

A community of metacommunities: exploring patterns in species distributions across large geographical areas

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Abstract. Ecological communities show extremely complex patterns of variation in space, and quantifying the relative importance of spatial and environmental factors underpinning patterns of species distributions is one of the main goals of community ecology. Although we have accumulated good knowledge about the processes driving species distributions within metacommunities, we have few insights about whether (and how) environmental and spatial features can actually generate consistent species distributional patterns across multiple metacommunities. In this paper we applied the elements of metacommunity structure (EMS) framework to identify and classify metacommunities according to multiple but discrete patterns of species distributions. Given that each pattern has unique underlying structuring mechanisms, exploring and comparing such patterns across multiple metacommunities spanning large geographical areas provides a way to test the existence of general principles underlying species distributions within metacommunities. In this study, we applied the EMS framework into a data set containing about 9000 lakes distributed across 85 fish metacommunities across Ontario, Canada, and estimated the relative importance of local and spatial factors in explaining their distributional patterns. Nested and Clementsian gradients were the patterns that fitted most metacommunities; nested metacommunities were distributed throughout the province, while Clementsian gradient metacommunities were concentrated in the southeastern region. Sixty-five percent of nested metacommunities were located in low-energy watersheds (i.e., colder climate and shorter growing season), whereas metacommunities representing Clementsian gradients were present in high-energy watersheds (i.e., relatively warmer climate and longer growing season). Taken together, our results reveal that the environmental and spatial properties in which metacommunities are embedded are at least partially responsible for their species distributional patterns.

Key words: biogeography; Clementsian gradients; community composition; distribution pattern; lake fish; metacommunity structure; nestedness; spatial variation; turnover.

INTRODUCTION

The processes that select species to assemble into local communities and how they vary across space have been a core theme in ecology as a science (Ricklefs 1987, Gaston 2000, Holyoak et al. 2005). In this context, the metacommunity framework serves to understand how the links between dispersal, environmental factors and species interactions determine the regional coexistence of species within landscapes (Leibold et al. 2004, Holyoak et al. 2005). One main feature of this framework is the analysis of multispecies distributional patterns along environmental gradients (Leibold and Mikkelsen 2002, Heino 2005, Presley et al. 2009), which seeks to identify the processes (e.g., biotic and abiotic) that account for different types of nonrandom species associations within

metacommunities (Gotelli and Graves 1996, Presley et al. 2009, Willig et al. 2011).

Several analytical tools have been developed to identify patterns of species distributions within metacommunities (Hoagland and Collins 1997, Haudsorf and Hennig 2007). However, in general, these frameworks evaluate one type of distributional pattern (e.g., nestedness) and as a consequence, a metacommunity may be found as randomly structured because other distributional patterns, which may fit the data equally well, were not considered (e.g., Gleasonian gradients, checkerboards; see Table 1 for a description of different types of metacommunities). Leibold and Mikkelsen (2002) created the elements of metacommunity structure (EMS) framework that serves to analyze multiple models simultaneously, comparing them against each other to assess which one best fits to a particular metacommunity. These models are based on the interaction of three different elements (coherence, turnover, boundary clumping) of the metacommunity structure as measured in a site-by-species, incidence

Manuscript received 26 April 2012; revised 4 September 2012; accepted 2 October 2012. Corresponding Editor: D. E. Schindler.

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TABLE 1. The expected statistical patterns and description of the six species distributional patterns considered by the elements of metacommunity structure (EMS) framework.

Metacommunity structure	Statistical pattern	Description
Random	<i>Coherence</i> is random, i.e., number of embedded absences in the metacommunity is not different than what is expected by chance.	Species within the metacommunity are randomly distributed according to the main gradient uncovered by correspondence analysis.
Checkerboard	<i>Coherence</i> is significantly negative, i.e., there are more embedded absences than what is expected by chance.	The metacommunity is composed of pairs of mutually exclusive species that occur independently of one another.
Nestedness	<i>Coherence</i> is significantly positive, i.e., there is less embedded absences than what is expected by chance. <i>Turnover</i> is significantly negative, i.e., there is a lower number of replacements than what is expected by chance.	The metacommunity is composed of species-poor sites that are predictable subsets of the species composition from richer sites.
Evenly spaced gradient	<i>Coherence</i> is significantly positive. <i>Turnover</i> is either random or significantly positive, i.e., more replacements than what is expected by chance. <i>Boundaries</i> are hyperdispersed, i.e., Morisita Index is lower than 1.	The metacommunity is composed of species that compete along an environmental gradient and their distribution is dictated by trade-offs in their ability to explore alternative resources.
Clementsian gradient	<i>Coherence</i> is significantly positive. <i>Turnover</i> is either random or significantly positive, i.e., more replacements than what is expected by chance. <i>Boundaries</i> are clumped, i.e., Morisita Index is greater than 1.	The metacommunity is composed of discrete biotic communities that show similar responses to environmental gradients and replace each other across space.
Gleasonian gradient	<i>Coherence</i> is significantly positive. <i>Turnover</i> is either random or significantly positive, i.e., more replacements than what is expected by chance. <i>Boundaries</i> are randomly distributed, i.e., Morisita Index is not significantly different from 1.	The metacommunity is composed of species that have somewhat idiosyncratic responses to abiotic factors and, as a consequence, communities gradually change in species' compositions across space.

matrix. From these elements, six different patterns of species distributions can emerge (Fig. 1, Table 1), and each can be linked to a particular way in which species interact and respond to biotic and abiotic factors along distributional gradients across patches (Leibold and Mikkelsen 2002).

The first element of the EMS framework, namely coherence, relates to the level in which species respond to the same environmental gradient (i.e., different habitat affinities). If species have completely independent (random) patterns of distributions, the metacommunity will present a noncoherent structure (Fig. 1, Table 1; Leibold and Mikkelsen 2002). If metacommunities are composed of pairs of mutually exclusive species that occur independently of other pairs along the gradient, thus having negative coherence, they are classified as checkerboards (Diamond 1975). Positive coherence indicates that species are responding to the same environmental gradient and characterizes the remaining EMS patterns. Turnover relates to the way species compositions change across communities. Nestedness occurs in metacommunities with low turnover rates, where the composition of species-poor sites represents subsets of progressively richer sites (Ulrich et al. 2009). When turnover rates are higher than expected, metacommunities can be classified as Clementsian, Gleasonian, or evenly spaced gradients based on a pattern of species clumping. Clumping measures the level of distinctiveness of blocks of species. Communities forming discrete species group showing similar responses within gradients, and that replace each other across

space, are termed Clementsian gradients (positive clumping), whereas communities composed of species that show idiosyncratic responses to the gradient and yield a metacommunity with a continuum of gradually changing composition are termed Gleasonian gradients. Finally, metacommunities with negative clumping are termed evenly spaced gradients and are composed of species likely competing along a gradient and trading off in their ability to explore alternative resources (Tilman 1982).

Although a large number of studies have assessed some of these distributional patterns separately (e.g., nestedness, Cook and Quinn 1995, Fernández-Juricic 2002; Clementsian gradients, Hoagland and Collins 1997), to date only a few studies have applied the EMS approach to test for multiple patterns (see Presley et al. 2009) or compared patterns across different metacommunities (e.g., Leibold and Mikkelsen 2002). Yet, the EMS approach is an extremely promising framework because it allows characterizing metacommunity patterns across different taxa and/or regions, and provides an exceptional venue to search for general rules in determining the structure of community assemblages across space (and also in time). Given that each EMS pattern can be considered as a "metacommunity trait" with unique underlying structuring mechanisms and theoretical foundations (Hoagland and Collins 1997, Leibold and Mikkelsen 2002), exploring and comparing such patterns across large geographical regions encompassing several metacommunities has the potential to enhance our understanding of how biolog-

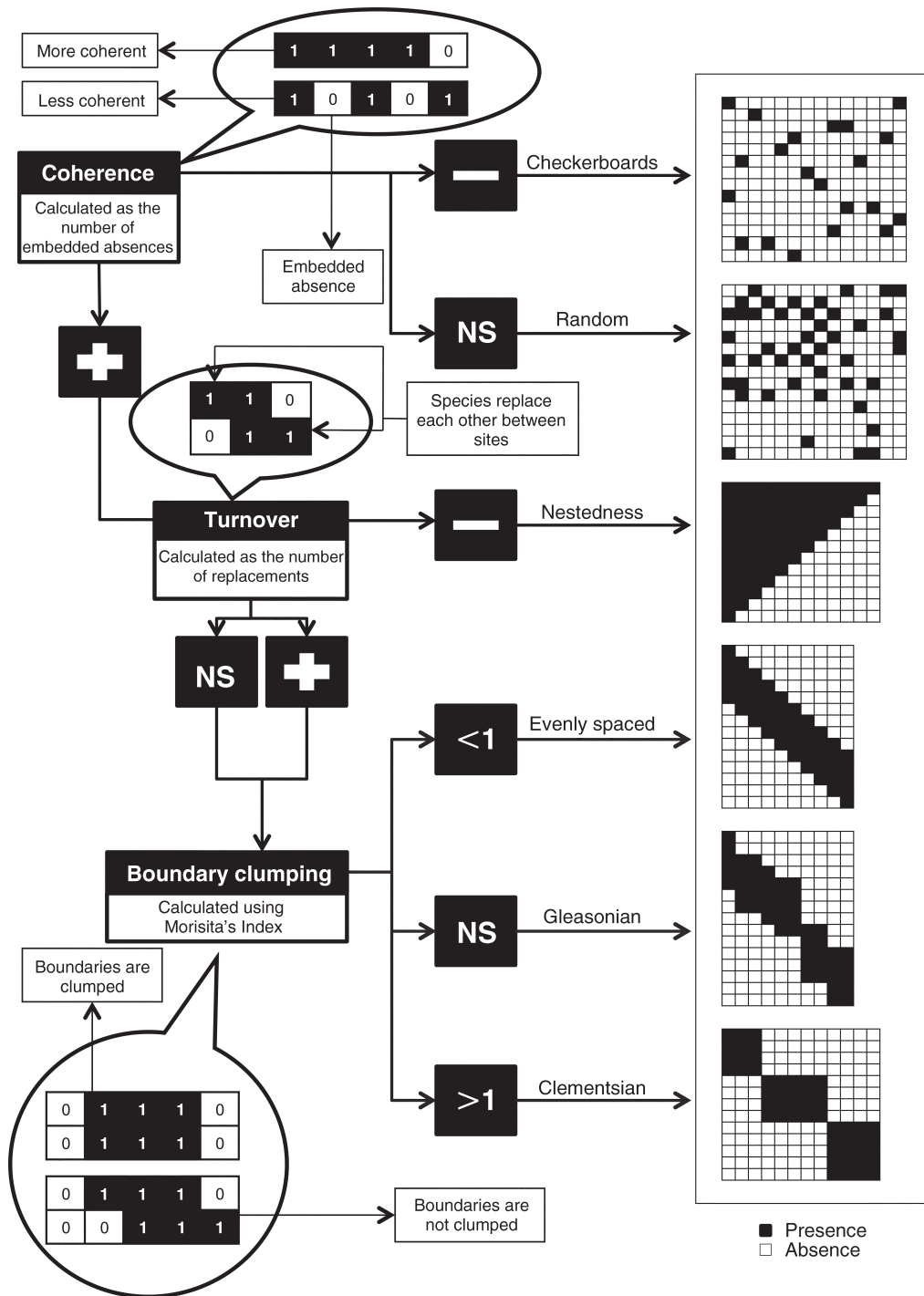


FIG. 1. General framework for the elements of metacommunity structure (EMS) analysis based on coherence, turnover, and boundary clumping. Columns represent sites, and rows represent species; NS stands for nonsignificant. A plus sign signifies “significantly positive,” and a minus sign signifies “significantly negative” ($P < 0.05$).

ical communities respond to environmental (Presley et al. 2009) and biogeographical variation.

Despite the large body of work regarding the drivers of community structure of local communities within metacommunities (e.g., direct gradient analysis, varia-

tion partitioning of environmental and spatial drivers), to our knowledge, our study is the first to investigate whether and how environmental and spatial features generate consistent distributional patterns across multiple metacommunities using lake fish distribution as a

study system. Lakes can be considered as “virtual islands” (Magnuson et al. 1998) varying in size, environmental features (Eadie et al. 1986), and degree of isolation (Olden et al. 2001), which may impose different environmental and spatial constraints that, in turn, will influence fish dispersal and probability of establishing viable populations, as well as their extinction vulnerability (Magnuson et al. 1998, Olden et al. 2001). We used a unique data set containing environmental and presence–absence data on fish distribution for ~9000 lakes from Ontario, Canada. The current Ontario fish fauna is a result of recent processes of colonization (and recolonization) at the end of the Pleistocene glacial period where lakes and rivers were formed from the meltwaters of the retreating glacial sheet (Mandrak and Crossman 1992b), with southern watersheds being ice free for a longer period of time and, as a result, have experienced an earlier period of recolonization. Moreover, there is a strong environmental gradient across the province with more extreme, but stable environmental conditions (i.e., harsher winter) in the north and a more favorable climatic condition, but less stable (e.g., seasonally variable temperature) in the southern region (Mandrak 1995). We predict that such contrasting environmental conditions and biogeographical processes associated with postglacial dispersal may have shaped species distributions into different metacommunity structures across Ontario watersheds and that recurrent patterns in metacommunity structure should occur for watersheds sharing similarities in such conditions. With this goal in mind, we first identified the EMS best describing the structure of 85 lake fish metacommunities and then explored how these patterns related to the spatial structure and environmental factors of these metacommunities.

From the six patterns tested by EMS analysis, we did not expect that checkerboards would be a predominant pattern in lake fish distributions due to the large number of widespread species in our data set that do not follow the “pairs of mutually exclusive species” pattern suggested by Diamond (1975). Moreover, there is strong evidence that the coexistence of lake fishes with similar niches is facilitated via habitat segregation rather than competitive exclusion (Werner 1984, Robinson and Wilson 1994). We expected that the northern conditions (i.e., harsher conditions) would likely shape fish species distributions according to a nested pattern characterized by a gradual species loss due to the lack of the necessary physiological adaptations to survive in this harsh environment. Conversely, we expected that the relatively milder environment conditions of southern lakes should allow for a greater variation in species compositions across lakes (i.e., greater species turnover), hence shaping species distributions as clumped (i.e., either as evenly spaced, Gleasonian, or a Clementsian gradient; see Fig. 1, Table 1).

METHODS

Metacommunity data

Data on fish communities across Ontario were gathered from the Ontario Fish Distribution Database (OFDD) maintained by the Ontario Ministry of Natural Resources (OMNR), which contains the presence–absence records of 134 fish species and the geographic positions for ~9900 lakes (inland only) from Ontario. Although records (160 000 indicating the presence of a single species at a specific lakes on a given date) span from 1900 to 1992, we used 67 000 records sampled in the summer between 1968 and 1985 in which fish community surveys and lake environmental characteristics were performed concurrently (see Mandrak and Crossman 1992a for the history of the data base and Goodchilde and Gale 1982 for sampling methods). Note that the majority of lakes were sampled only once, and in cases where lakes were sampled multiple times, we considered only the fish records for the year in which environmental characteristics were assessed. As we include all species collected across all sampling gears, only presence and absence data was used (see Jackson and Harvey 1997 for rationale). The OFDD is known to have sampling biases, where sport fishes are overrepresented and small-bodied species, such as cyprinids, are underrepresented (Minns 1986). Yet despite the potential sample biases, the large-scale nature of this data set has provided important insights in many different types of ecological questions (Mandrak 1995, Gardezi and Gonzalez 2008, Sharma et al. 2009, Layeghifard et al. 2012). We removed species that were present in less than an arbitrary value of 0.5% of all lakes, and any introduced species from our analyses. Rare and endemic species are somewhat uninformative due to their idiosyncratic nature, and they can affect EMS analysis in ways that are discussed elsewhere (Presley and Willig 2010). Introduced species do not follow any historical contingency experienced by the native species. In total, 53 extant native species were used in the analyses. Finally, lakes with missing geographic coordinates ($n = 514$) or without species ($n = 277$) were also removed from the analyses.

Local lake characteristics consisted of lake geography (e.g., elevation), water quality (i.e., total dissolved solids, pH, Secchi depth, oxygen concentration, morpho-edaphic index), lake morphology (surface area, maximum depth, mean depth, perimeter and island perimeter within lakes), and climate (growing-degree days). Missing values were replaced by the mean value of that variable within the watershed (0.2% of lakes on average per variable). Note that the environmental information of lakes treated in this way became uninformative given the total number of lakes used in the analysis. Moreover, additional climatic variables (e.g., mean annual daily temperature, mean July temperature, and mean August temperature) were acquired from the Intergovernmental Panel on Climate

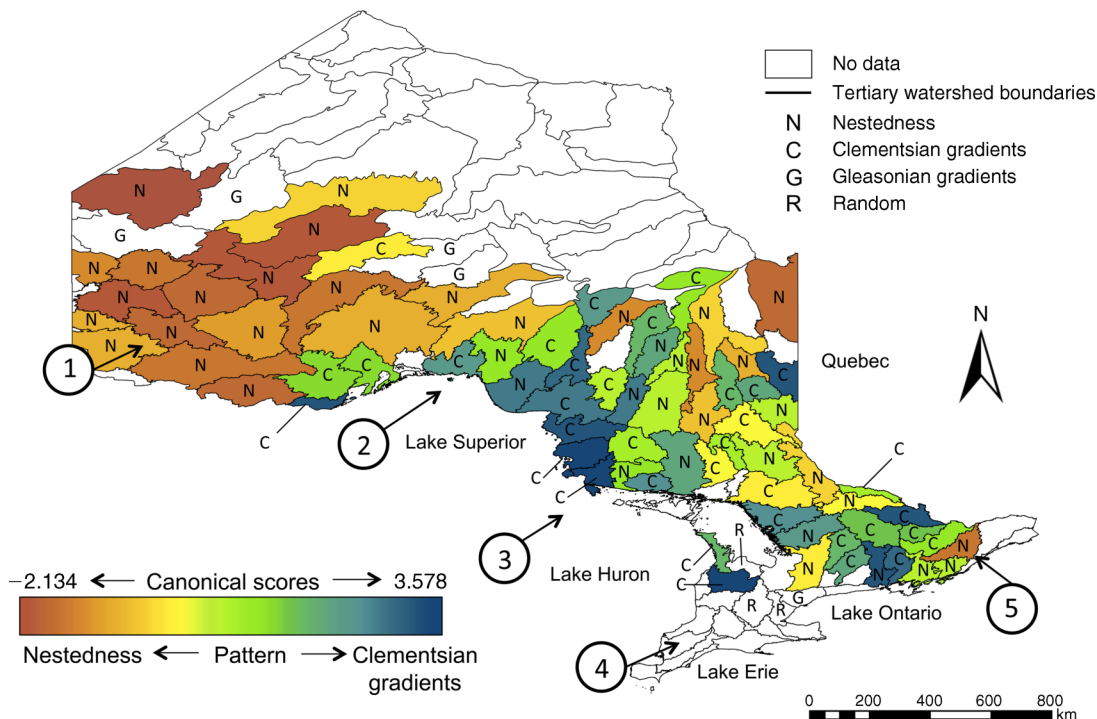


FIG. 2. A map of Ontario, Canada, showing the spatial distribution of each tertiary watershed. Colors represent their canonical scores along a discriminant analysis separating Clementsian and nestedness patterns using local and regional variables together (see *Methods*), whereas letters represent the original results from the EMS analysis. The circled numbers refer to the entry locations of postglacial dispersal routes (see Mandrak and Crossman 1992b, Mandrak 1995): 1, Glacial Lake Agassiz; 2, Brule-Portage Outlet; 3, Grand Valley Outlet; 4, Fort Wayne Outlet; and 5, Champlain Outlet.

Change (IPCC) Data Distribution Centre as 1961–1990 averages and interpolated from meteorological stations using thin-plate splines (Sharma et al. 2011).

The environmental variables considered here (see Appendix A: Table A1 for further details) all have the potential to affect the type of metacommunity structure. Lake morphometry and limnological variables are associated with habitat complexity, and resource and oxygen availability (Jackson et al. 2001), which can influence fish species richness and productivity (Eadie et al. 1986, Minns 1989). Climatic variables, mainly the ones related to growing-season length and temperature, can constrain the potential range of species (Jackson et al. 2001) and are important for the young-of-the-year critical growth needed for successfully overwintering (Shuter et al. 1980). Elevation may influence fish dispersal (e.g., headwater lakes are less accessible for fish; Minns 1989) and is also associated with variation in temperature and chemical variables (Mandrak 1995). Finally, percent of crown canopy cover (crown in Appendix A: Table A1) as an index of the amount of vegetation around the lake can be used as a proxy of anthropogenic impacts on lakes.

There are three primary watersheds in Ontario, 28 secondary watersheds nested within the primary, and the 144 tertiary watersheds that are nested within the secondary watersheds (Cox 1978). As in other studies

based on this data set (e.g., Minns 1989, Chu et al. 2005, Gardezi and Gonzalez 2008), we have considered tertiary watersheds as the scale unit of the analysis (i.e., as metacommunities; Fig. 2). Unlike secondary watersheds, the delineation of tertiary ones does present some level of arbitrariness (Minns 1989). As a consequence, some lakes across two spatially close tertiary watersheds could potentially share a greater fish dispersal history than within their own designated watersheds; however, we expect that lakes within tertiary watersheds should still share, on average, a greater dispersal history than lakes across watersheds. In order to test this assertion, we developed a null model approach (see Appendix B for computational details) that shows that lakes within metacommunities (tertiary watersheds) are more connected than lakes across metacommunities. Therefore, tertiary watersheds, for our studied system, represent a reasonable scale for lake fish metacommunities; not so large that species distributions might respond to different gradients, but large enough that the EMS analysis can detect distributional structure with relevant ecological and biogeographical properties. Finally, our results showed very strong EMS patterns within tertiary watersheds (see *Results* section), indicating that this scale does represent an important ecological unit for their fish assemblages. All tertiary watersheds with data for fewer than 20 lakes were

excluded from the analysis (183 lakes), as the EMS technique has low statistical power to detect patterns on small matrices (Leibold and Mikkelsen 2002), resulting in a database of 8911 boreal lakes distributed across 85 tertiary watersheds. Hereafter, metacommunity and watershed will be used interchangeably.

The analysis of elements of metacommunity structure

The first step in EMS is to produce an ordination of the species distribution matrix (lakes-by-species). Given that differences in community structure are determined by multiple factors (e.g., environment, dispersal, competition) and because these factors cannot all be assessed, the use of multivariate ordination techniques is essential to create gradient constructs that are expected to integrate these multiple factors into common patterns of variation across sites and species within metacommunities. In this study, each metacommunity (watershed) was analyzed via a separate correspondence analysis (Gauch et al. 1977) that maximizes the positioning of sites along axes based on the degree in which their communities share species compositions and the positioning of species sharing similar ranges (Leibold and Mikkelsen 2002). The final solution is a compromise between minimizing interruptions within ranges and within communities (Leibold and Mikkelsen 2002). As in previous studies (e.g., Leibold and Mikkelsen 2002, Presley and Willig 2010), sites and species within incidence matrices were ranked according to their position along the primary ordination axis, which maximizes their correlation (Gauch et al. 1977). Other axes of ordination were not used, as they explained a much reduced variation in species distributions across sites.

The elements of metacommunity structure and their respective significances were evaluated in a hierarchical way using null model analysis based on permutation tests (Fig. 1). The first element, coherence, was evaluated as the number of embedded absences in all species ranges and community compositions of each watershed. If the observed coherence was significantly lower than in the null distribution, it suggested a checkerboard pattern (Fig. 1; Leibold and Mikkelsen 2002). A nonsignificant coherence would suggest that the metacommunity is randomly structured regarding the gradient (ordination) analyzed (Fig. 1). Finally, a significantly positive coherence suggests that species are distributed according to the same gradient (Leibold and Mikkelsen 2002), which is further contrasted to turnover and boundary clumping patterns (Fig. 1). These two elements can be evaluated using two perspectives (species range or community [site] composition [Leibold and Mikkelsen 2002]), and here we used only the community perspective, as we were interested in assessing the potential roles of lake characteristics on metacommunity structure (but see Presley et al. 2009). Turnover was calculated by counting the number of times one species was replaced by another species across two sites. For example, in Fig.

1, the first species (first row) is present in the first site (first column) but is absent in the third site (third column), whereas the second species (second row) is absent in the first site (first column) but is present in the third (third column); this pattern is counted as one replacement. Note that a replacement is only counted between the “edges” of lake composition (i.e., first and last species) and not on embedded absences as these are not related to the primary axis of correspondence (see Presley et al. 2010 for further details on rationale). The empirical number of replacements was then compared to the ones calculated from the null distribution. If a metacommunity showed significantly low turnover, it suggested a nested distribution (Fig. 1); conversely, if it exhibited a moderate (i.e., not significant) or high turnover (positive), we evaluated boundary clumping to classify the metacommunity according to the remaining patterns (Fig. 1). The final step was performed using the Morisita's Index (Morisita 1971), which has a null expectation of 1. If the value obtained was not significantly different from 1, it indicated that community boundaries were randomly distributed, thus suggesting Gleasonian gradients. However, if the index value was significantly greater (clumped boundaries) or smaller (over-dispersed boundaries) than 1, it suggested that the metacommunity was distributed according to a Clementsian or evenly spaced gradient, respectively (Leibold and Mikkelsen 2002). Significance was assessed on the basis of an alpha of 0.05.

In order to test the significance of each EMS pattern, we applied a null model that permutes species across sites but that keeps site richness as fixed (i.e., equal to the observed values). Thus, the chosen null model included some site property such as species richness, which in lakes is highly correlated with surface area (Barbour and Brown 1974, Eadie et al. 1986). Note that there are several ways in which to permute incidence matrices, but the procedure used here has correct Type I error rates and appropriate levels of power in detecting distributional patterns (Gotelli and Graves 1996). For each watershed, we generated 999 random matrices. Each random matrix was also ordinated via correspondence analysis and used to calculate the appropriate element (i.e., under random expectation) to be contrasted against its observed value.

Observed values were then contrasted against the random distribution to estimate their probability of rejection. The test is one tailed and the direction depends on the type of EMS pattern being tested (e.g., positive vs. negative coherence; Fig. 1). Depending on the direction, probabilities were calculated as (number of values [Coherence, Turnover, or Clumping] equal to or smaller than the observed + 1)/(number of permutations + 1); or (number of values [Coherence, Turnover, or Clumping] equal to or greater than the observed + 1)/(number of permutations + 1), where 1 represents the observed value for the index being evaluated and is also included as a value of the randomized distribution.

Drivers of metacommunity structure

Local predictors were simply based on the mean value of each environmental variable across lakes within watersheds. All variables were log-transformed prior to the analysis, except for elevation, mean depth, maximum depth, and Secchi depth, which were normally distributed. Regional predictors were based on the spatial connectivity, distances to postglacial routes, and environmental structure of the entire watershed. Potential evapotranspiration (PET) was estimated as in Gardezi and Gonzalez (2008), and averaged values for each watershed were used. Spatial connectivity across lakes within watersheds was based on a modification of Hanski's (1994) connectivity measure as follows:

$$\text{Avg. Con.} = \frac{1}{n} \sum_{\substack{i=1 \\ i \neq j}}^n p_{jk} \exp(-d_{ij})$$

where Avg. Con. (average connectivity) measures the average geographic distance (based on latitude/longitude) across lake i for the k th species across all other $n - 1$ lakes within any given watershed; p indicates the presence (1) and absence (0) of the k th species in the j th lake. In cases where species i was found only in one lake, we assigned for that species the maximum distance between any two sampled lakes within any given watershed as its connectivity value (i.e., smallest connectivity). For each lake, overall connectivity was calculated as the average connectivity values for all species present in it. The overall connectivity of any given watershed was then calculated as the average connectivity of their lakes.

Due to the Pleistocene glaciation (Mandrak and Crossman 1992b), we expected that the distance between postglacial routes (i.e., refuges) and watersheds might have influenced the likelihood of postglaciation recolonization by fish species. Mandrak and Crossman (1992b) suggested five postglacial dispersal routes used by fish to recolonize Ontario (Fig. 2). Such postglacial dispersal routes were determined by comparing present-day species distributions to the locations of glacial waterbodies that acted as dispersal corridors. Moreover, each postglacial route was used by a slightly different group of species (see Mandrak and Crossman 1992a), and it has been shown previously that regions that are located near these routes have greater species richness than farther ones (Mandrak 1995) as they were the first to be colonized when the ice sheet retreated from them. Therefore, to assess the general influence of these refuges in structuring metacommunity patterns, we calculated the following two indices: MeanDP as the mean Euclidean distance between any given watershed and all five postglacial routes, and MinDP as the minimal Euclidean distance between any given watershed and its closest postglacial route.

Regarding the environmental gradient of each watershed, we calculated an index that measures the variation

in environmental conditions (gradient size) across lakes within a watershed (hereafter referred to as Env. Grad. Size). For this analysis, variables correlated to lake size were not considered (surface area, shoreline perimeter, and island perimeter), because these variables should not follow a coherent environmental gradient. This index was based on the average environmental Euclidean distance among lakes within metacommunities (variables were standardized prior to analysis, i.e., mean = 0 and variance = 1), which can be seen as the "length" (or extension) of their environmental gradients.

In order to determine how much of the variation in lake fish distribution was explained by environmental vs. spatial factors other than lake connectivity (e.g., the spatial signature of important but missing environmental, see Peres-Neto and Legendre 2010, and Jacobson and Peres-Neto 2010 for a recent discussion) within each watershed, we performed a variation partitioning scheme in order to estimate the unique and combined contributions of environmental and spatial predictors (Borcard et al. 1992). Environmental variables (except PET, which was not available for a substantial amount of lakes) from all lakes within each metacommunity were used as environmental predictors, and the MEM (Moran's Eigenvector Maps) method was used to model spatial variation (Dray et al. 2006, Peres-Neto and Legendre 2010). Species data (the response variable) were Hellinger transformed (Legendre and Gallagher 2001) prior to analysis, and reported values are based on the adjusted R^2 (Peres-Neto et al. 2006). Statistical significance, as before, was based on 999 permutations and assessed on an alpha of 0.05. When a fraction was found to be negative, which is often the case in the case of adjusted values of nonsignificant fractions, we assigned a zero to its value instead of the observed value (see Peres-Neto et al. 2006). Finally, we averaged the explained variation from spatial and environmental predictors across watersheds across patterns uncovered by the EMS analysis.

Based on EMS analysis and associated null model probabilities under an alpha = 0.05, each metacommunity was discretely classified into one of six metacommunity patterns (Fig. 1). This classification was then used in a discriminant function analysis (DFA; Legendre and Legendre 1998) to determine the environmental features that maximized their differences at the local and regional scales. A variation partitioning using the DFA scores as the response variable was performed across watersheds using the average values for the environment (local predictors) or indices (regional predictors) and MEM based on the latitude/longitude of the center of the watershed as predictors. Our interest here was to understand the factors that maximized the differences across metacommunity patterns, and therefore we used the canonical scores from the discriminant function as a response.

EMS patterns and their associated null models (coherence and turnover) were performed using a

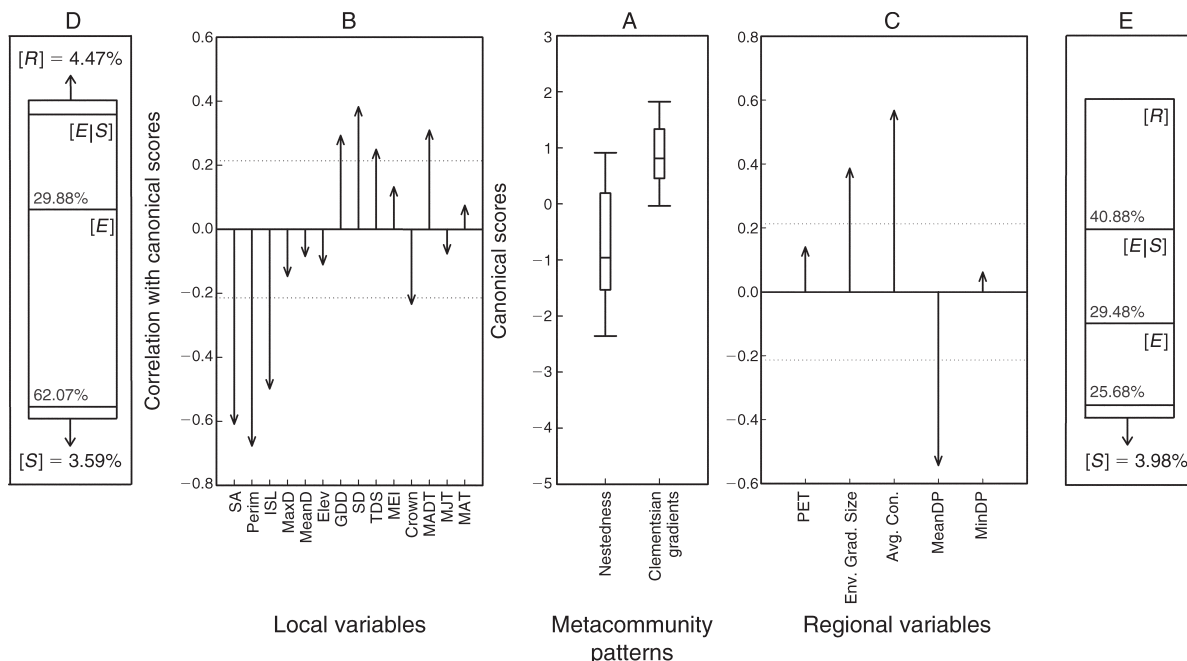


FIG. 3. Discriminant analysis on the basis of local and regional variables between nestedness and Clementsian gradients. (A) Score differences among metacommunity types ($F_{1,76} = 49.19$, $P < 0.001$). The lower boundaries of the boxes indicate the 25th percentile, the lines within the boxes represent their medians, and the upper boundaries of the boxes represent the 75th percentile. Whiskers above and below the boxes represent the 90th and 10th percentiles, respectively. (B, C) Correlations (B) between local variables and the canonical axis of the discriminant function and (C) between regional variables and the canonical axis of the discriminant function. The arrow length indicates the correlation level, and any correlation arrow crossing the dashed line is significant at $\alpha = 0.05$. Abbreviations are: SA, surface area; Perim, shoreline perimeter; ISL, island perimeter; SD, Secchi depth; MaxD, maximum depth; MeanD, mean depth; Crown, crown canopy cover; Elev, elevation; GDD, growing-degree days; TDS, total dissolved solids; MEI, morpho-edaphic index; MADT, mean annual daily temperature; MJT, mean July temperature; MAT, mean August temperature; PET, potential evapotranspiration; Env. Grad. Size, environmental gradient size; Avg. Con., average connectivity; MeanDP, mean distance from postglacial routes; and MinDP, minimal distance from postglacial route. Panels (D) and (E) show the resulting fractions from the variation partitioning using the canonical scores from the discriminant analysis as the response variable and Moran's Eigenvector Maps based on the mean geographical coordinates and (D) mean environmental variables (local variables) and (E) the regional variables as the environmental predictors. Definitions of fractions are given in Table 2.

MATLAB code developed by Presley et al. (2009). The calculation of Avg. Con., Env. Grad. Size, and variation partitioning were performed with functions written in Matlab (Mathworks 2010) by the authors. All remaining statistical analyses were performed using Statistica (Statsoft 2001).

RESULTS

Among the 85 metacommunities analyzed with the EMS framework, four patterns were uncovered: 42 watersheds were consistent with nested distributions, 35 with Clementsian gradients, 5 with Gleasonian gradients, and 3 were random (Fig. 2). Here we focus the analysis of the two most common patterns, namely nested and Clementsian gradients (but see the *Discussion* section for further explanation regarding the nonsignificant patterns).

The results supported our initial expectations whereby the discriminant function analysis (DFA) clearly demonstrated that environmental conditions and the levels of spatial connectivity are quite distinct between nested and Clementsian watersheds ($F_{20,56} = 1.83$, $P < 0.039$;

Fig. 3A), and that these patterns also have a strong spatial component (Fig. 2). Although it is clear that nested metacommunities are dominant in the northwestern part of the province (Fig. 2), they are also present in smaller numbers in the southeastern region; Clementsian gradient watersheds are largely concentrated in the southeastern region along the Great Lakes (Fig. 2). Nested watersheds (negative canonical scores) were associated with larger lakes and lower temperatures (Fig. 3B), whereas Clementsian gradient watersheds (positive canonical scores) were associated with these variables in the opposite direction. Moreover, nested watersheds were negatively associated with Environmental Gradient Size and Average Connectivity, and positively associated with mean distance to postglacial dispersal routes (Fig. 3C). These results indicate that nested metacommunities have a lower degree of spatial connectivity and environmental variation, and are, on average, located farther from postglacial dispersal routes. Conversely, Clementsian metacommunities present the opposite association with these variables, demonstrating a higher degree of spatial connectivity

and environmental variation, and are geographically closer to postglacial dispersal routes (Fig. 3C). Furthermore, the variation partitioning applied on the DFA canonical scores (Fig. 3D, E) showed that the differences between Clementsian and nested metacommunities are better explained by local environment ($[E] = 62.07\%$, where $[E]$ represents the fraction of variation explained solely by the environment; Fig. 3D) rather than regional components ($[E] = 25.68\%$; Fig. 3E), although the shared variation between local or regional variables and space ($[E|S]$) were about the same in both cases ($\sim 29.5\%$ for both type of variables; Fig. 3D, E). Finally, spatial variation alone (other than connectivity) described by MEM did not explain much variation across nested or Clementsian watersheds ($\sim 4\%$; Fig. 3D, E), indicating that there are no missing spatial predictors that could further explain their differences. The low spatial connectivity observed in nested metacommunities (Fig. 3C) also suggests that their species are dispersal limited in contrast to Clementsian ones. Taken together, these results indicate that connectivity is an important structuring factor in nested but not on Clementsian metacommunities.

Although nested and Clementsian metacommunities are clearly distinct in terms of their environments and levels of spatial connectivity, they cannot be distinguished on the basis of how their species distributions (rather than their structure) are explained by the environmental and spatial variation within watersheds (Table 2).

DISCUSSION

The expectation that metacommunity patterns could be explained by their environmental and spatial differences across their landscapes (watersheds) was clearly upheld by our analyses. This is the first time that a study applied the EMS framework over an entire biogeographic region, thus encompassing several metacommunity systems. To our knowledge, only one study has looked at how these metacommunity structures compare across different regions for the same taxa (i.e., bat metacommunity structure on Caribbean islands; Presley and Willig 2010). However, their study was somewhat limited by the fact that they only considered three regions, and therefore, little inference could have been made about how differences among regions could have explained the observed patterns. Here, given the large number of metacommunities, we were able to determine the environmental and spatial drivers corresponding to different patterns of species distributions (EMS). Our initial expectations regarding the spatial distribution of metacommunity patterns across the province were well supported, demonstrating that Clementsian metacommunities were mostly encountered in the southeastern part of Ontario and near to the Great Lakes (Fig. 2), while nested metacommunities were the dominant pattern in northwestern Ontario,

TABLE 2. Variation partition results within watersheds.

Pattern	Fractions (%)			
	$[E]$	$[S]$	$[E S]$	$[R]$
Clementsian	15.96	1.30	3.20	79.54
Nestedness	16.58	1.12	2.43	79.86

Notes: Values represent the average variation explained of adjusted fractions for all watersheds within each pattern. $[E]$ represents the fraction of variation explained solely by the environment; $[S]$ is the unique fraction of variation explained by space; $[E|S]$ is the common fraction of the variation shared by space and environment; and $[R]$ is the residual variation.

though they still occurred in considerable numbers in the southeastern region.

Lakes within watersheds at higher latitudes undergo more severe winters, with ice cover lasting longer periods of time, greater periods of oxygen depletion, and shorter growing seasons relative to lakes occurring at lower latitudes (Magnuson et al. 1998, Fang and Stefan 2000). This process can account for the majority of watersheds classified as nested in northwest Ontario because lakes with harsher temperature regimes preclude species with young-of-the-year that cannot attain a minimum size to survive winter starvation in the first year (Shuter et al. 1980). Because nested watersheds were characterized by more homogeneous and harsher environment (Fig. 3C; see also Mandrak 1995) and contained less energy (relatively colder climate and shorter growing season), they may decrease the opportunity for specialist species to colonize these metacommunities (Chase 2007, Gardezi and Gonzalez 2008). Such unfavorable environmental conditions are more deterministic and, coupled with a hierarchy in breadth of species-specific tolerances in which the distribution of less tolerant species are nested within the distribution of species having greater niche breadth, could result in a strongly nested metacommunity (Fernández-Juricic 2002, Smith and Brown 2002, Chase 2007). Here, species that can tolerate the broadest range of conditions would be more widespread, and the least tolerant species would present a restricted distribution. Vulnerable species may survive in larger lakes, which are more stable (Shurin et al. 2010), present greater habitat complexity (Eadie et al. 1986), and provide more winter refuges for species to survive through this period (Magnuson et al. 1998). Larger lakes are far more common in northwestern nested watersheds compared to the southern region (Fig. 3B), and this is likely to be one of the factors structuring nestedness.

The spatial and biogeographic predictors assessed in this study were also important for explaining the dominance of nested and Clementsian metacommunities in the studied region. The effects of historic biogeographic processes were strongly supported (i.e., greater distance on average between nested watersheds and postglacial dispersal routes) in which the average distance to the five postglacial routes was the most

important predictor (Fig. 3). The Mississippian refugium is the major contributor to the present-day Ontario fish fauna (Mandrak and Crossman 1992b). Historically, northwestern watersheds had less time available for species to colonize as they deglaciated after the retreat of the Wisconsin ice sheet and were close to only two dispersal routes (Fig. 2). Additionally, the low degree of connectivity among lakes within nested metacommunities (Fig. 3D) suggests that dispersal limitation is (and was) an important structuring factor, constraining poor dispersers to colonize only a few well connected lakes, whereas good dispersers are also present in more isolated lakes (e.g., species colonization hypothesis; Cook and Quinn 1995, Ulrich et al. 2009). In general, lakes that are more connected can be accessed by a greater number of species than more isolated ones (Olden et al. 2001).

Clementsian watersheds are located at lower latitudes, which observe lower winter severity (i.e., less oxygen depletion through winter under ice cover, larger growing season), have higher productivity, and are closer to postglacial dispersal routes. This relatively more “benign” environment (Mandrak 1995) may allow species to specialize in the exploitation of different resources and therefore increase the importance of stochasticity in community assembly that may lead to a higher species turnover (Chase 2007). Moreover, lake within Clementsian metacommunities were more spatially connected (Fig. 3D) and were close to four out of five postglacial dispersal routes (Fig. 2) indicating that species were less dispersal limited and suggesting that these watersheds were more accessible to recolonization after the end of the glacial period. Additionally, these watersheds were colonized by species of both the Mississippian refuge (dispersal routes 2, 3, and 4; Fig. 2) and the Atlantic refuge (dispersal route 5; Fig. 2); the latter having a lower species pool, but nevertheless contributing to the greater fish biodiversity of southern Ontario (Mandrak and Crossman 1992b). If species are not dispersal limited, but lakes differ in their compositions, then the local environment should be acting as a filter and species should distribute themselves according to their niches and thus suggest species sorting dynamics (sensu Leibold et al. 2004). This was also supported by the fact that these watersheds have a greater environmental variation (i.e., larger Env. Grad. Size; Fig. 3C), which increases the likelihood of species sorting (Leibold et al. 2004). Another possible explanation for Clementsian gradients is that pairs of competing species (i.e., “forbidden combinations”; Diamond 1975) do not occur independently of each other, rather forming “clusters of forbidden combinations” (Gilpin and Diamond 1982). However, in order to assess the possible role of competition, further research is needed and perhaps phylogenetic or trait-based approaches may provide further insights into limiting similarity of species within these metacommunities (Mason et al. 2008).

Finally, spatial segregation between southern nested (under 48° latitude) and Clementsian metacommunities was less clear as these watersheds shared environmental characteristics in common, though nested watersheds presented on average greater species richness across their lakes (one-way ANOVA; $F_{1,48} = 6.0$; $P = 0.0181$), which might produce patterns of species composition of poorer communities being subsets of progressively richer communities (Ulrich et al. 2009). Although beyond the scope of this paper, additional analysis on the distribution of species traits and phylogenetic structure of communities and habitat specialization of species might shed some light on the relative importance of historical biogeographic patterns and ecological mechanisms that might be causing the emergence of these two distinct patterns in somewhat similar environments.

Our results from the variation partitioning applied within watersheds suggest that variation in species composition is explained mainly by environmental factors (Table 2). Similarly, Magnuson et al. (1998) concluded that for temperate-lake fishes, environmental factors are more important than spatial factors in explaining lake fish composition, because extinctions are likely to occur at a faster rate than colonization events in boreal-lake fish assemblages. Although the explained variance seems relatively low (~16%), we argue that these results are not negligible in absolute numbers, considering the size of the data set ($n = 8911$ lakes). Surprisingly, the spatial (~1%) and shared variation (~2.5%) at the watershed level was low. It is important to point out that, although geographic coordinates alone may ignore key spatial components such as waterway distances (Olden et al. 2001) and geographic barriers, which were not measured due to issues of feasibility for the amount of lakes ($n = 8911$) in the data set, the two most relevant metacommunity patterns were significantly different on the basis of their connectivity levels (Fig. 3C). Thus, even if spatial variation could not explain variation in species distributions, our connectivity metric, jointly with Env. Grad. Size and MeanDP (Fig. 3D, E), proved to be relevant in driving their metacommunity structure. Indeed, regional variables explained ~25% (Fig. 3E) of the variation in DFA canonical scores related to the differences in metacommunity patterns. Thus, we suggest that the structure of nested metacommunities, due to a more stable and less variable environment (Mandrak 1995), should be more affected by historical and current dispersal limitation of species among lakes than Clementsian metacommunities, in which the environmental variation plays a larger role.

As expected, the majority of metacommunities appeared either as nested or clumped (i.e., either Gleasonian or Clementsian). The absence of metacommunities having evenly spaced gradients (see Fig. 1 for an example) indicates that there is no trade-off between species competitive abilities and their environmental tolerances along distributional gradients. In this case,

dispersal limitation may not allow species to find their optimal conditions where they could outcompete species with slightly different optima for any given lake environment. Indeed, dispersal in lake fishes is less likely than in stream fishes where evenly spaced gradients can emerge across longitudinal stream gradients. For instance, Taniguchi et al. (1998) found that a number of fish species presented longitudinal replacement in Rocky Mountains streams due to a trade-off in competitive ability and tolerance to temperature. Moreover, Magnuson et al. (1998) found that the rate of extinction is potentially greater than the rate of colonization in lake fishes. Note that many lakes in the studied region are not connected to other lakes, hence hindering natural recolonization, however, historical colonization was possible due to past glacial connections during the receding glacial ice sheet. Finally, many species having similar niches in the studied system coexist via niche partitioning rather than outcompeting each other (Robinson and Wilson 1994).

The three randomly distributed metacommunities uncovered in southern-Ontario are likely due to watersheds being highly impacted by anthropogenic activities, which may have generated strong mismatches between environmental and spatial gradients, and species distribution in these metacommunities. Combined, these three random metacommunities have the smallest average percentage of lake shoreline covered by vegetation (i.e., Crown in Appendix A: Table A1; 6.97% vs. 77.8% average coverage for all other metacommunities) and smallest mean averages (1.93 m for random vs. 4.96 m for the other metacommunities) and maximum depths (5.20 m vs. 16.14 m). Low crown vegetation in this region is due to anthropogenic activities and patterns of species co-occurrences tend to be random in disturbed habitats (see Sanders et al. 2007 for a discussion and associated references). The emergence of a few Gleasonian gradients on northeastern Ontario (Fig. 2) was unexpected. Given the low degree of environmental heterogeneity on northern watersheds and considering that environmental harshness is expected to be a highly deterministic process (e.g., Chase 2007), it would appear unlikely that species in this region would have differential responses to the environmental gradients, which is necessary for the emergence of a Gleasonian structure at the metacommunity level. We believe that the low number of lakes sampled on these watersheds (between 21 and 36 lakes) combined with the large matrix fill (i.e., the ratio between the number of presences and number of records) of these metacommunities (between 34% and 43%) might have restricted the null space (number of potentially different matrix under the null hypothesis) to detect a pattern of significant low turnover. Indeed, three out of five of these Gleasonian metacommunities were somewhat marginally nested ($P=0.0909$, 0.1085, and 0.2247), but considered as clumped and consequently Gleasonian (Fig. 1).

The EMS framework is an effective tool to distinguish among six metacommunity patterns (Leibold and

Mikkelsen 2002, Presley et al. 2009) and represents substantial progress in contrast to analyses that are restricted to one distributional pattern (e.g., traditional analyses of nestedness, Patterson and Atmar 1986; checkerboards, Diamond 1975, Gilpin and Diamond 1982). Despite the uniqueness of ecological systems (Lawton 1999), the species within should ultimately be distributed according to one of the metacommunity patterns (or some variant of them; Presley et al. 2010). Even when particular species distributions do not coincide exactly with a particular pattern, there is always one that best fits the data, facilitating the exploration of the mechanisms underlying species distributions. We have shown that the EMS framework is capable of assessing multiple hypotheses about the structure of metacommunities, and as presence-absence data sets are becoming increasingly available, ecologists should find useful the framework implemented here.

ACKNOWLEDGMENTS

We thank Sapna Sharma for her help with the Ontario Fish Distribution Database and the calculation of climatic variables. P. R. Peres-Neto was supported by the Canada Research Chair program (Chair in Spatial Modelling and Biodiversity) and NSERC Discovery grants. The Groupe de Recherche Interuniversitaire en Limnologie et Environnement Aquatique (GRIL) at Université du Québec à Montréal provided partial financial support to R. Henriques-Silva. Helpful reviews from two referees greatly improved the manuscript.

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SUPPLEMENTAL MATERIAL

Appendix A

Details on the environmental variables used in the study ([Ecological Archives E094-055-A1](#)).

Appendix B

Computational details of the null model showing that lakes within watersheds are more connected than across watersheds ([Ecological Archives E094-055-A2](#)).