird species make up approximately 5% of all global species (of approximately 9700 species) (Gaston and Blackburn, 2003) and the 25% most abundant species in the European breeding bird assemblage make up approximately 96% of individuals (Gaston, 2002). For British breeding birds specifically, the 25% most abundant species comprise 95% of all individuals, 88% of all biomass, and 60% of all occurrence records at a 10 × 10 km resolution (Gaston and Fuller, 2008).

Not only do common species appear to be strongly dominant, but there is also empirical evidence for birds, trees, and fishes, that widespread species influence variation in overall species richness and that common species are more closely related to geographic variation, reflecting responses to environmental conditions, or to the environmental variables that strongly covary with overall richness than rare species (Jetz and Rahbek, 2002; Evans *et al*., 2005; Mora and Robertson, 2005; Kreft *et al*., 2006; Rahbek *et al*., 2007). Thus, common species may be better indicators of overall biodiversity than rare species (McGeoch, 2007; Pearman and Weber, 2007), and their abundances may perform well as indicators of overall habitat quality (Gaston and Rodrigues, 2003; McGeoch, 2007).

Not surprisingly, common species are important in ecosystem function. Increases in downstream transport of organic carbon and primary production and respiration were observed due to natural and experimental removal of a common detritivorous fish (Taylor *et al*., 2006). Removal and density reductions of a dominant grass in prairie tallgrass experiments reduced total above-ground net primary productivity but similar influences by rare species were not observed (Smith and Knapp, 2003).

Common species act as an indicator of both response and explanatory variables, depending on the context, and hence reflect both affects and effects of species richness and ecosystem properties and processes. Investigation of common species and their roles can elucidate the dynamics between biodiversity and ecosystem function. Use of synoptic sampling, which highlights biodiversity of common species, and incorporating functional diversity data into ecological studies would greatly advance ecological knowledge and conservation endeavours and may be more informative than use of exhaustive sampling designs that attempt to emphasize the quantity of rare species and their role as indicators of biodiversity.

CONCLUSIONS

The findings from this study that sampling insufficiency prevented accurate species richness estimation and rigorous testing of the rarefaction slope-evenness hypothesis based on datasets produced from intensive sampling effort suggest that ultimately, surveys cannot provide true measures of biodiversity. Biodiversity research programs would benefit from studies that provide a closer examination of the influence of detectable species (i.e., common species) on species interactions and community function, rather than those that endeavour to identify rare and/or transient species.

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Table 4.1: Summary of mean sample size, total number of samples collected, observed total richness, and scaled performance measures for amphibian, bird, and fish study areas. Performance measures calculated for bias, precision, and accuracy were scaled mean error (SME), coefficient of variation (CV), and scaled mean square error (SMSE), respectively (as per Walther and Moore, 2005).

Taxonomic group	Site	Mean Number of Individuals per Sample	Total Number of Samples	Total Richness	Performance Measure		
					Bias (SME)	Precision (CV)	Accuracy (SMSE)
Amphibian	IL005	2.8	11	5	0.691	32.219	0.487
	MI030	5.8	5	5	0.640	64.789	0.464
	MI122	3.3	6	3	0.667	0.000	0.444
	MI129	8.2	6	4	0.583	44.721	0.375
	NY021	4.8	58	6	0.707	43.932	0.516
	NY033	8.8	23	8	0.750	41.703	0.573
	NY078	3.5	21	6	0.762	34.641	0.587
	NY086	2.2	6	3	0.611	31.944	0.389
	OH063	9.2	5	5	0.600	31.623	0.376
	OH066	4.0	9	5	0.622	52.613	0.427
Bird	IN001	15.4	24	46	0.860	29.977	0.741
	MI024	34.2	6	24	0.694	41.411	0.498
	MI100	6.4	8	9	0.778	61.237	0.623
	MI107	11.7	11	17	0.690	26.932	0.483
	MN001	24.9	12	28	0.702	37.094	0.506
	NY017	8.0	31	14	0.737	34.109	0.552
	NY024	14.4	24	26	0.779	32.633	0.612
	NY073	17.2	20	36	0.782	30.752	0.616
	OH010	44.3	20	45	0.771	19.921	0.597
	WI033	13.2	6	11	0.530	13.300	0.285
Fish	Allouez Bay Inner	246.4	24	31	0.692	28.378	0.487
	Allouez Bay Outer	414.5	24	29	0.599	24.684	0.369

Table 4.2: Site evenness values (Hurlbert's probability of interspecific encounter, Δ_1), parameter estimates (mean asymptotic species richness, b_1, and the growth coefficient, b_2) based on rarefaction curves using the best richness estimator, and comparison with observed species richness for amphibian, bird, and fish study areas. Explanation of the various richness estimators are given in Appendix 2.

Taxonomic group	Site	Δ_1	b_1	b_2	Richness Estimator	Simulated Total Number of Individuals	Simulated Total Number of Samples	Observed Total Richness (% of asymptotic richness)
Amphibian	IL005	0.42	5.03 SE=0.128	0.19 SE=0.031	Chao-1	31	11	5 (99.4)
Amphibian	MI030	0.25	5.05 SE=0.376	0.18 SE=0.069	Chao-1	29	5	5 (99.0)
Amphibian	MI122	0.00	3.42 SE=0.318	0.11 SE=0.046	Chao-1	20	6	3 (87.7)
Amphibian	MI129	0.30	7.35 SE=0.731	0.03 SE=0.003	Jack-1	49	6	4 (54.4)
Amphibian	NY021	0.38	6.07 SE=0.031	0.07 SE=0.002	Chao-1	277	58	6 (98.8)
Amphibian	NY033	0.45	7.79 SE=0.645	0.03 SE=0.023	Bootstrap	202	23	8 (1.03)
Amphibian	NY078	0.28	6.08 SE=0.077	0.08 SE=0.013	Chao-1	74	21	6 (98.7)
Amphibian	NY086	0.13	3.05 SE=0.116	0.33 SE=0.026	Chao-1	13	6	3 (98.4)
Amphibian	OH063	0.42	5.67 SE=0.168	0.05 SE=0.003	Chao-1	46	5	5 (88.2)
Amphibian	OH066	0.58	5.12 SE=0.085	0.09 SE=0.005	Bootstrap	36	9	5 (97.7)
Bird	IN001	0.78	56.95 SE=0.876	0.01 SE=0.000	Bootstrap	370	24	46 (80.8)
Bird	MI024	0.73	40.02 SE=0.735	0.01 SE=0.000	ACE	205	6	24 (60.0)
Bird	MI100	0.35	43.57 SE=4.376	0.01 SE=0.001	Jack-1	51	8	9 (20.7)
Bird	MI107	0.82	19.50 SE=0.178	0.03 SE=0.001	Bootstrap	129	11	17 (87.2)
Bird	MN001	0.84	32.04 SE=0.487	0.01 SE=0.001	Bootstrap	299	12	28 (87.4)
Bird	NY017	0.70	14.38 SE=0.108	0.03 SE=0.001	Chao-1	248	31	14 (97.4)
Bird	NY024	0.82	40.56 SE=0.856	0.01 SE=0.001	Jack-2	345	24	26 (64.1)
Bird	NY073	0.83	48.39 SE=0.893	0.01 SE=0.001	Jack-1	344	20	36 (74.4)
Bird	OH010	0.82	43.62 SE=0.657	0.01 SE=0.001	Chao-1	885	20	45 (1.03)
Bird	WI033	0.81	12.83 SE=0.171	0.04 SE=0.002	Bootstrap	79	6	11 (85.7)
Fish	Allouez Bay Inner	0.55	40.75 SE=0.708	0.01 SE=0.001	Jack-2	5914	24	31 (76.1)
Fish	Allouez Bay Outer	0.53	28.73 SE=0.400	0.00 SE=0.000	Bootstrap	9947	24	29 (1.01)

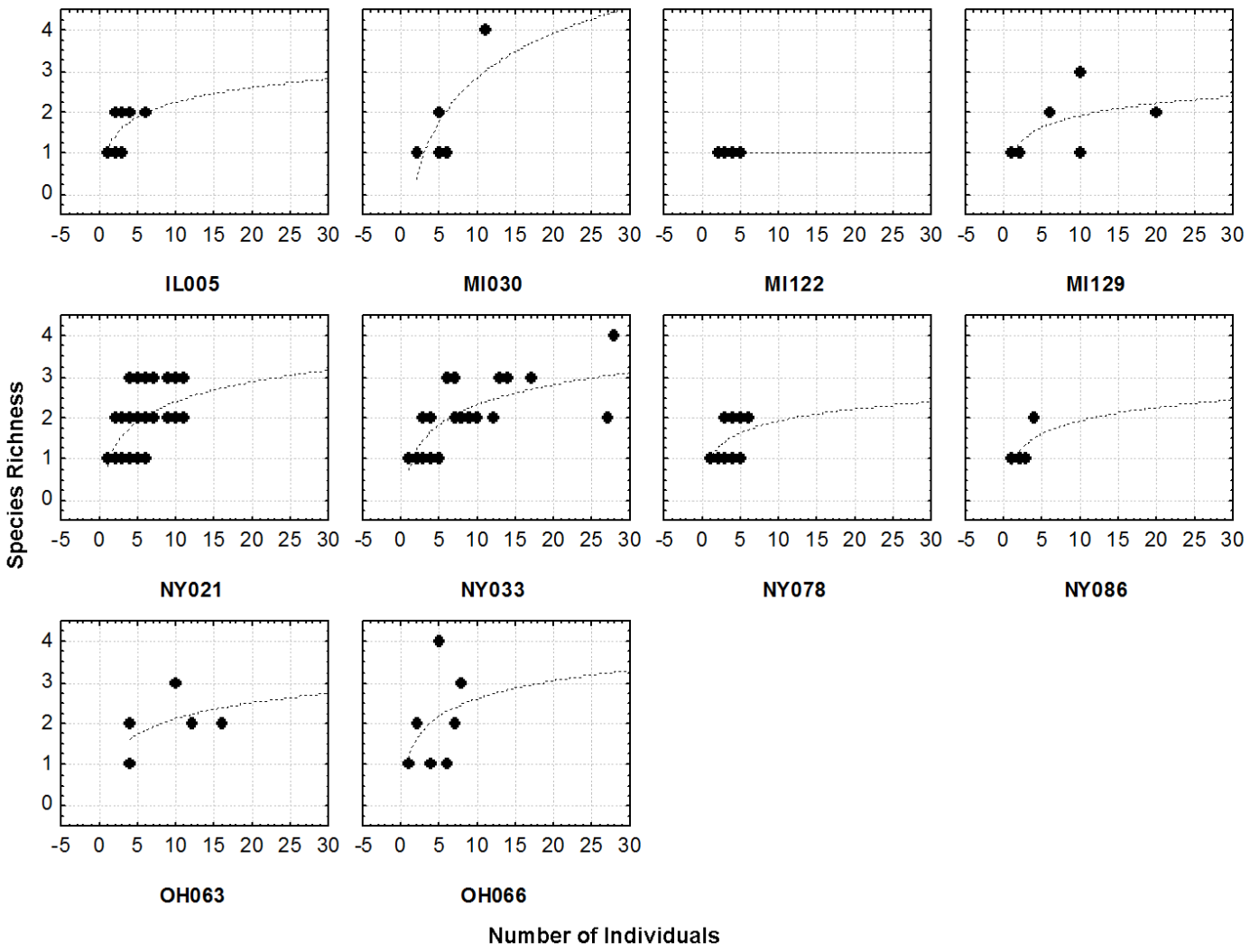
Table 4.3: Linear regression relationships between rarefaction curve parameters (asymptotic species richness, b_1, and the growth coefficient, b_2) and Hurlbert's probability of interspecific encounter (Δ_1) and between rarefaction curve parameters and slope (b_1 b_2).

Taxonomic group		Independent Variable		
	Dependent Variable	b_1 b_2	b_1	b_2
All n=22	Δ_1	ns	$p<0.005$, $r^2=0.41$ m=0.0091 SE=0.21	$p<0.005$, $r^2=0.39$ m=-1.94 SE=0.20
Amphibian n=10	Δ_1	ns	ns	ns
Bird n=10	Δ_1	ns	ns	ns

Table 4.4: Proportions of the 3 most abundant and widespread amphibians, birds, and fishes in terms of relative abundance and site frequency from synoptic and intensive sampling. Values relating relative abundance and site frequency are given in parentheses. Widespread and abundant species identified by both synoptic and intensive sampling protocols are marked with an asterisk.

Taxonomic group	Relative Abundance (% of individuals)		Site Frequency (% of sites)	
	Synoptic	Intensive	Synoptic	Intensive
Amphibians (Synoptic n=610, Intensive n= 198)	**Rana sylvatica,* wood frog (40)	**Rana clamitans melanota,* green frog (67)	**Rana clamitans melanota,* green frog (61)	**Rana clamitans melanota,* green frog (83)
	**Rana clamitans melanota,* green frog (40)	*Pseudacris crucifer*, spring peeper (65)	**Pseudacris crucifer,* spring peeper (57)	**Pseudacris crucifer*, spring peeper (74)
	Pseudacris triseriata & Pseudacris maculate, chorus frog (39)	**Rana sylvatica*, wood frog (64)	*Hyla versicolor*, gray (tetraploid) treefrog (46)	*Bufo americanus*, American toad (73)
Birds (Synoptic n=493, Intensive n= 227)	*Agelaius phoeniceus,* red-winged blackbird (29)	*Euphagus cyanocephalus*, Brewer's blackbird (52)	**Agelaius phoeniceus*, red-winged blackbird (90)	**Agelaius phoeniceus*, red-winged blackbird (95)
	Larus argentatus, herring gull (22)	*Ammodramus leconteii*, Le Conte's sparrow (50)	*Geothlypis trichas*, common yellowthroat (80)	*Tachycineta bicolor*, tree swallow (76)
	Cistothorus platensis, sedge wren (19)	*Buteo lineatus,* Red-shouldered hawk (50)	**Melospiza melodia*, song sparrow (76)	**Melospiza melodia*, song sparrow (75)
Fishes	**Notropis atherinoides,* emerald shiner (43)	**Perca flavescens,* yellow perch (42)	NA	NA
	Percopsis omiscomaycus, trout perch (12)	*Ameiurus nebulosus,* brown bullhead (20)	NA	NA
	**Perca flavescens,* yellow perch (10)	**Notropis atherinoides,* emerald shiner (14)	NA	NA

a)


Species Richness
Number of Individuals
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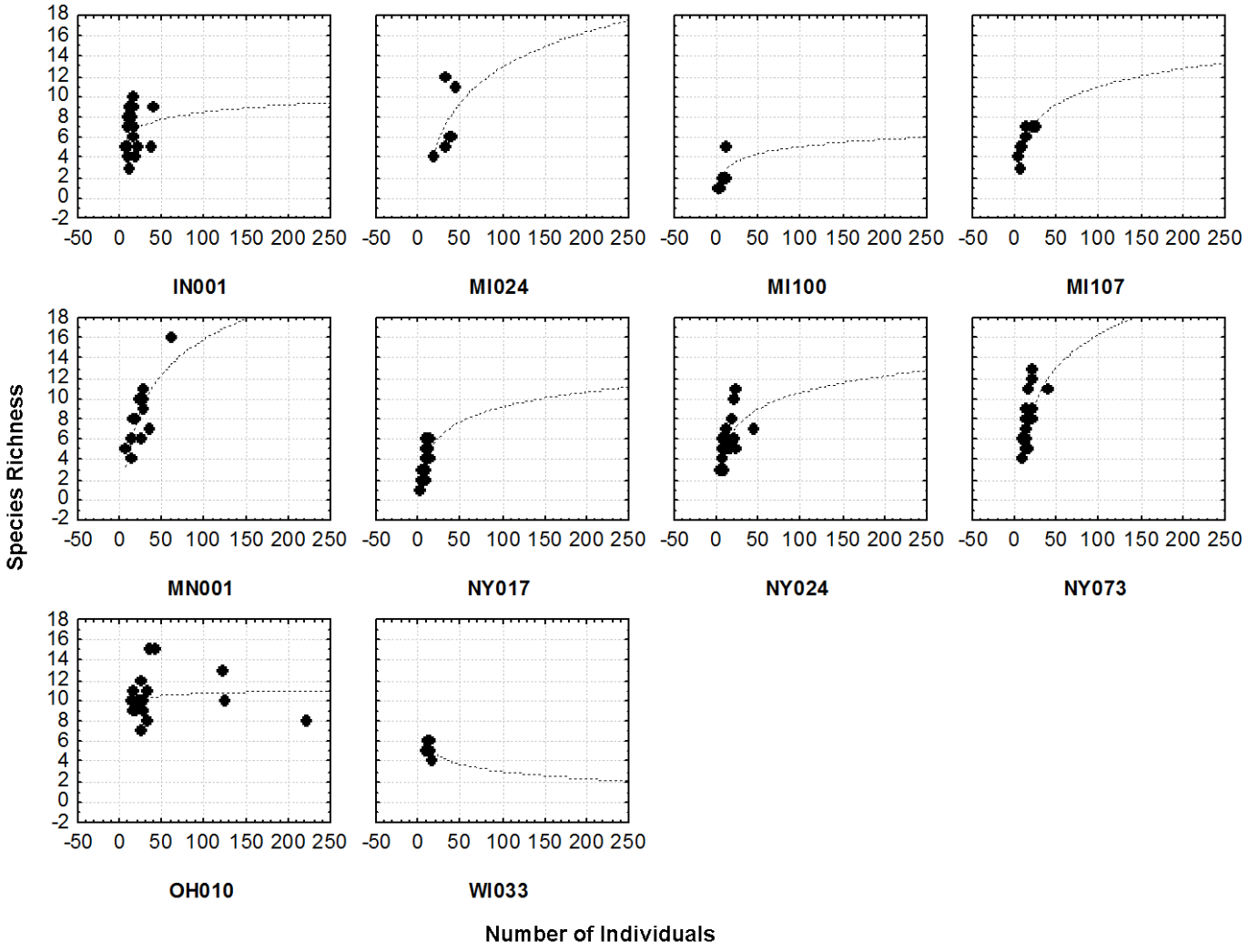
MI030
MI122
MI129
NY021
NY033
NY078
NY086
OH063
OH066

b)


Species Richness
Number of Individuals
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MI024
MI100
MI107
MN001
NY017
NY024
NY073
OH010
WI033

c)

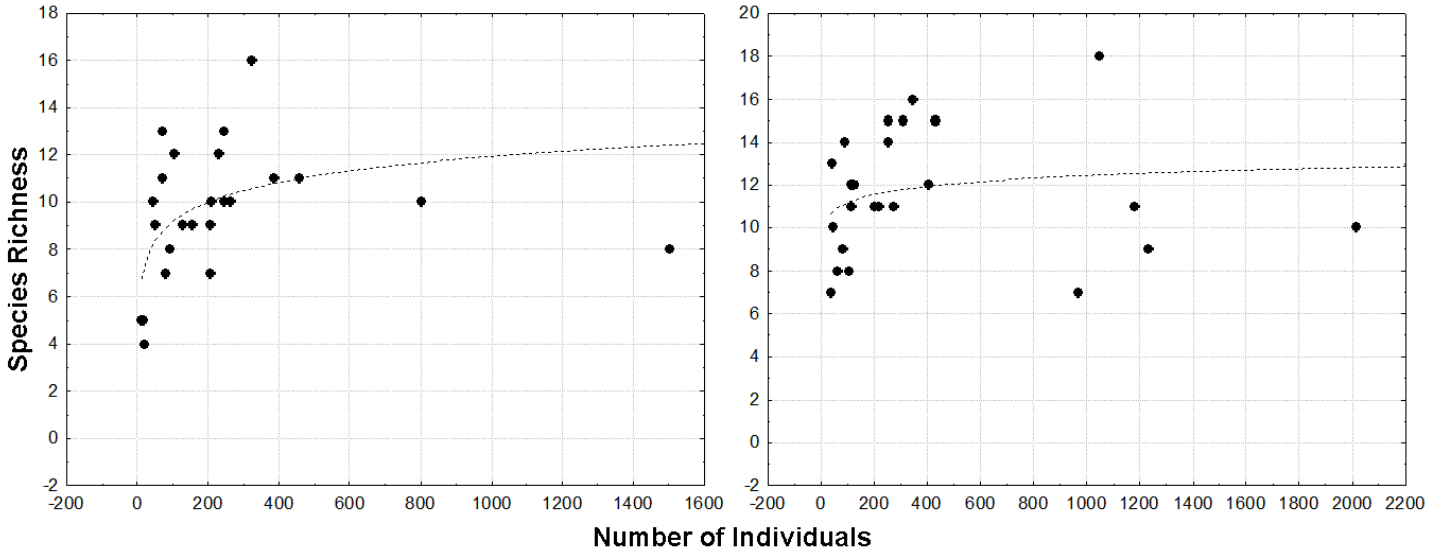


Figure 4.1: Species accumulation curves for amphibian (a), bird (b), fish (c) study areas. Curves fail to reach an asymptote suggesting lack of sampling sufficiency for species richness estimation.

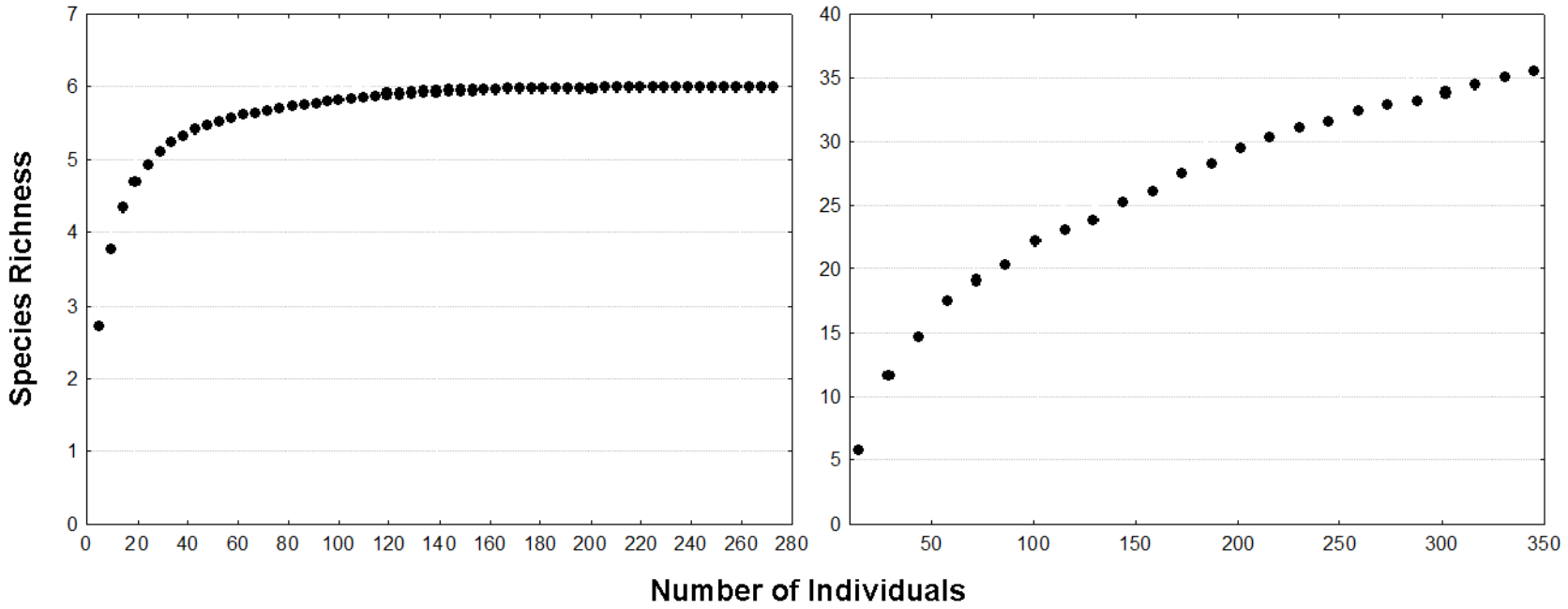
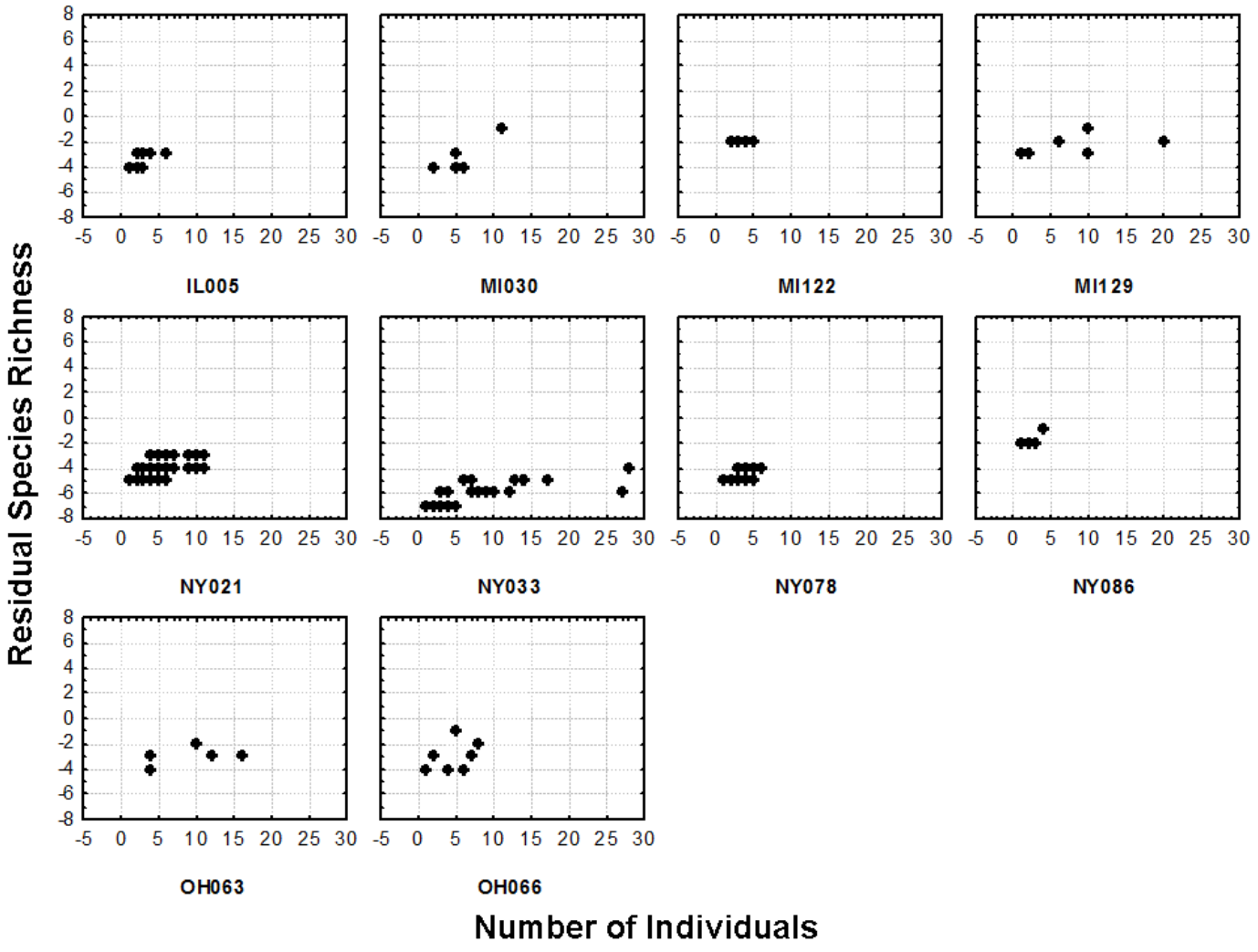


Figure 4.2: Representative rarefaction curves of a) accurate species richness estimation of amphibian site NY021 by Cole estimator that reaches an asymptote and b) inaccurate species richness estimation of bird site NY024 by Jack 1 estimator that fails to reach an asymptote.

ai)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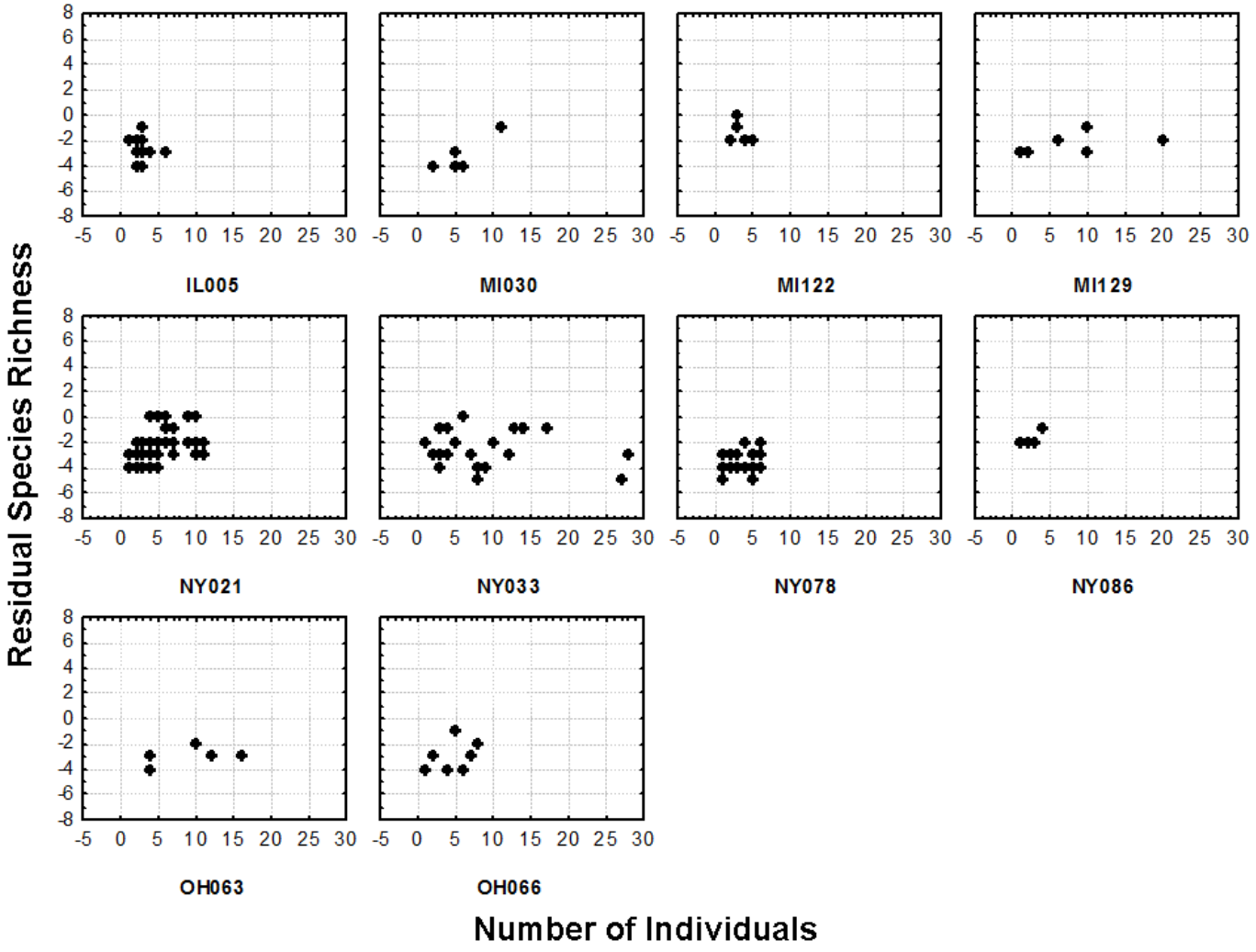
MI030
MI122
MI129
NY021
NY033
NY078
NY086
OH063
OH066
Number of Individuals

aii)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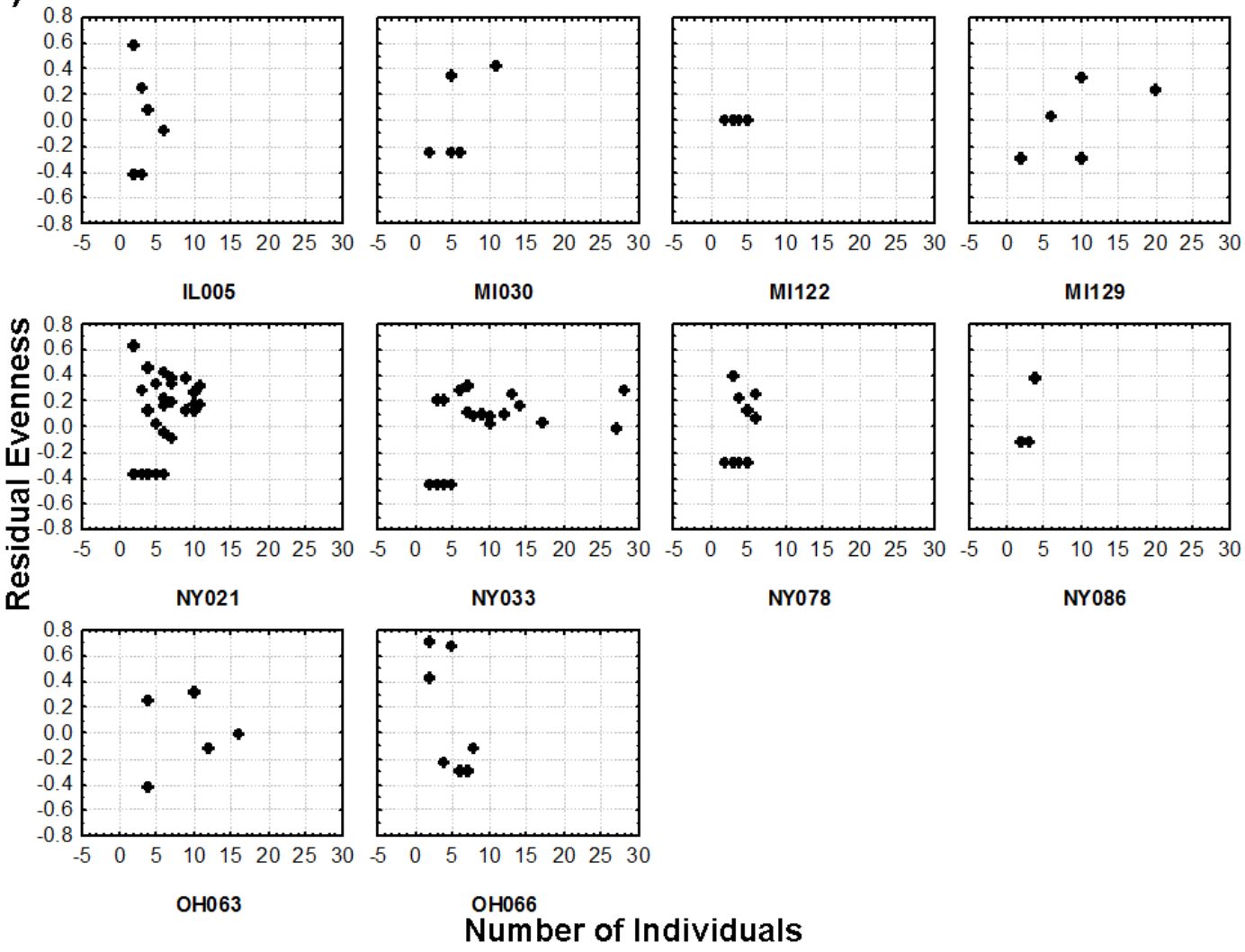
MI122
MI129
NY021
NY033
NY078
NY086
OH063
OH066
Number of Individuals

aiii)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NY021
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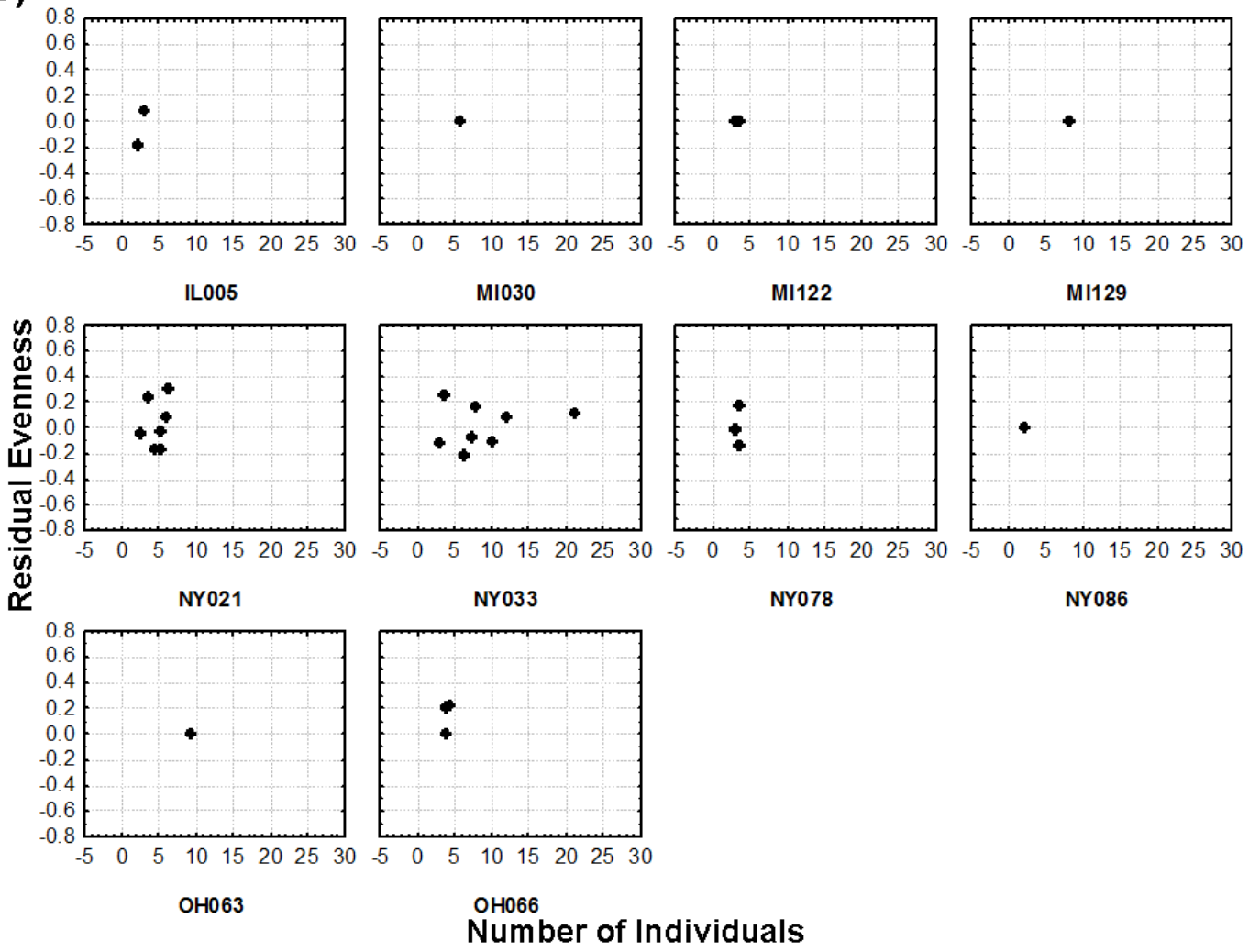
OH066

aiv)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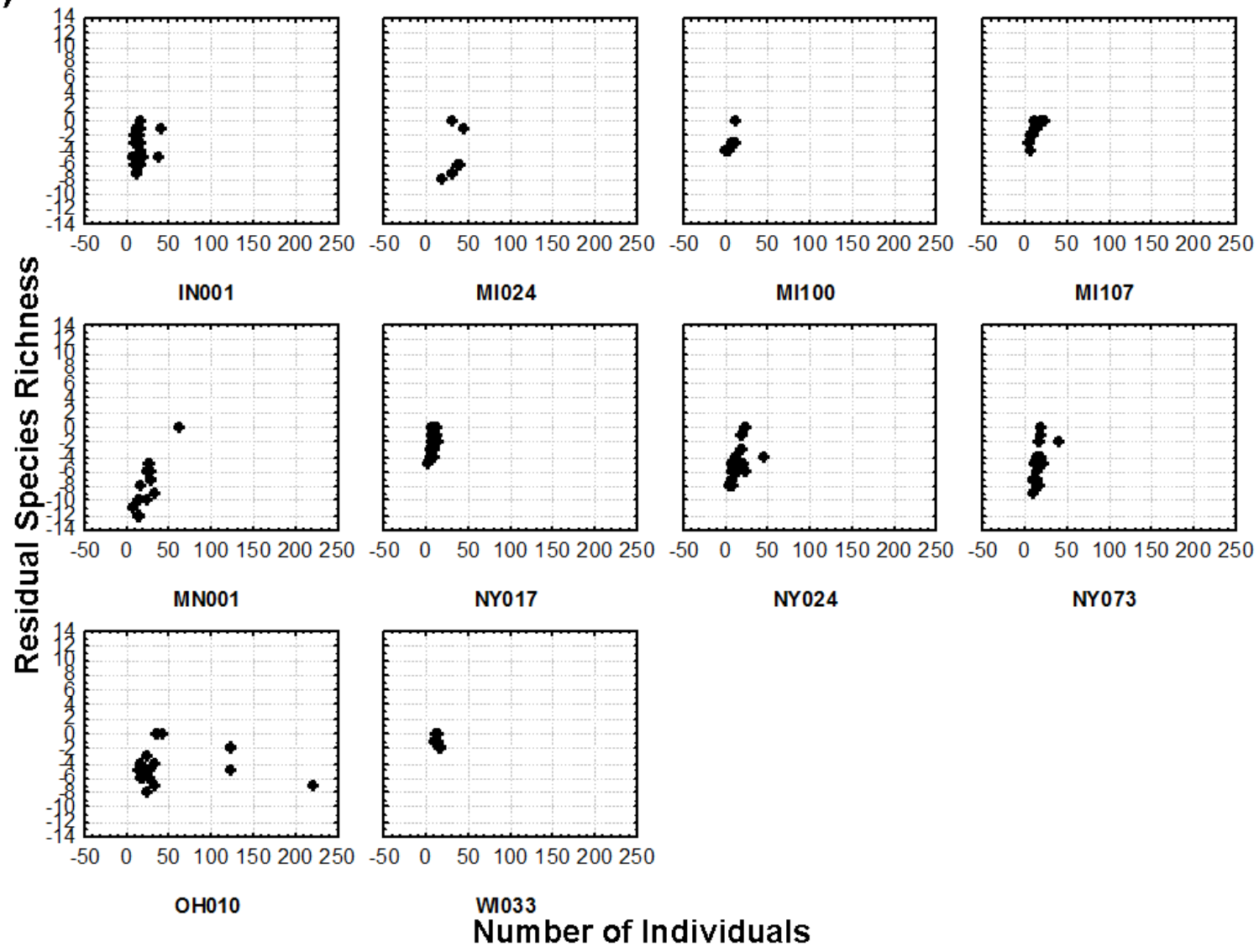
0.6
0.4
0.2
0.0
-0.2
-0.4
-0.6
-0.8
-5 0 5 10 15 20 25 30
IL005
MI030
MI122
MI129
NY021
NY033
NY078
NY086
OH063
OH066
Number of Individuals

bi)


Residual Species Richness
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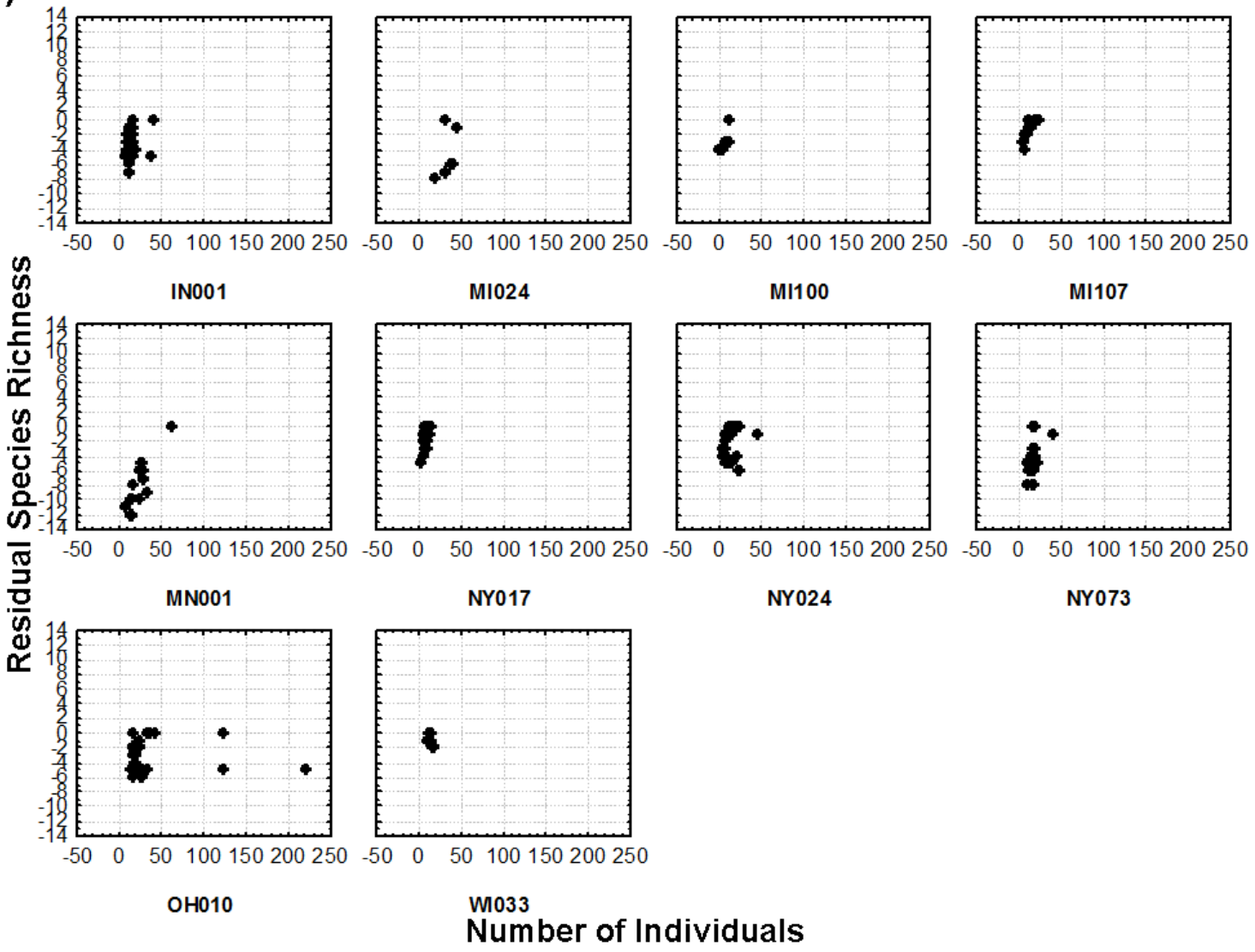
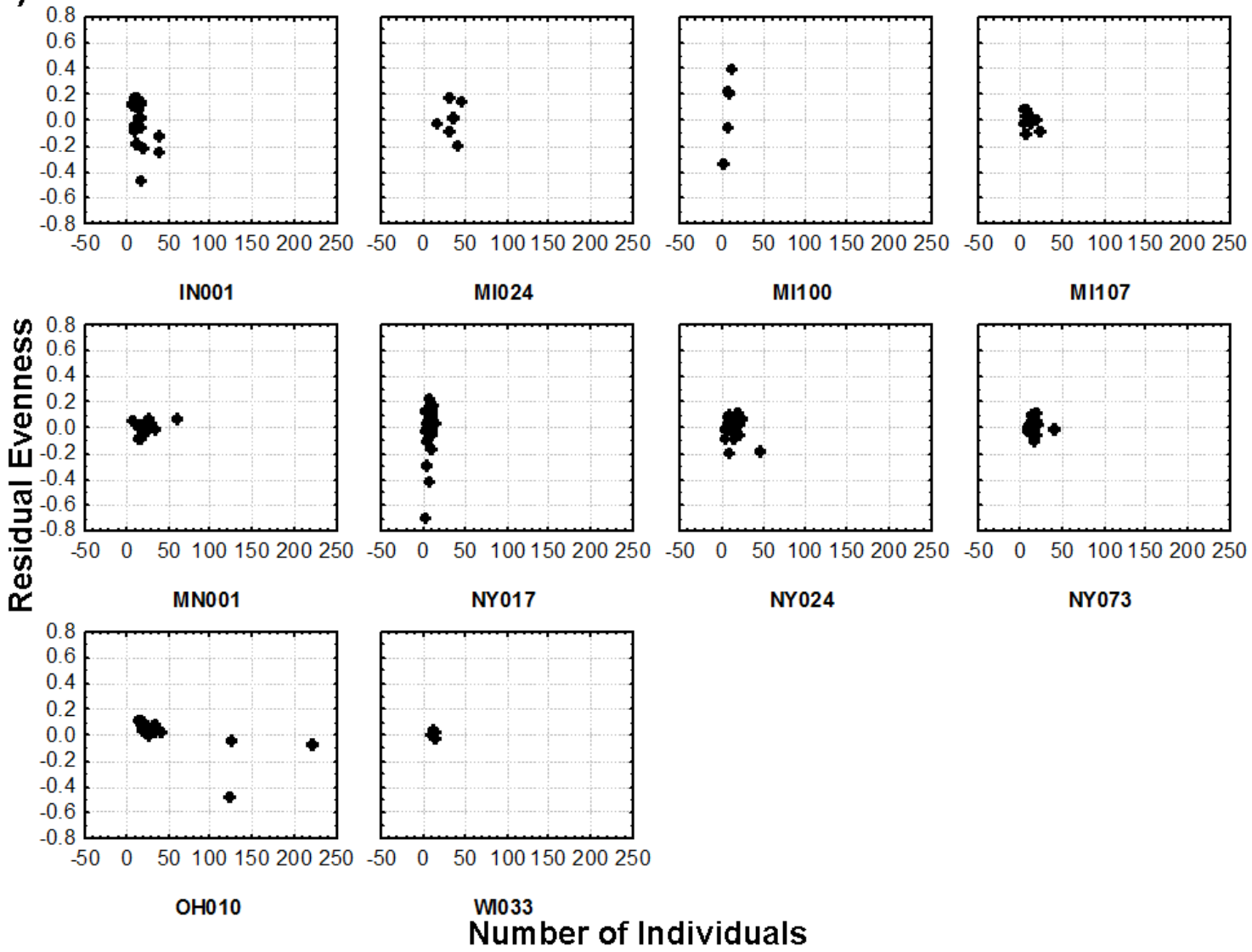
MI024
MI100
MI107
MN001
NY017
NY024
NY073
OH010
WI033
Number of Individuals

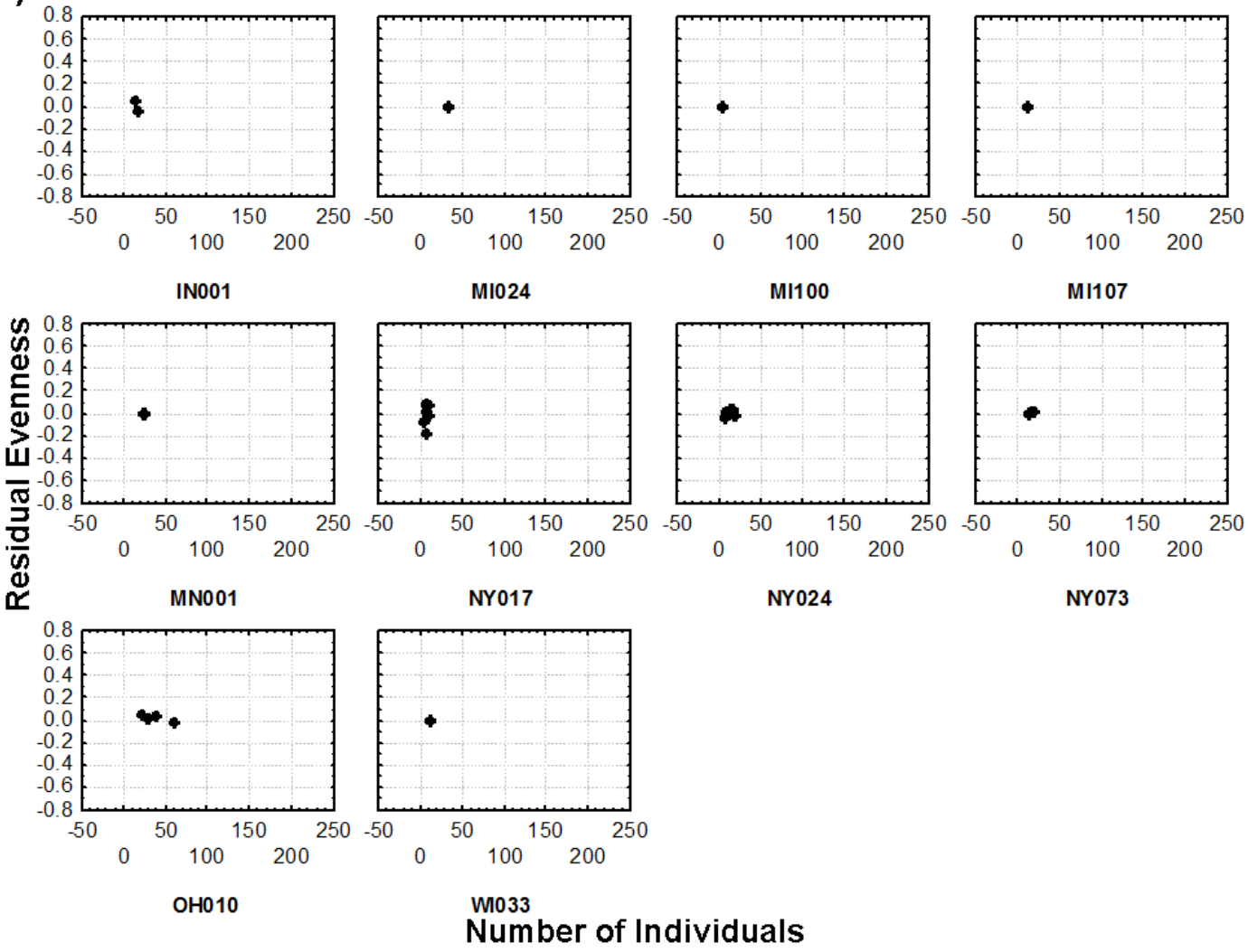
bii)


Residual Species Richness
IN001
MI024
MI100
MI107
MN001
NY017
NY024
NY073
OH010
WI033
Number of Individuals

biii)


Residual Evenness
0.8
0.6
0.4
0.2
0.0
-0.2
-0.4
-0.6
-0.8
-50 0 50 100 150 200 250
IN001
MI024
MI100
MI107
MN001
NY017
NY024
NY073
OH010
WI033
Number of Individuals

biv)


Residual Evenness
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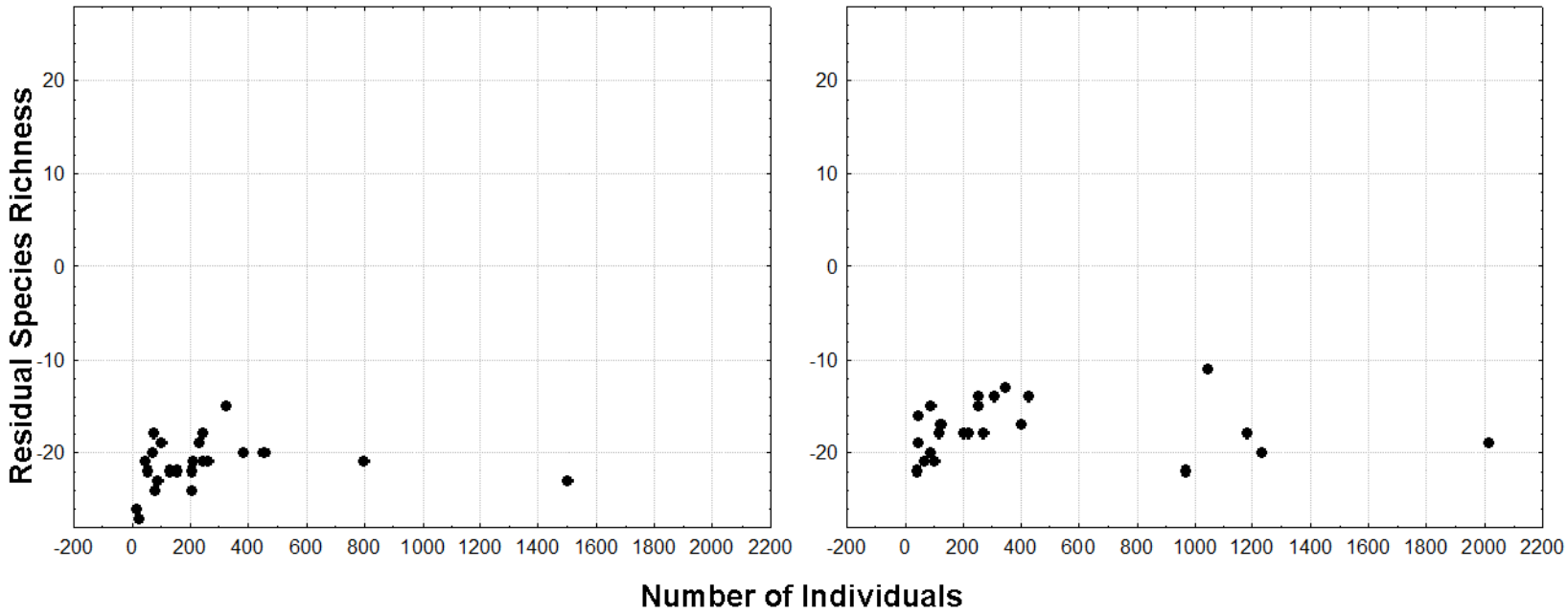
0.6
0.4
0.2
0.0
-0.2
-0.4
-0.6
-0.8
-50
50
150
250
0
100
200
IN001
MI024
MI100
MI107
MN001
NY017
NY024
NY073
OH010
WI033
Number of Individuals

ci)


Residual Species Richness
20
10
0
-10
-20
-200
0
200
400
600
800
1000
1200
1400
1600
1800
2000
2200
Number of Individuals

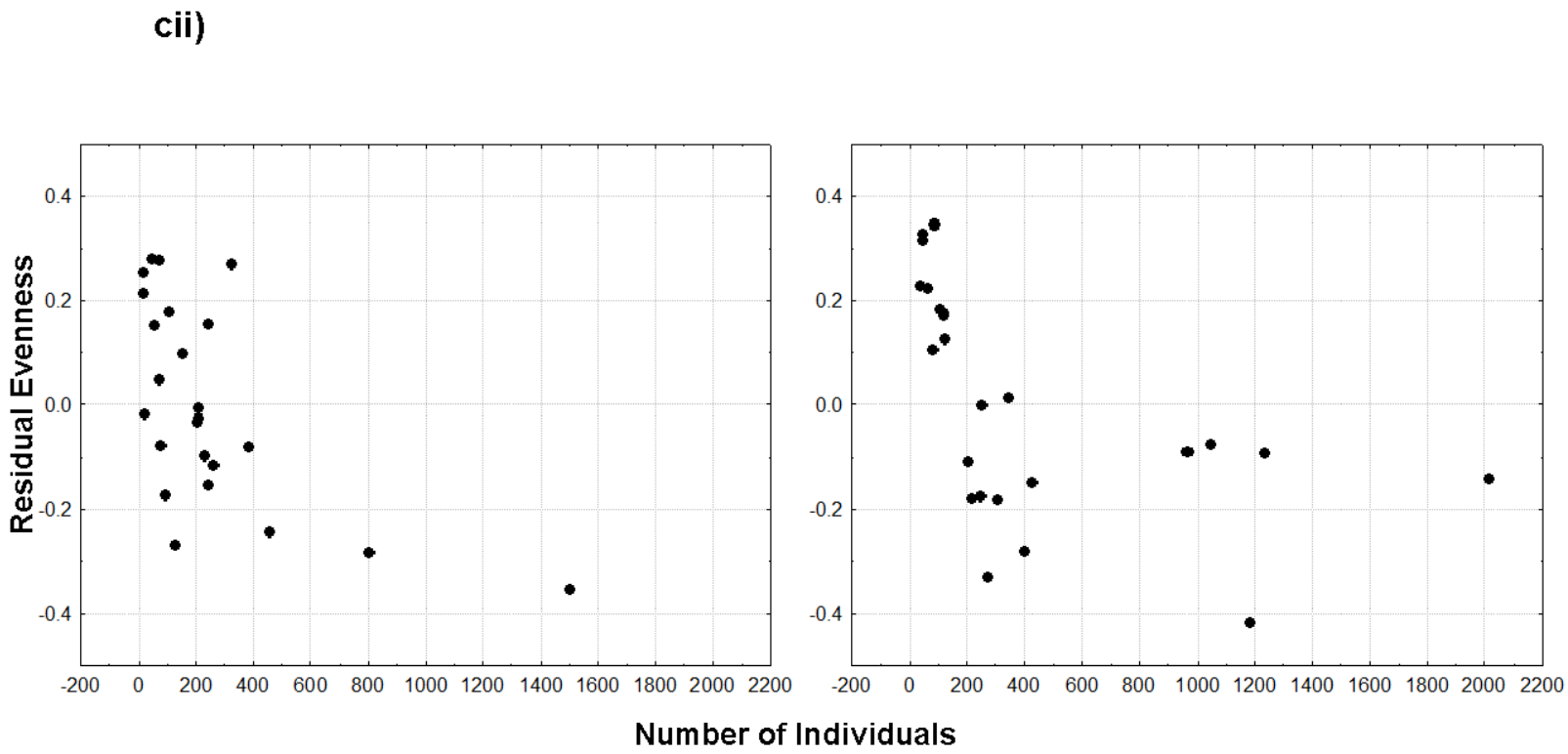
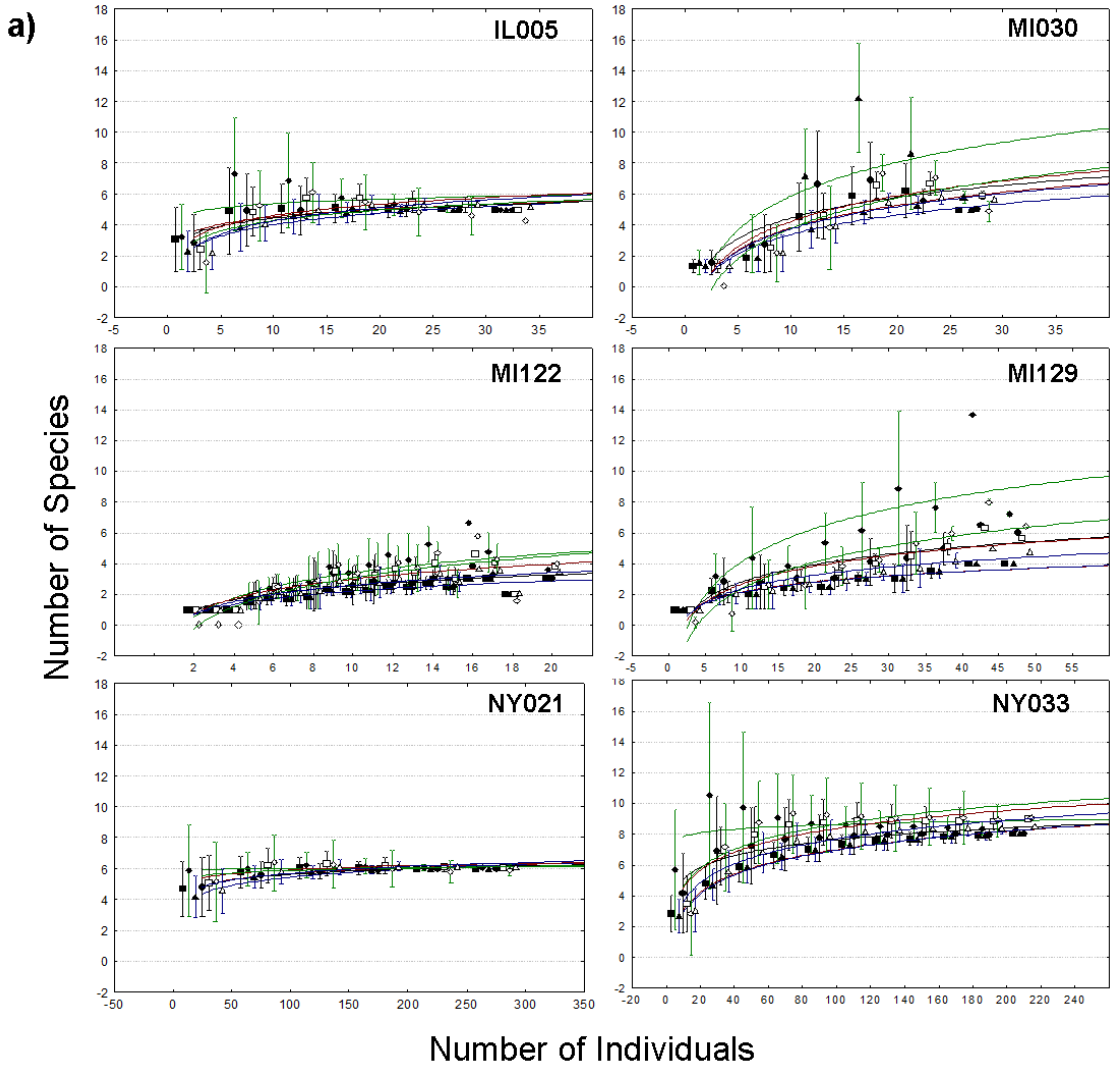
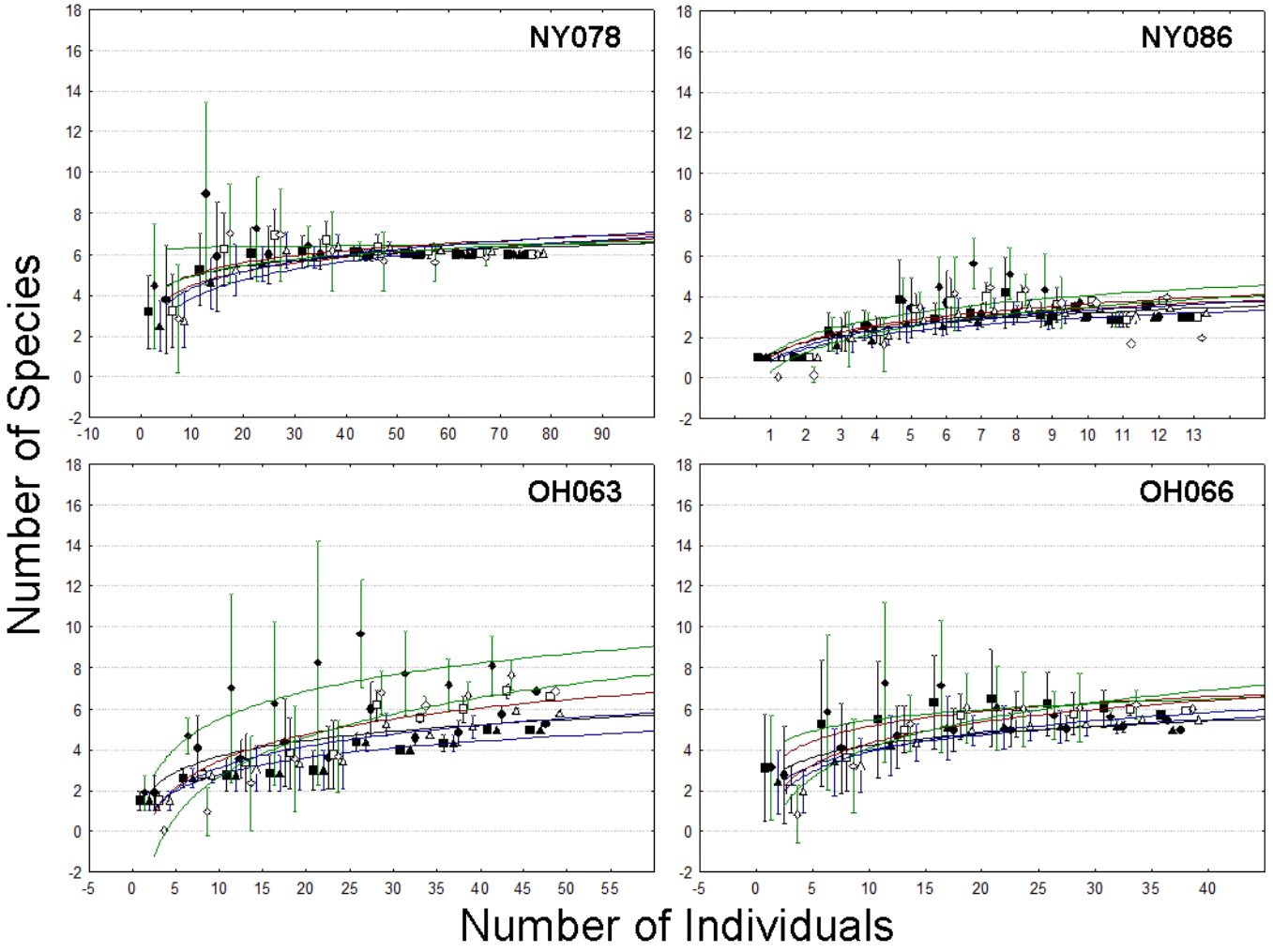
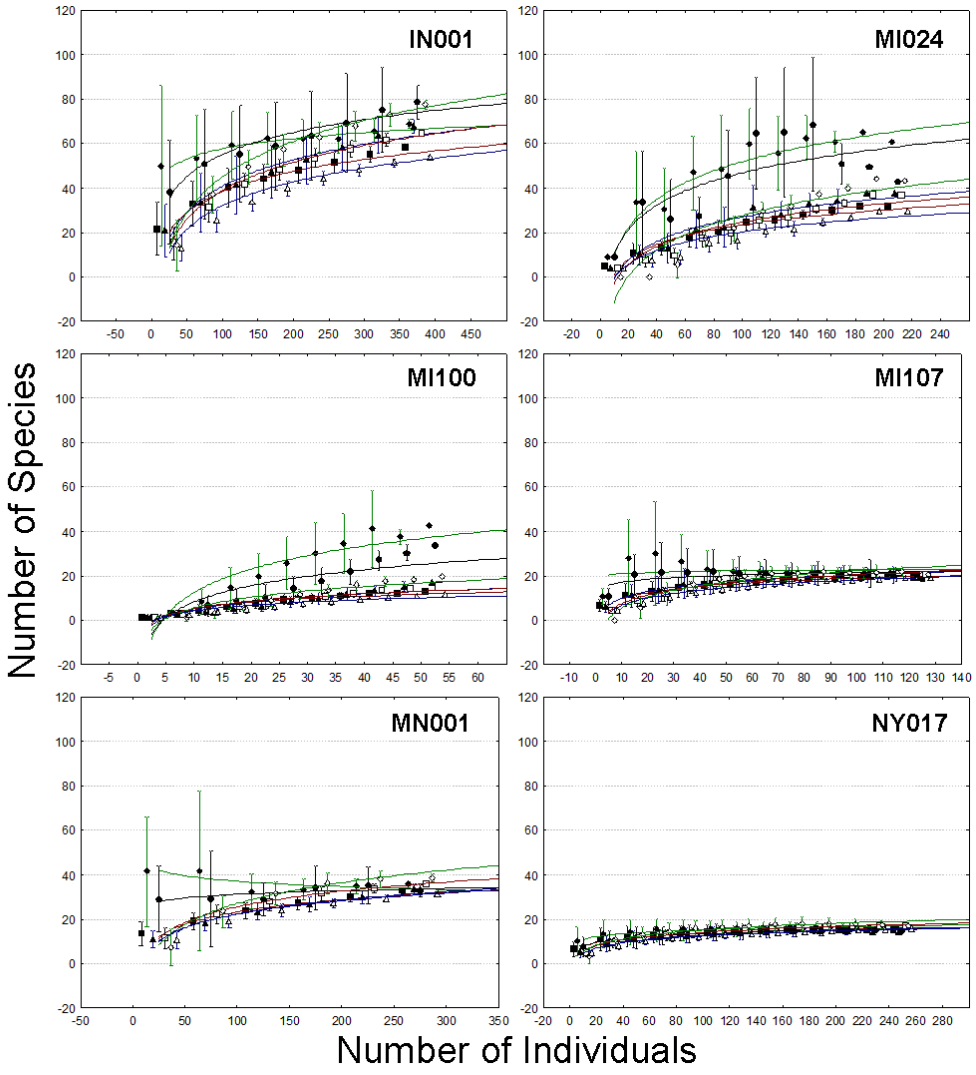


Figure 4.3: Scatterplots of the relationship between residual species richness and evenness with sampling effort for amphibians (ai, aiii), birds (bi, biii), fish (ci). Yearly trends of the relationships for each taxonomic group are also shown (aii, aiv, bii, biv, cii). The zero line represents mean richness and mean evenness.


a)
IL005
MI030
MI122
MI129
NY021
NY033
Number of Species
Number of Individuals


NY078
NY086
OH063
OH066
Number of Species
Number of Individuals

b)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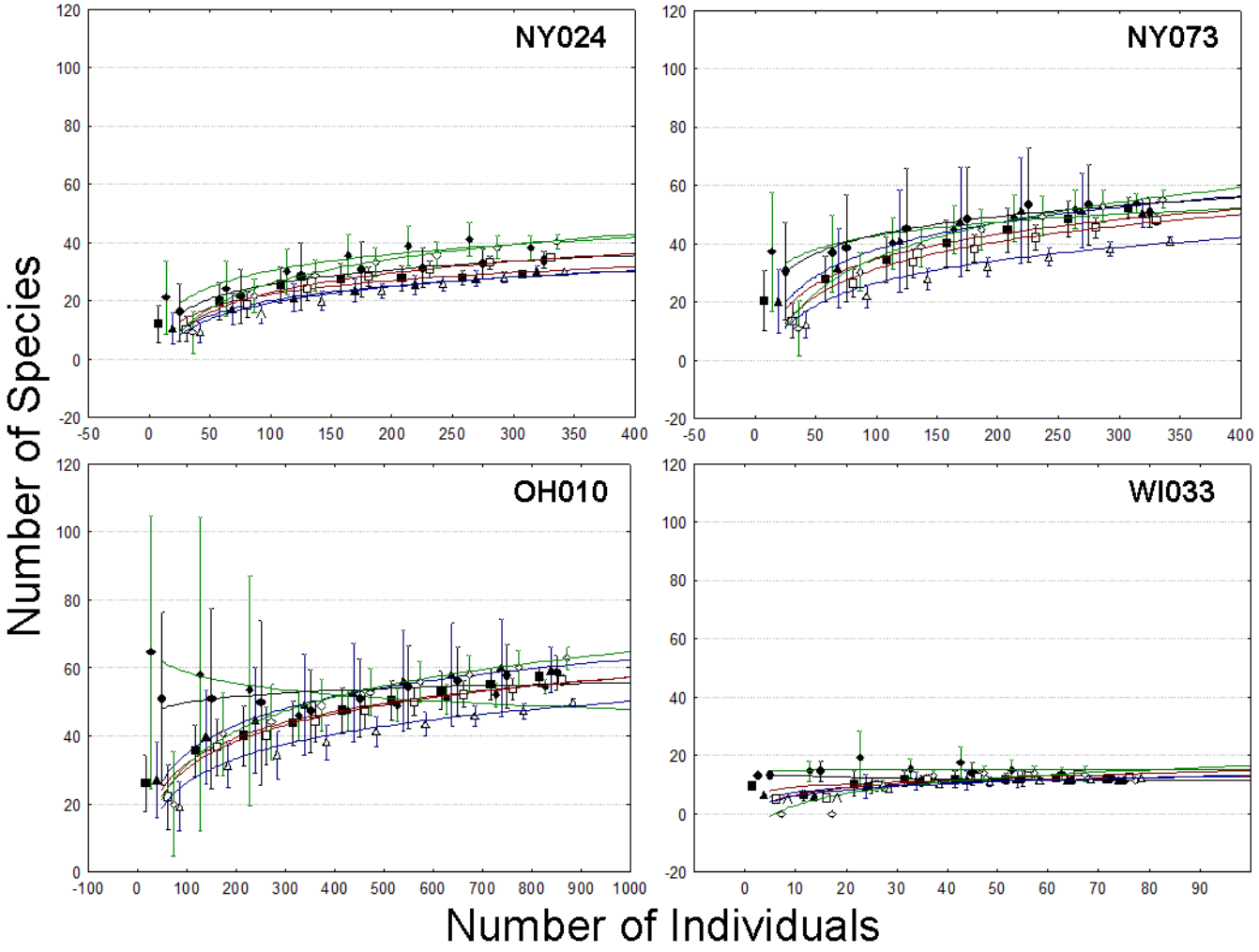
MI024
MI100
MI107
MN001
NY017
Number of Species
Number of Individuals


NY024
NY073
OH010
WI033
Number of Species
Number of Individuals

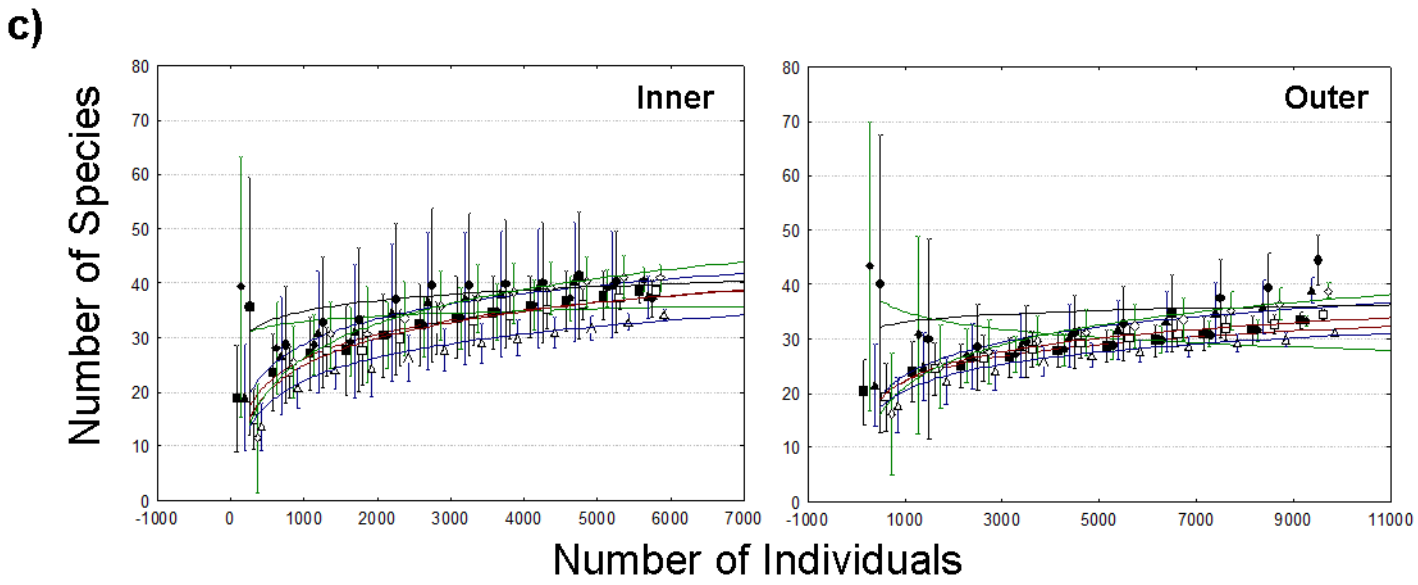
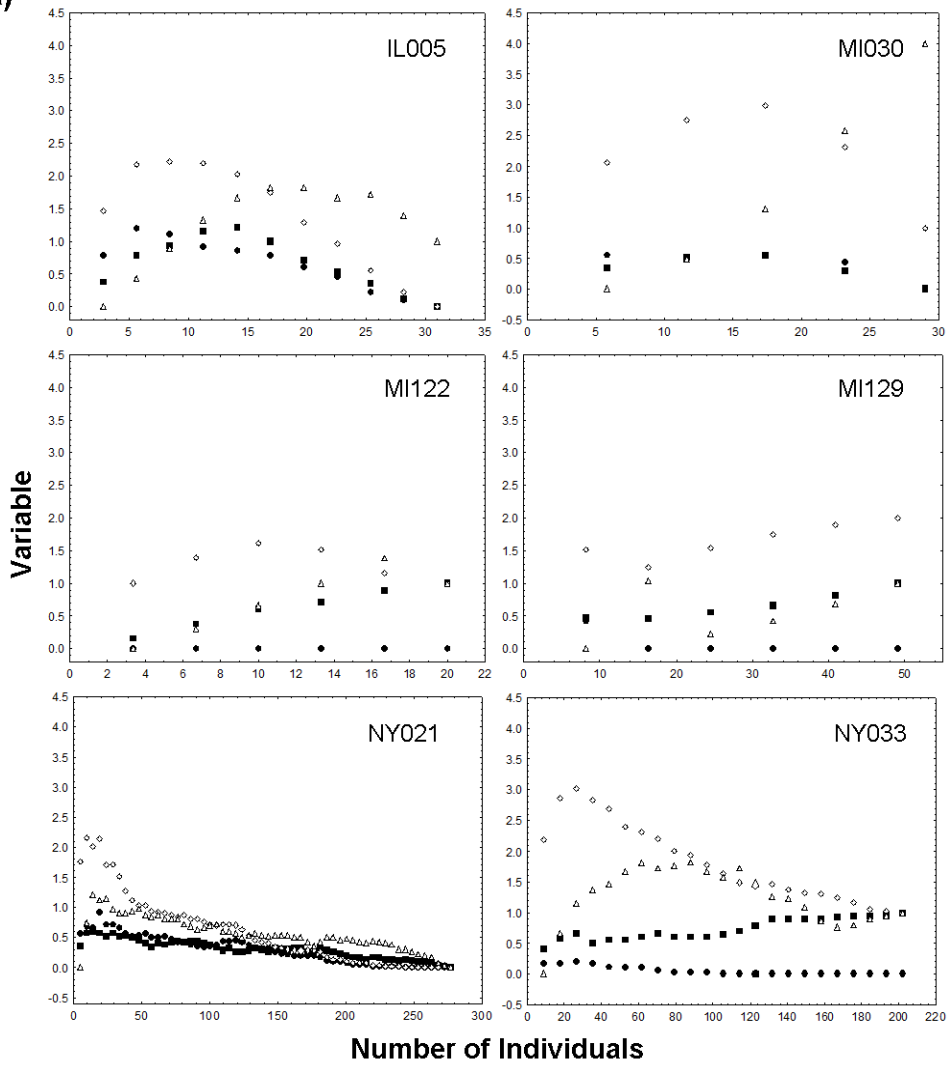
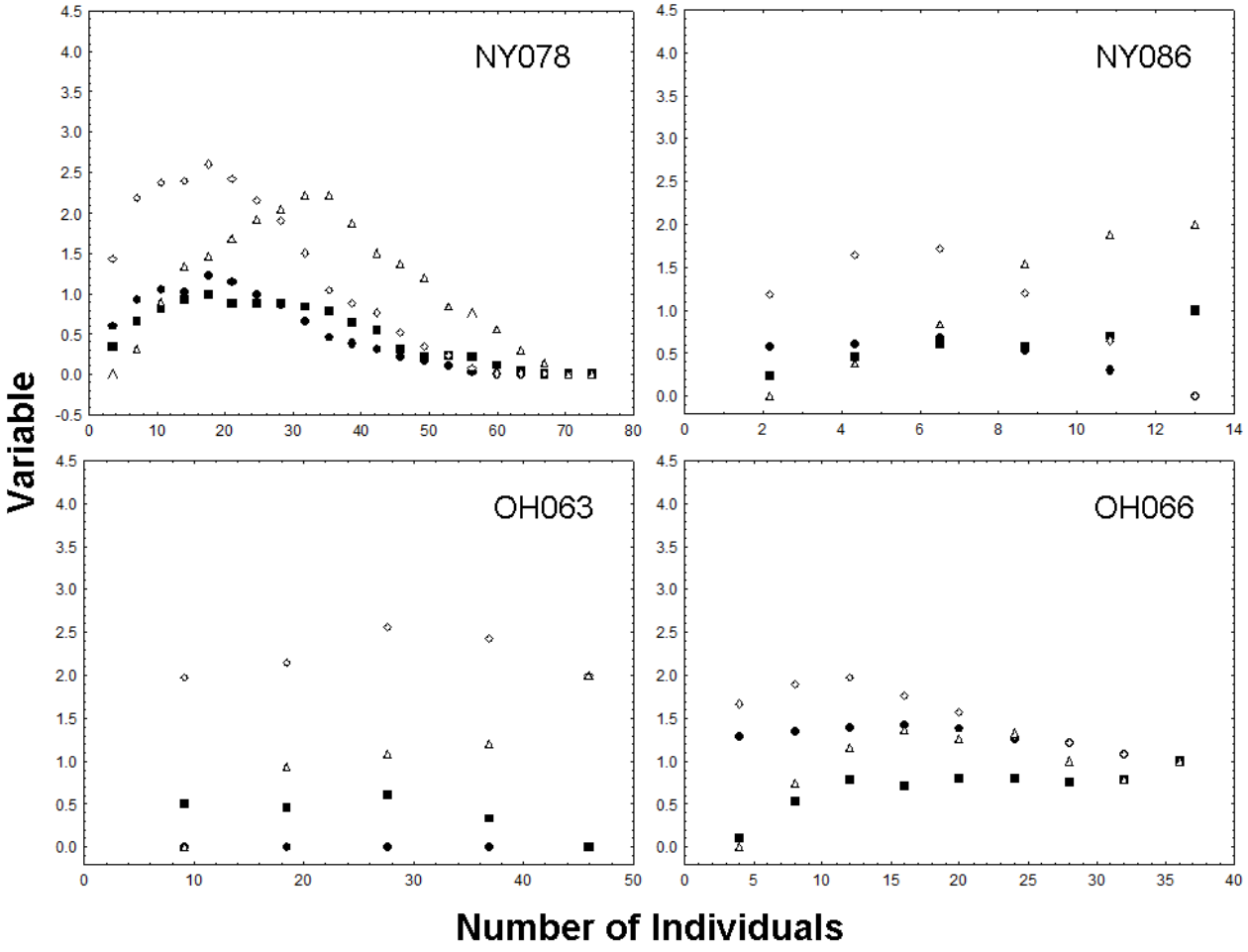


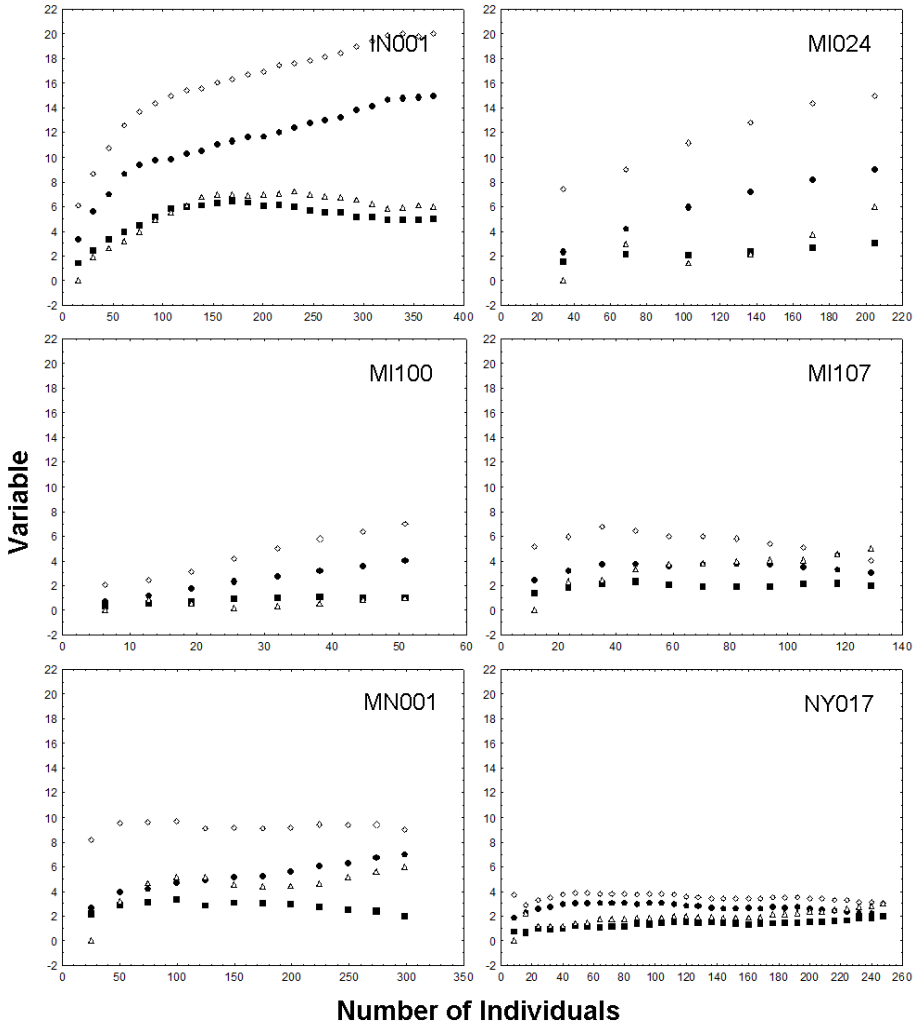
Figure 4.4: Performance of richness estimators for a) amphibians, b) birds, and c) Fish. Richness estimators were ACE (■), ICE (♦), Chao-1 (▲), Chao-2 (●), Jack-1 (□), Jack-2 (◊), and Bootstrap (△).

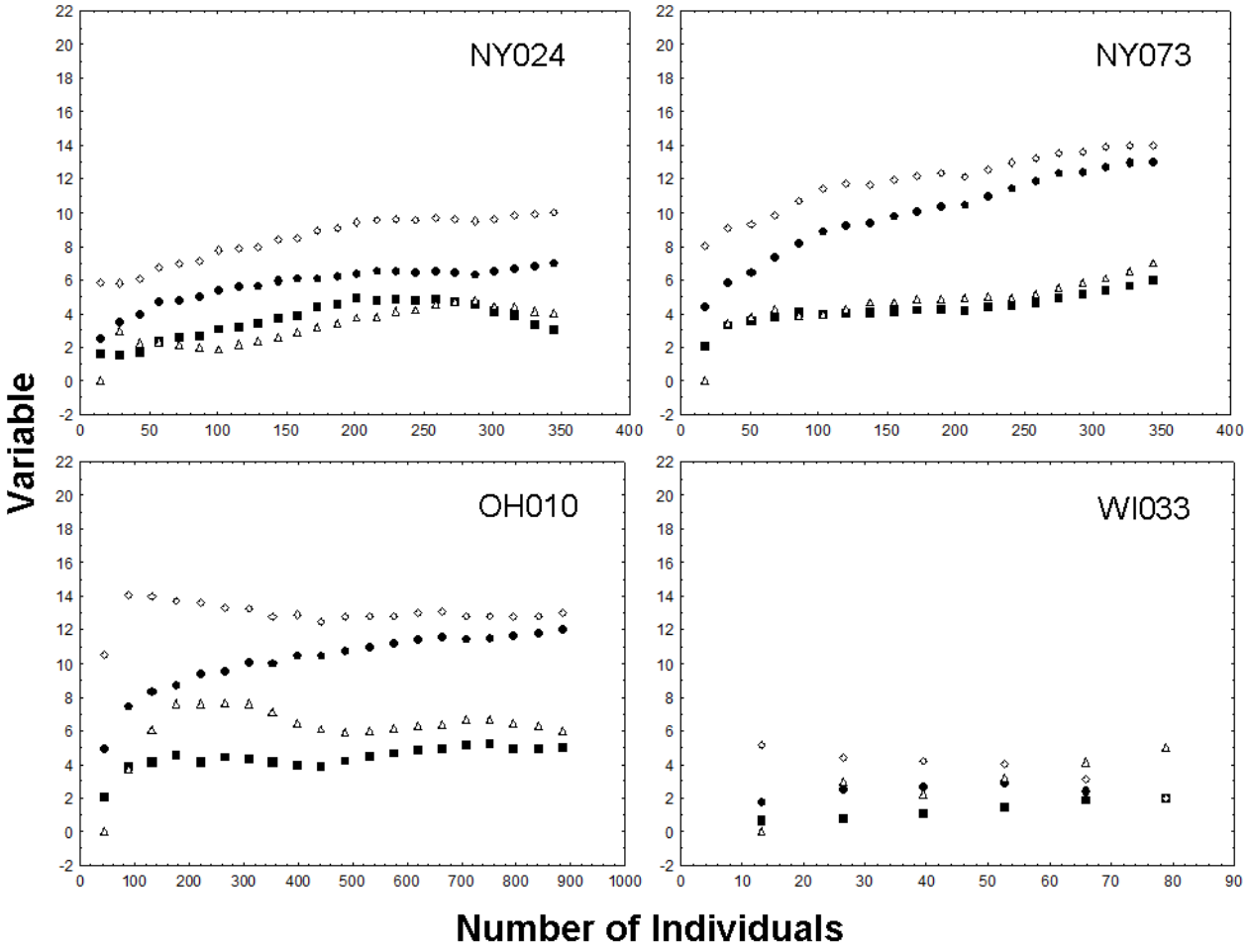
a)


IL005
MI030
MI122
MI129
NY021
NY033
Variable
Number of Individuals


NY078
NY086
OH063
OH066
Variable
Number of Individuals

b)


IN001
MI024
MI100
MI107
MN001
NY017
Variable
Number of Individuals


NY024
NY073
OH010
WI033
Variable
Number of Individuals

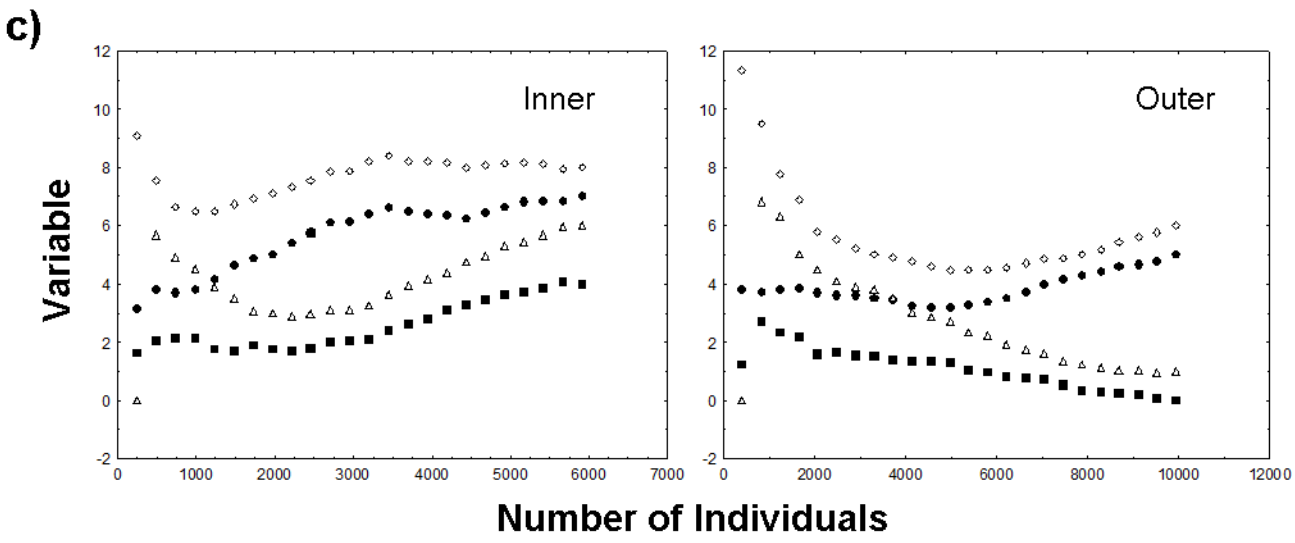


Figure 4.5: Scatterplots of the relationship between sampling effort for a) amphibian, b) bird, and c) fish samples and rare species variables: singleton (●), doubleton (■), unique (◇), and duplicate (△) species.

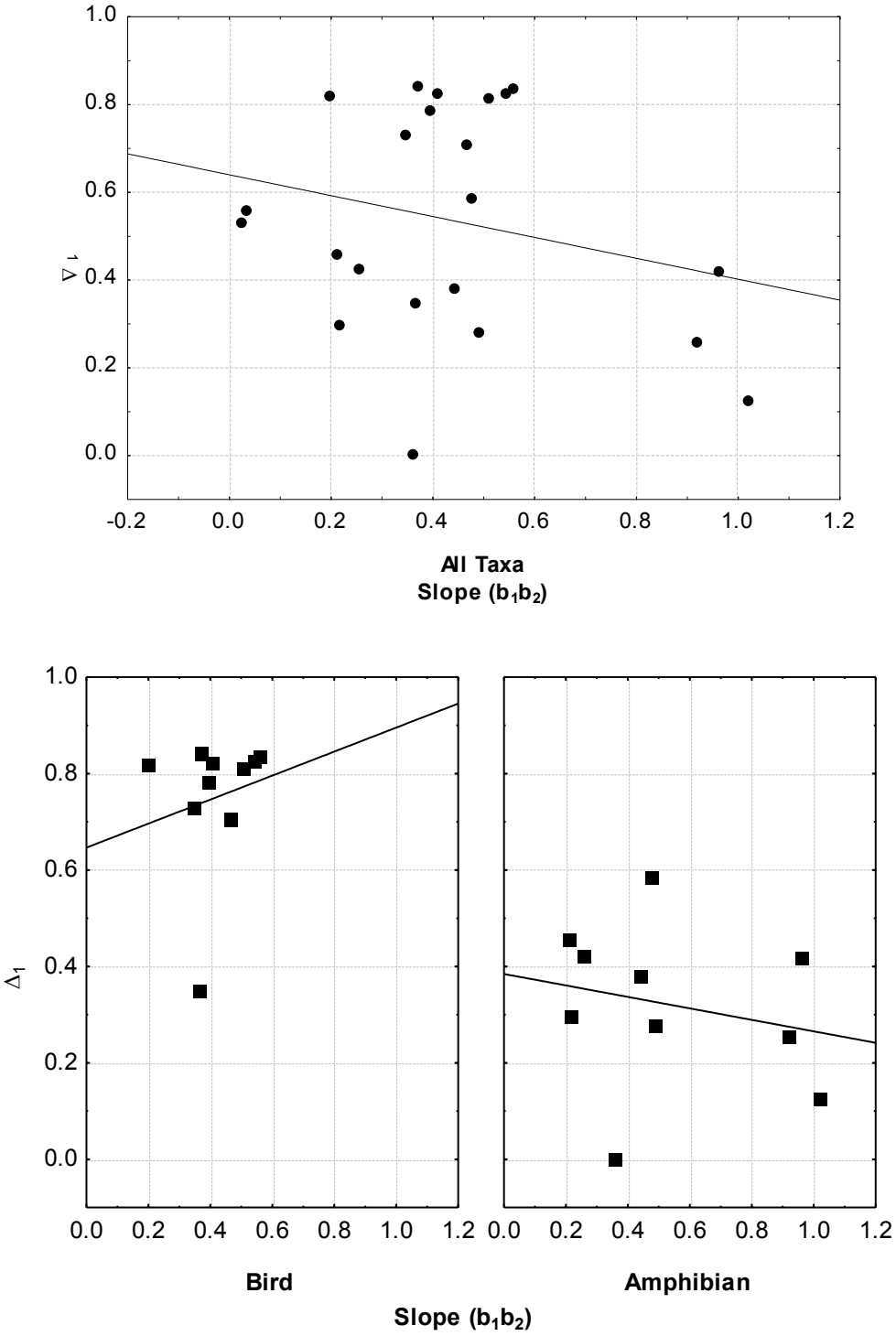


Figure 4.6: Relationship between slope of the rarefaction curve and evenness (Hurlbert's (1971) probability of interspecific encounter, Δ_1) of all taxonomic groups, bird, and amphibian study areas.

Appendix 4.1: Demonstration that the initial slope of a rarefaction curve is equivalent to Hurlbert's (1971) probability of interspecific encounter (Δ_1) by showing that $E(s_m; m=2) - E(s_m; m=1) = \Delta_1$ (from Olszewski, 2004).

$$E(s_2) - E(s_1) = \sum_{i-1}^{s} \left[1 - \frac{\binom{N - n_i}{2}}{\binom{N}{2}} \right] - 1$$

$$= \sum_{i=1}^{S} \left[1 - \frac{\frac{(N - n_i)!}{2!(N - n_i - 2)!}}{\frac{N!}{2!(N-2)!}} \right] - 1$$

$$= \sum_{i=1}^{S} \left[1 - \frac{(N - 2)!(N - n_i)!}{N!(N - n_i - 2)!} \right] - 1$$

$$= \sum_{i=1}^{S} \left[1 - \frac{(N - n_i)(N - n_i - 1)}{N(N - 1)} \right] - 1$$

$$= \sum_{i=1}^{S} \left[\frac{2Nn_i - n_i^2 - n_i}{N(N - 1)} \right] - 1$$

$$= \frac{2N \sum_{i=1}^{S} n_i - \sum_{i=1}^{S} n_i - \sum_{i=1}^{S} n_i^2}{N(N - 1)} - 1$$

$$= \frac{2N}{N - 1} - \frac{1}{N - 1} - \frac{\sum_{i=1}^{S} n_i^2}{N(N - 1)} - 1$$

$$= \frac{N}{N - 1} - \frac{\sum_{i=1}^{S} n_i^2}{N(N - 1)}$$

$$= \frac{N}{N - 1} \left(1 - \frac{\sum_{i=1}^{S} n_i^2}{N^2} \right)$$

$$= \frac{N}{N - 1} \left(1 - \sum_{i=1}^{S} p_i^2 \right) = \Delta_1$$

Appendix 4.2: Description of species richness estimators used for rarefaction.

CHAO-1[1]

CHAO-1 is an abundance-based, nonparametric estimator that relies on the distribution of individuals among species and incorporates into the estimate the number of species caught once (singletons) or twice (doubletons) in a particular lake (Chao, 1984). The estimator is

$$\text{CHAO-1} = \begin{cases} S_{\text{obs}} + \dfrac{F_1^2}{2F_2} & \text{if } F_2 > 0 \\ S_{\text{obs}} + \dfrac{F_1(F_1 - 1)}{2} & \text{if } F_2 = 0 \end{cases},$$

where S_{obs} is the number of species observed, F_1 is the number of species with one individual (singleton) when all samples are pooled, and F_2 is the number of species with two individuals (doubleton) when all samples are pooled.

CHAO-2[1]

CHAO-2 is an incidence based estimator that relies on the distribution of species among samples and requires only presence–absence data (Chao, 1987). This method also incorporates the number of species captured in only one (uniques) or two (duplicates) sampling stations within a lake. The estimator is

$$\text{CHAO-2} = \begin{cases} S_{\text{obs}} + \dfrac{Q_1^2}{2Q_2} & \text{if } Q_2 > 0 \\ S_{\text{obs}} + \left(\dfrac{m-1}{m}\right)\dfrac{Q_1(Q_1 - 1)}{2(Q_2 + 1)} & \text{if } Q_2 = 0 \end{cases},$$

where S_{obs} is the number of species observed, Q_1 is the number of species that were captured in only one sampling station in a lake (uniques), Q_2 is the number of species that were captured in only two sampling stations in a lake (duplicates), and m is the number of samples.

First-order jackknife estimator (Jack-1)[2]

The first-order jackknife (JACK-1) estimator is another nonparametric incidence-based estimator that relies on the number of species that occur in only one sample (Burnham and Overton, 1978, 1979; Heltshe and Forrester, 1983; Smith and van Belle, 1984). The estimator is

$$\text{JACK-1} = S_{\text{obs}} + Q_1\left(\frac{m-1}{m}\right),$$

where S_{obs} is the number of species observed, Q_1 is the number of species that were captured in only one sampling station in a lake (uniques), and m is the number of samples.

Second-order jackknife estimator (Jack-2)[2]

The second-order jackknife (JACK-2) estimator is a nonparametric incidence-based estimator that relies on the number of species that occur in one only sample and in exactly two samples (Burnham and Overton, 1978, 1979; Smith and van Belle, 1984; Palmer, 1991), that is

$$\text{JACK-2} = S_{\text{obs}} + \left[\frac{Q_1(2m-3)}{m} - \frac{Q_2(m-2)^2}{m(m-1)}\right],$$

where the variables are defined as before.

Bootstrap estimator (BS)

The bootstrap (BS) estimator is an incidence-based estimator that relies on the proportion of samples containing each species (Smith and van Belle 1984), that is,

$$\mathrm{BS} = S_{\mathrm{obs}} + \sum_{k=1}^{S_{\mathrm{obs}}} (1 - p_k)^m,$$

where S_{obs} is the number of species observed, p_k is the proportion of samples with species k, and m is the number of samples.

Abundance-based coverage estimator (ACE)[1]

The abundance-based coverage estimator (ACE) relies on those species with 10 or fewer individuals in the sample (Chao *et al.,* 1993), that is,

$$\mathrm{ACE} = S_{\mathrm{abund}} + \frac{S_{\mathrm{rare}}}{\left(1 - \frac{F_1}{N_{\mathrm{rare}}}\right)} + \frac{F_1}{\left(1 - \frac{F_1}{N_{\mathrm{rare}}}\right)} \gamma^2_{\mathrm{ACE}},$$

where S_{abund} is the number of species with more than 10 individuals when all samples are pooled, S_{rare} is the number of species with 10 or fewer individuals when all samples are pooled, N_{rare} is the number of individuals belonging to rare species that are not singletons, and γ^2 ACE is the coefficient of variation of F_1.

Incidence-based coverage estimator (ICE)[1]

The incidence-based coverage estimator (ICE) relies on species found in 10 or fewer sampling units (Lee and Chao,1994), that is,

$$\mathrm{ICE} = S_{\mathrm{freq}} + \frac{S_{\mathrm{infreq}}}{\left(1 - \frac{Q_1}{N_{\mathrm{infreq}}}\right)} + \frac{Q_1}{\left(1 - \frac{Q_1}{N_{\mathrm{infreq}}}\right)} \gamma^2_{\mathrm{ICE}},$$

where S_{freq} is the number of species found in more than 10 samples, S_{infreq} is the number of species found in 10 or fewer samples, N_{infreq} is number of occurrences of infrequent species, and γ^2 ICE is the coefficient of variation of Q_1.

[1]These estimators were designed to estimate a lower bound for species richness

[2]These estimators were designed to reduce bias

CHAPTER 5: GENERAL DISCUSSION AND CONCLUSIONS

GENERAL DISCUSSION

The classical paradigm of ecology views patterns in the distribution and abundance of species as a function of abiotic (i.e., physical and chemical conditions) and biotic factors (i.e., interactions among species - competition, predation, mutualism, disease). These abiotic and biotic factors combined can be viewed as ecosystem properties and processes. The classical paradigm set biodiversity as a passive dependent variable of extrinsic structuring forces governed by ecosystem properties and processes. Ecological studies have been directed towards predicting biodiversity's response to environmental change. Recent work has challenged this idea by supporting the hypothesis that biodiversity is important to ecosystem functioning (Schulze and Mooney, 1993) and has considered the functional role of biodiversity by viewing it as the independent variable, influencing ecosystem attributes such as biomass accumulation (Tilman, 2000), invasibility (Elton, 1958), energy flow (Carpenter *et al.,* 1987), material flow (Chapin, 1986). Work under the new paradigm includes studies investigating the effects of biodiversity loss on productivity and stability (e.g., Tilman *et al.,* 1996; Vitousek, 1997) and the role of biodiversity in influencing invasion by nonindigenous species (NIS), revisiting the classic hypothesis proposed by Elton (1958) (e.g., Stachowicz *et al.,* 1999; Levine, 2000). This dissertation provides insight to the details of the dynamics between feedback loops of abiotic and biotic factors of the new biodiversity-functioning paradigm, as well as community processes.

In Chapter 2, I tested various hypotheses relating NIS establishment to biotic resistance and environmental suitability of the new habitat by comparing distributions of the nonindigenous amphipod, *Echinogammarus ischnus*, with that of a widespread amphipod, *Gammarus fasciatus*, at sites influenced by varying types and levels of anthropogenic stress. *Echinogammarus* occurred wherever environmental conditions were suitable and that were concurrently occupied by dreissenids. This is consistent with the environmental suitability hypothesis (Baltz

and Moyle, 1993) but not with the disturbance hypothesis (Elton 1958) as an explanation for the distribution of *Echinogammarus* at Great Lakes coastal margins. Prior establishment and strong facilitation imparted by dreissenids likely aided the amphipod's establishment in the Great Lakes, in concert with sufficient propagule pressure. This case study provides a good example of the dynamics between biodiversity and function. Both suitable abiotic and biotic conditions governed the establishment success of a NIS, and this could also apply to the dispersal of a native species entering a new range of its habitat.

Chapter 3 expanded on findings from Chapter 2 by testing hypotheses relating native species (NS) diversity, dominance, and interaction-neutral processes to communities' invasibility. This was the first study to test the various hypotheses linked to invasion using numerous taxonomic groups at comparable sampling locations that took sampling artifacts into account. Hence, the results bear on interpretation of factors governing invasion, and biodiversity-ecosystem function processes. I found that suitable conditions (sufficient dispersal/propagule pressure and suitable habitat) that allow for establishment of a population, are the primary determinants of invasion success. These suitable conditions are not unlike the conditions that are needed for the dispersal of NS. Thus, the same conditions of necessity pertain to both NS and NIS. The identity of an individual does not predetermine the likelihood of its success in a new environment. Evidently, dispersal and environmental factors most strongly regulate the distribution of biota that I investigated.

Findings from Chapter 4 illustrated the inaccuracy of species richness estimation by a number of methods using datasets compiled from intensive sampling. Most biodiversity studies likely expend less sampling effort in collecting samples than was used in this study. Therefore, the accuracy of these datasets for total species estimation is likely lower. Hence, even intensive survey studies produce biodiversity estimates that are inaccurate, particularly when research focuses on the biodiversity of rare species. Yet, surveys do accurately portray the biodiversity of common species. Biodiversity studies overall would benefit from a stronger focus on common species, that is, the proportion of the community that

accounts for much of the ecosystem functioning and biodiversity dynamics (e.g., Smith and Knapp, 2003; Taylor *et al*., 2006; Gaston, 2008).

The functional roles of NIS, especially those that become keystone species, can be significant (Drake *et al.,* 1989). By altering habitats, NIS can affect the fluxes of resources in ecosystems in a variety of ways (Mack and D'Antonio 1998; Crooks 2002; Bais *et al.,* 2003). Measures are critically needed to prevent introductions, especially since NIS can have significant and unpredictable effects, as history has shown with introductions of ecosystem engineers, such as dreissenid mussels, *Neogobius melanostomus* (round goby), and *Typha angustifolia* L (narrow-leaf cattail), *Carassius auratus* (goldfish), and *Cyprinus carpio* (common carp). Nonindigenous species rarely establish, but the impacts that successful keystone invaders may have can be so strong that measures should be in place to prevent introductions, especially since post-establishment dynamics in new habitat are unknown. Time and money would be efficiently invested in research to prevent NIS introductions rather than in NIS detection/monitoring or control/eradication. Studies of predictive models that determine the likelihood of successful introduction of potential NIS based on invasion history, propagule pressure, and habitat suitability are beneficial (Grigorovich *et al.,* 2003; Ricciardi, 2003). Measures to prevent those species that have high potential for invading the Great Lakes must be screened from ballast and other dispersal vectors, especially those that may enter even with ballast water exchange and other dispersal prevention measures.

Conversely, my synoptic evaluations suggest that the contribution of detectable aquatic NIS to Great Lakes biodiversity estimates is negligible. When all species are viewed equivalently and biodiversity is assumed to be the importance of richness and evenness, the identity of species in terms of their native status is not important. The functional roles of NIS are equivalent to those of native species. Native species contribute to ecosystem function differently from one another, with some having strong effects while others have negligible effects. Similarly, this differential influence on ecosystem function has been shown with NIS. For example, an NIS, such as *Dreissena polymorpha* (zebra mussel) has a

markedly different effect on Great Lakes ecosystem function than does *Echinogammarus ischnus*.

Dreissena polymorpha is a highly efficient filter feeder that increases water clarity. The resulting change in transparency promotes the growth of macrophytes that act as substrate for settling mussel larvae, while species adapted to turbid water conditions (e.g. *Sander vitreus*, walleye) are excluded from the new habitat (Vanderploeg *et al.,* 2002). *Dreissena polymorpha* also attach to hard substrates, such as the shells of other mollusks, which can act as foci for initial settlement. Zebra mussels create expanding clusters of byssally-attached shells which are preferred substrate for larvae (Berkman *et al.,* 1998). Attached zebra mussels add successively greater surface area to clusters and promote subsequent colonization (Ricciardi *et al.,* 1995). This fouling activity hinders feeding, respiration, excretion, and valve movement of native mussels and can cause mortality.

In contrast, studies predicted (Witt *et al.*, 1997) or demonstrated (Dermott *et al.*, 1998; Stewart *et al.*, 1998; Burkart, 1999) that *Gammarus fasciatus* would be replaced by *E. ischnus* on *Dreissena* substrata and subsequent changes in littoral food web organization or transfer efficiencies were anticipated (Dermott *et al.*, 1998; Nalepa *et al.,* 2001). However, more recent studies suggest that *E. ischnus* is not systematically replacing *G. fasciatus* in the Great Lakes (Chapter 2; Palmer and Ricciardi 2004, Palmer and Ricciardi 2005, Limen *et al.,* 2005). *Echinogammarus ischnus* has been found in the stomachs of yellow perch and whitefish collected in Lake Michigan (Pothoven *et al.,* 2001) but their biomass transfer contribution is unknown. The impact of the amphipod on the ecosystem of the lakes may be minor, and certainly less dramatic than that of *Dreissena* (Dermott *et al.*, 1998).

Some NIS are common/dominant like some native species. Although findings from Chapter 3 indicated that NIS generally do not dominate invaded habitats, NIS occasionally become common and invasive (i.e., have a propensity to become widespread and abundant to the detriment of other species) in some communities. Similarly, some common native species have negative influences

on other species and can in turn be invasive. The two NIS discussed above are different in their invasiveness, as well as contribute differently to the ecosystem function of the Great Lakes. *Dreissena polymorpha* is invasive and common, while *E. ischnus* is inconspicuous. In Chapter 4, I discussed the significance of investigation of common species and their roles for elucidation of the dynamics between biodiversity and ecosystem function. It is clear that invasive NIS are more detectable than rare NIS, so NIS contributions (and similarly native species contributions) to the biodiversity and ecosystem functioning of the Great Lakes may be marked by a few invasive and/or keystone species.

Many NIS have long been present in the Great Lakes. Biodiversity trends of invaded sites that include both new and older NIS show that habitats are relatively resilient since NIS have not influenced the biodiversity of the locations they invade (Chapter 3). Native species that have strong impacts on community structure disperse to new areas as well, but research efforts have primarily been focused on dispersal of NIS, rather than on understanding how species become problematic, since propagule pressure and dispersal of NIS are perceived to have far greater impacts than that of NS. This is mainly due to the reputation of NIS as being invasive. Invasive NIS can provide valuable biodiversity-function information and make good case studies of establishment since they have high research profiles and are more readily distinguishable from native species. Studies linking invasiveness of NIS and their functional roles would contribute greatly to biodiversity-functioning research.

Giller *et al.,* (2004) proposed that experiments that manipulated local and regional richness, as well as dispersal rate, would help to add realism to biodiversity-functioning research. Assessment of comparable effects of propagule pressure and NIS addition to local and regional richness would contribute similarly to elucidation of biodiversity-functioning.

GENERAL CONCLUSIONS

Determination of the relative importance of the abiotic and biotic factors that regulate community processes has been a major endeavour in ecological research and more recently in the study of invasions. Given that ecology's view of biodiversity has shifted from the classic paradigm, where biodiversity is a function of ecosystem properties and processes, to one where biodiversity is both a response and explanatory variable of ecosystem properties and processes, a parallel shift in focus by the study of invasions is inevitable.

Invasion is a common event and a natural part of community dynamics. However, NIS rarely have strong impacts on their new habitat or act as ecosystem engineers. Just as ecologists have emphasized rare species, they have also scrutinized NIS, preferentially focusing on studies of attributes of NIS and invaded habitats, as though the factors that regulate NIS distributions are different from the factors regulating native species. The NIS that become widespread and abundant are likely governed by the same factors that regulate common native species. Ecology would benefit from linking studies of the factors that regulate the distribution and abundances of common species, both native and nonindigenous, and the dynamics between biodiversity and ecosystem properties and processes, as under the new biodiversity-function paradigm.

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