ORIGINAL ARTICLE

Unravelling the effects of multiple types of disturbance on an aquatic plant metacommunity in freshwater lakes

Jason D. Lech[1] | Michael R. Willig[1,2]

[1]Department of Ecology and Evolutionary Biology, University of Connecticut, Storrs, CT, U.S.A.

[2]Center for Environmental Sciences & Engineering and Institute of the Environment, University of Connecticut, Storrs, CT, U.S.A.

Correspondence
Jason D. Lech, Center for Environmental Sciences & Engineering, 3107 Horsebarn Hill Road, U-4210, Storrs, CT 06269-4210, U.S.A.
Email: jason.lech@uconn.edu

Abstract

1. Lakes and ponds experience numerous forms of disturbance, including land use (anthropogenic), invasive species (biotic), and eutrophication (abiotic). Although these disturbances act independently or synergistically to affect native species composition, their effects generally are not considered simultaneously, thereby failing to account for appreciable variation or inaccurately attributing joint effects to a single type of disturbance.

2. We assessed defining characteristics (coherence, turnover, and boundary clumping) of a metacommunity of 67 native aquatic macrophyte species that inhabit 104 lakes to determine the extent to which species respond to the same latent environmental gradient and the association of that gradient with multiple interrelated types of disturbance.

3. Species generally responded to the same latent environmental gradient, with their distributions replacing one another along that gradient, resulting in a compartmentalised structure (i.e. Clementsian pattern). The latent environmental gradient was associated with disturbance; different functional or phylogenetic groups of species were associated with high or low levels of disturbance.

4. We used variation partitioning to evaluate whether spatial or environmental attributes were more important in driving variation among lakes along the latent environmental gradient. We accounted for 78.7% of variation among lakes in species composition of native aquatic plants, with 10.0% due to unique attributes of space, 16.4% due to unique attributes of environment, and 52.2% due to spatially structured environmental attributes, highlighting the importance of species sorting.

5. We separated environmental attributes into three subcategories: abiotic (water quality), biotic (invasive species), and anthropogenic (land use). We used variation partitioning on the three environmental subcategories and on spatial attributes to disentangle their independent and joint effects. We then used hierarchical partitioning to unravel the independent and joint effects of each attribute within each subcategory.

6. Abiotic (water quality), biotic (invasive species), and anthropogenic (land use) disturbances each had significant total effects that are highly conflated with each other. Importantly, each subcategory of disturbance had significant unique effects on native aquatic plant composition.

7. By using spatial characteristics as well as abiotic, biotic, and anthropogenic attributes that are related to disturbance, we accounted for most of the variability in species composition among lakes. Of particular importance, invasive species independently, and interactively with other environmental characteristics, affected the metacommunity structure of native species. The emergent compartmentalised structure (Clementsian) of native species in the metacommunity arises because of species-specific differences in response to a disturbance gradient, resulting in species with distinctive functional characteristics and phylogenetic histories at different ends of a disturbance gradient.

1 | INTRODUCTION

Freshwater is an essential resource, yet freshwater systems are among the most modified and threatened ecosystems on the planet (Albert et al., 2020; Reid et al., 2019). Nearly all major forms of anthropogenic disturbance affect freshwater systems, with overexploitation, water pollution, flow modification, land use change, and invasive species being among the leading causes of decline in freshwater populations (Dudgeon, 2019; Dudgeon et al., 2006). Consequently, freshwater systems are more threatened than are terrestrial or marine systems, and freshwater organisms suffer extinction rates 3.9 times greater than that of terrestrial species (Reid et al., 2019; WWF, 2018). This is particularly problematic because freshwater ecosystems contain 35% of vertebrates and 9.5% of named animal species, despite covering <1% of the Earth's surface (Balian et al., 2008).

Land use and invasive species are the first and second most frequent causes of native species endangerment in the U.S.A., respectively (Levine et al., 2003). Land use is a ubiquitous form of anthropogenic disturbance, with over 77% of the terrestrial biosphere modified by humans (Ellis et al., 2010). Land use can affect freshwater species indirectly by affecting water quality (Bennett et al., 2001; Soininen et al., 2015) or by influencing dispersal of aquatic species (Carlson et al., 2016). Invasive species are a major driver of global change (Vilà et al., 2011) and competitively dominate in certain habitats (Pimentel et al., 2005), compromising local biodiversity (Hejda et al., 2009), ecosystem functions (Ehrenfeld, 2010), and ecosystem services (Vilá et al., 2011). Aquatic macrophytes in particular are some of the most problematic invasive plants in the world (Chambers et al., 2008).

Water quality, invasive species, and land use are related to anthropogenic disturbance to various degrees and are highly interrelated with one another in freshwater systems. Land use is a direct form of anthropogenic disturbance, typically in the form of buildings, roads, lawns, or agriculture. Land use indirectly affects native and invasive aquatic plants by providing nutrients and other pollutants to freshwater systems, which can act as abiotic disturbances by causing rapid eutrophication and shifts in critical water quality parameters. Anthropogenic activity also indirectly affects native aquatic plants by enhancing dispersal (via transportation on boats) and growth of invasive plants (via fragmentation while boating), subsequently altering biotic processes such as interspecific competition. Altered abiotic filtering (via changes in water quality) and interspecific competition (via changes in invasive species) that are both mediated by anthropogenic disturbance (as represented by land use) can be strong enough to extirpate species from lakes, thereby influencing species composition. Despite the conflated relationship of anthropogenic disturbance with abiotic and biotic processes, we hereafter use anthropogenic to represent the direct form of disturbance (i.e. land use) from which we distinguish indirect consequences associated with water quality and invasive species.

1.1 | Metacommunity ecology

Understanding how regional and local processes affect spatiotemporal dynamics of species distributions is a dominant theme in ecology (Mittelbach & McGill, 2019), and is increasingly critical for conservation of freshwater ecosystems and the biota that they harbor. The metacommunity concept offers a comprehensive framework for understanding how species distributions are organised along environmental gradients, and how such organisation is shaped by combinations of regional and local processes. A metacommunity is a set of local communities that are linked by the dispersal of multiple interacting species (Leibold et al., 2004). This framework unifies a number of ecological theories by recognising that many processes operate at multiple scales, with both local and regional processes affecting the composition of communities (Leibold et al., 2004). Freshwater systems, particularly lakes and ponds, represent ideal systems for advancing metacommunity theory because of a number of critical characteristics. First, lakes possess discrete boundaries

that delineate local communities. Second, spatial variation in abiotic characteristics is small within lakes compared to differences in abiotic characteristics among lakes. Third, a number of mechanisms facilitate dispersal among lake communities, including transport by birds or boats or via stream connections.

Two complementary approaches characterise the metacommunity framework: one focuses on mechanistic processes, and the other on patterns of species distributions. In the pattern-based approach (Leibold & Mikkelson, 2002), differentiation of six idealised metacommunity structures (i.e. random, checkerboard, nested, evenly spaced, Clementsian, and Gleasonian) is the goal (Figure 1). The six idealised structures were initially developed to clarify the nature of metacommunities and to make inferences about particular mechanisms that drive the distributional patterns of species.

In the mechanistic approach (Cottenie, 2005; Leibold et al., 2004), the degree to which regional versus local mechanisms are important is reflected in four idealised processes: species sorting, mass effects, patch dynamics, and neutrality (Figure 1). These four processes represent various positions on a hypothetical continuum, but are not the only processes worthy of consideration (Brown et al., 2017). The metacommunity continuum proposed by Logue et al., (2011) is flexible, synthetic, and utilitarian. In it, three axes show the extent to which variation in species composition in a metacommunity is determined by dispersal (regional), environmental heterogeneity (local), and species equivalence (stochasticity). In application, environmental heterogeneity is generally measured by abiotic attributes, despite the importance of biotic and anthropogenic characteristics.

Although biotic interactions (e.g. interspecific competition) affect species composition, the role of invasive species (representations of biotic disturbance) has not been studied comprehensively in a metacommunity context, and the effects of invasive species on a metacommunity of native species are poorly known. Anthropogenic disturbance such as land use also affects species composition, but biotic and anthropogenic attributes are rarely considered separately or together in metacommunity studies. Furthermore, the extent to which biotic disturbance (invasive species), anthropogenic disturbance (land use), and the abiotic environment (water quality) interact with each another and with space to drive patterns of species composition is not understood. Metacommunities of aquatic plants generally display a Clementsian pattern in many regions of the globe (García-Girón et al., 2020), but how functional or phylogenetic groups of aquatic plants correspond to such structure is largely unknown, despite evidence that patterns of β diversity relate to taxonomic, functional, and phylogenic attributes of species (García-Girón et al., 2019). Consequently, we evaluated patterns and processes in a metacommunity of native aquatic plants to comprehensively address three overarching goals: (1) determining the role of invasive aquatic plants in affecting the metacommunity; (2) unravelling the roles of space and three subcategories of local environmental disturbance (abiotic, biotic, and anthropogenic) on species composition; and (3) assessing if functional or phylogenetic groups of native aquatic plants are associated with metacommunity structure.
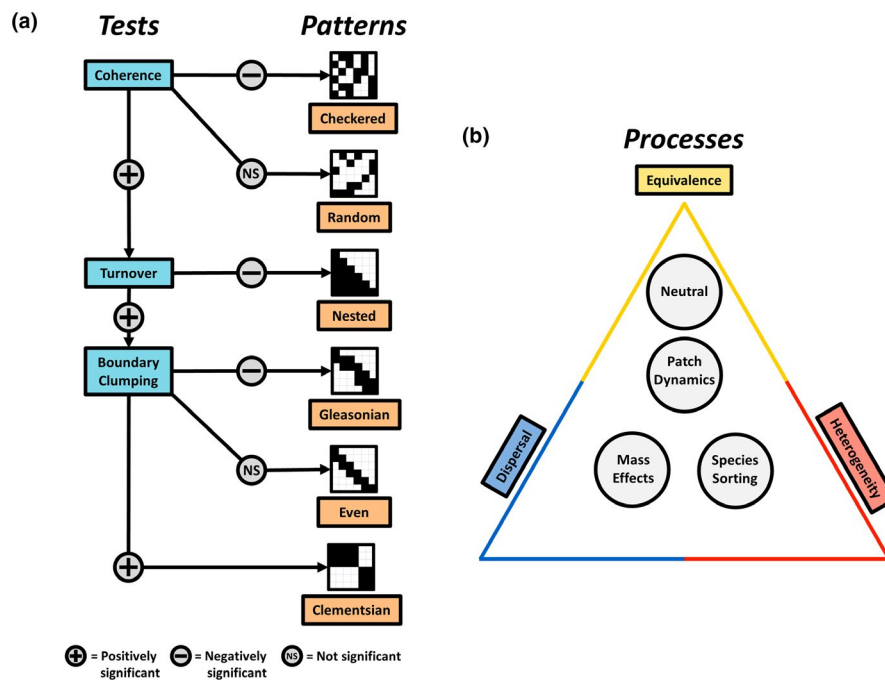

FIGURE 1 Using an incidence matrix ordinated by reciprocal averaging, metacommunity structure is evaluated via a decision tree that assesses three elements of structure (species coherence, turnover, and boundary clumping), as indicated by light blue boxes in the graphic on the left (a; modified from Presley et al., 2010). Each of six metacommunity patterns corresponds to a unique combination of statistical outcomes. The graphic on the right (b) diagrammatically represents the effects of environmental heterogeneity, dispersal, and species equivalence on metacommunity structure (modified from Logue et al., 2011). The relative positions of four metacommunity processes are illustrated with respect to those environmental characteristics

2 | METHODS

2.1 | Data collection

We used 104 surveys of aquatic plants in lakes of Connecticut (Figure 2, Table S1) that were performed by personnel of the Connecticut Agricultural Experiment Station from late June to late September in 2004 and in 2005. Capers et al., (2010) analysed these data to explore variation in species composition but did not consider anthropogenic attributes as a cause of inter-lake variation. Although lakes were selected nonrandomly (not all lakes are accessible and some surveys were requested), they represent the typical range of morphometric attributes (e.g. area, depth, slope), environmental conditions (e.g. alkalinity, conductivity, phosphorus), and biotic and anthropogenic disturbances (e.g. invasive species, land use, boating activity) found throughout the region (Capers et al., 2007; Table 1). Each lake was surveyed by propelling a small boat through areas that were shallow enough to support plant growth (boating surveys). All observed plants (i.e. submerged, floating, and emergent macrophytes) in each lake were recorded, including native and invasive taxa. Species incidence was determined using visual inspection and

collection with an extendible handheld rake (3.7 m maximum length). Areas too deep for sampling with a rake were surveyed using a grapple, but these areas were typically unable to support plant growth (median Secchi depth was 2.0 m). Additionally, line transects were used to survey plant communities. One transect (10 points) was surveyed for every 24 ha of lake surface area (with a minimum of one transect per lake). Each transect was positioned perpendicular to the shoreline such that points increased in depth as they increased every 10 m in distance from the shore. Species incidence for a lake was based on the combined data from boating surveys and transects. Voucher specimens were collected for every species in each lake, dried, mounted, and deposited in the herbaria of the University of Connecticut (CONN) and the Connecticut Agricultural Experiment Station (NHES).

A total of 96 aquatic plant species representing 39 genera, 27 families, and 16 orders were obtained from the 104 surveyed lakes. Of those species, eight are invasive and three are hybrids (two native and one invasive hybrid). The median, minimum, and maximum number of native species per lake is 10, 1, and 27, respectively. Overall, 63% lakes contained at least one invasive species (median, one; maximum, four). Invasive species include *Cabomba caroliniana*,
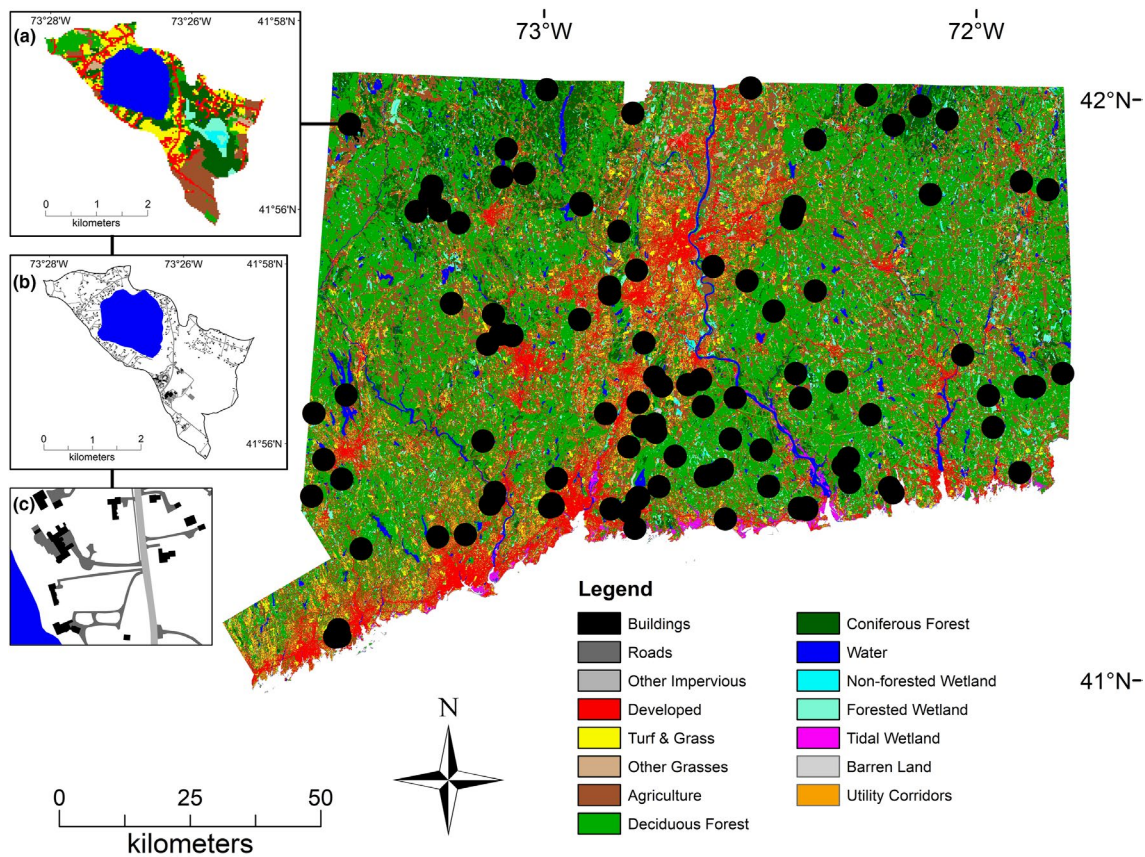

FIGURE 2 Location of each of 104 lakes (circles) in Connecticut that were surveyed in 2004–2005 for aquatic plants and water quality. Map colours correspond to land cover types. The source of land cover maps is the UConn Center for Land Use Education and Research (CLEAR). We used maps based on 30-m LandSAT imagery from 2006 to most closely match survey dates. Inset a represent the land cover of a single catchment. Inset b represents the same catchment using 1-m resolution LiDAR imagery to distinguish three types of impervious surface (i.e. buildings, roads, and others such as sidewalks and driveways). Inset c shows a portion of inset b, but at a higher magnification

TABLE 1 Spatial and environmental attributes of lakes in Connecticut

Attribute	Mean	SD	Min	Max
Areal				
Lake area (ha)	48.26	202.12	0.07	2,058.23
Catchment area (ha)	338.01	547.39	12.81	5,455.59
Plants				
Invasive species richness	1.06	1.04	0.00	4.00
Native species richness	11.52	6.27	1.00	27.00
Water quality				
Alkalinity (mg/L)	29.85	25.55	0.75	100.50
Conductivity (µS/cm)	127.54	72.68	19.40	375.00
pH	6.58	0.84	4.80	9.30
Total phosphorus (ppb)	36.53	54.86	0.00	333.83
Land use				
Agriculture (%)	4.88	8.22	0.00	47.91
Buildings (%)	2.02	1.78	0.00	7.28
Grass and turf (%)	9.37	7.53	0.14	41.01
Other impervious cover (%)	6.07	5.09	0.00	26.68

Note: Water quality was measured from samples taken at the surface of the deepest part of each lake.

Abbreviations: Max, maximum; Min, minimum; *SD*, standard deviation.

Eichhornia crassipes, *Glossostigma cleistanthum*, *Marsilea quadrifolia*, *Myriophyllum heterophyllum*, *Myriophyllum spicatum*, *Najas minor*, and *Potamogeton crispus*. The invasive hybrid *M. heterophyllum × laxum* can occur in Connecticut, but is indistinguishable from *M. heterophyllum* in the absence of molecular analysis (Moody & Les, 2002); therefore, both were considered to be *M. heterophyllum* in all analyses. Identification to the species level in several genera requires inspection of flowering parts. Because reproductive organs were not apparent at the time of all surveys, these taxa are recognised as *Alisma* spp., *Callitriche* spp., *Cardamine* spp., *Eleocharis* spp., *Sagittaria* spp., *Sparganium* spp., or *Wolffia* spp. Lastly, because species with only one occurrence have a poorly defined environmental distribution, those species (11 native species total) were not included in the site-by-species matrix. The final site-by-species matrix for native aquatic plants includes 67 taxa in 104 lakes whereas the final site-by-species matrix for invasive species includes eight invasive taxa in 104 lakes (invasives were only present in 65 lakes).

For abiotic attributes, we used aspects of water quality that are of known importance to aquatic plants and that are known to be influenced by anthropogenic disturbance. We used water quality measurements from samples obtained during plant surveys, which were collected, stored, and analysed by personnel of the Connecticut Agricultural Experiment Station (full details in Capers et al., 2007). Two water samples were taken from a single location at the deepest part of each lake, one 0.5 m below the surface and the other 0.5 m above the bottom. Of those available data, we used the surface samples. Many of the surveyed lakes transition from being homogenously mixed during most of the year to stratified during the summer (when they are surveyed). The water quality at the bottom of each lake can become different from the surface, but the surface samples represent the layer where aquatic plants grow. This upper layer is generally well mixed and homogenous in the surveyed lakes because they are not large, thereby allowing a single surface sample to be representative of the water quality experienced by macrophytes in a particular lake. Longitude and latitude at the deepest part of each lake were obtained during water sampling. Each lake was characterised by four water quality parameters: alkalinity (mg/L), conductivity (µS/cm), pH, and total phosphorus (ppb). Attributes of lake sediment can influence aquatic plants, but were not included because they were rarely measured during surveys from 2004 to 2005, and because many groups of aquatic plants are not rooted to the sediment.

We used invasive species within each lake as an environmental subcategory representing a biotic form of disturbance that is an indirect result of anthropogenic activity. Invasive species are those identified as such by the Connecticut Invasive Species Council (https://cipwg.uconn.edu/ipc).

Land use was an environmental subcategory that represents direct anthropogenic disturbance in the surrounding catchment of each lake. We considered three major types of land use: impervious cover; grass and turf; or agriculture. Impervious cover represents development (e.g. buildings, roads, sidewalks, driveways, parking lots); grass and turf represent manicured open areas (e.g. lawns, golf courses, sports fields); and agriculture represents fields for crops or livestock. For development, we used 2012 maps (http://cteco.uconn.edu/projects/ms4/impervious2012.htm) of impervious cover from the Center for Land Use Education and Research (CLEAR) of the University of Connecticut (UConn) that include all buildings and other impervious cover types (e.g. roads, driveways, sidewalks, parking lots). We used 2012 maps because they had a substantially higher spatial resolution (0.3048 m) than did impervious cover maps created closer to the time of plant surveys (30 m). Moreover, development in Connecticut has only changed 1.1% from 2006 to 2015 (http://clear.uconn.edu/projects/landscape/CT/stats.htm#download). We used ArcGIS 10.6 (Esri Inc, 2018) to measure the percent of each type of impervious cover within the catchment of each lake based on local drainage basin maps (the most detailed delineation of drainage basins in Connecticut) from the Connecticut Department of Energy and Environmental Protection (http://cteco.uconn.edu/guides/Basin.htm). We separately considered buildings from other forms of impervious cover because they probably represent distinctive anthropogenic effects. For example, buildings are more indicative of the number of septic systems, people, and pets around a lake, whereas roads and other forms of impervious cover are more

characteristic of vehicular traffic and management such as road salt application in winter. For grass and turf, as well as agriculture, we used 2006 maps (https://clear.uconn.edu/projects/landscape) from CLEAR, as these were the closest years to those of the plant surveys (2004–2005). Fragstats (McGarigal & Marks, 1995) was used to determine the percent of grass and turf as well as agriculture in the catchment of each lake.

2.2 | Quantitative analyses

We characterised metacommunity structure from a site-by-species incidence matrix of native plants. We used the *metacom* package (Dallas, 2014) in R (R Core Team, 2019) to perform the following procedures. The incidence matrix was ordinated by reciprocal averaging (RA), which rearranges the rows and columns so that species with similar spatial distributions are in close proximity to each other, and sites with similar species compositions are in close proximity to each other (Leibold & Mikkelson, 2002). From the ordinated matrix, three elements of metacommunity structure were quantified: coherence, turnover, and boundary clumping (Leibold & Mikkelson, 2002; Presley et al., 2010). Coherence measures the extent to which all species respond to the same environmental gradient. Coherence is measured based on the number of embedded absences (i.e. gaps in the environmental distributions of species) in the ordinated matrix. Coherence is evaluated for significance by statistical comparison of metrics for the empirical metacommunity to a null distribution of such metrics that were generated by randomising the empirical incidence matrix, and then repeating the procedure for 100,000 iterations (Leibold & Mikkelson, 2002). Turnover quantifies the extent to which species distributions replace one another along the latent gradient. Turnover is measured as the number of times that one species replaces another between sites for each pair of species and for each pair of sites. These observed replacements were statistically compared to a null distribution generated by randomly shifting the entire ranges of species (Leibold & Mikkelson, 2002). Boundary clumping quantifies the extent to which species replacements along the gradient occur in compartments. Boundary clumping assesses if range boundaries are more clumped (hyperdispersed) or less clumped (hypodispersed) than expected by chance, and is evaluated for significance via a χ^2 goodness-of-fit test with respect to an even distribution of boundaries, followed by an estimation of Morisita's (1971) index (when χ^2 is significant, an index >1 indicates hyperdispersion, whereas an index <1 indicates hypodispersion).

Many null models can be used to evaluate non-random patterns. These null models form a continuum from liberal to conservative, with trade-offs in susceptibility to Type I or Type II errors (Leibold & Mikkelson, 2002; Presley et al., 2010). The most liberal null model (equiprobable-equiprobable) assigns equiprobable occurrences to each species and to site richness; this creates an ecologically unrealistic model with little structure and high susceptibility to Type I error (Gotelli, 2000; Presley et al., 2010). A moderate null model (fixed-equiprobable) constrains species richness of each site to equal

empirical values, but incorporates equiprobable occurrences for each species, providing a more ecologically realistic model that balances susceptibility to Type I or Type II errors (Presley et al., 2010). The most conservative null model (fixed-fixed) constrains column and row totals from the incidence matrix to equal empirical values; this creates a highly constrained null space with a high susceptibility to Type II error (Gotelli & Graves, 1996; Presley et al., 2010). Importantly, the susceptibility of fixed-fixed null models to Type II error decreases as the empirical incidence matrix increases in rank (Hausdorf & Hennig, 2007; Ulrich & Gotelli, 2007). A fixed-fixed null model was used in this study, as the incidence matrix was sufficiently large (104 lakes x 67 taxa) to appreciably reduce concerns about Type II error rates.

We used the first axis from RA to characterise differences among lakes in species composition. In this context, the axis represents the latent environmental gradient that determines species occurrence (Leibold & Mikkelson, 2002) and the score of each lake with respect to that axis represents its position along the most important gradient that structures incidence. We grouped plants by order to represent phylogenetic information, and by a combination of leaf and root form to represent functional information. To identify the environmental attributes of lakes that were represented by the latent gradient, we executed analyses in a 3-part hierarchical fashion using variation partitioning (Peres-Neto et al., 2006) and hierarchical partitioning (Chevan & Sutherland, 1991).

Variation partitioning (Peres-Neto et al., 2006) is a valuable technique for assessing the relative importance of dispersal (unique spatial effects), environmental heterogeneity (unique environmental effects), and species equivalence (unexplained variation). We performed variation partitioning using the *vegan* package (Oksanen et al., 2020) in R to quantify the relative contribution of spatial and environmental attributes to the differences in species composition among lakes (Analysis 1). Subsequently, we subdivided the environmental category of attributes into three subcategories—abiotic (water quality), biotic (invasive species), and anthropogenic (land use)—to determine how local environmental attributes interact with each other and with space to affect species composition (Analysis 2). Although variation partitioning decomposes unique and interactive effects of space, environment, and spatially structured environmental characteristics on variation in species composition, it can only provide assessments of significance for: (1) unique contributions of each category or subcategory of attributes (i.e. those without interactive effects); (2) overall contributions (i.e. the sum of unique and interactive effects) for each category or subcategory of attributes; and (3) the total model (i.e. the cumulative unique and interactive effects of all categories or subcategories).

For the first two analyses using variation partitioning, we executed logistic principal components analysis (PCA; Landgraf & Lee, 2020) on the site-by-species matrix of invasive species to convert from binary to continuous representations, and to reduce the number of variables representing invasive species. This reduced the number of variables from eight to four, while retaining 97.3% of variation in invasive species incidence.

Spatial attributes collected for each lake (i.e. longitude, latitude, and elevation) capture broad-scale patterns. Although trend surface analysis (Gittins, 1968) can be useful for generating spatial predictors for attributes of metacommunity structure, they are problematic for a number of reasons. Trend surfaces are based on subjective decisions associated with selection of polynomial functions to inform spatial characteristics, and they are only appropriate with homogenous sampling areas, regular sampling designs, and simple gradients (Dray et al., 2006). We used spatial attributes derived from Moran's eigenvector maps (MEMs) based on the geographic position of each lake to overcome these limitations, whereas Capers et al., (2010) used trend surfaces to generate spatial predictors for the same metacommunity. MEMs enable the distinction of simple and complex spatial patterns in neighbourhood relationships at multiple scales, including broad and fine spatial scales (Dray et al., 2006; Griffith & Peres-Neto, 2006). MEMs were calculated from the geographic coordinates of lakes, based on principal coordinate analysis of neighbour matrices (Dray et al., 2006) using the *adespatial* package (Dray et al., 2021) in R. Lakes were sampled opportunistically due to various levels of public access. Nonetheless, their spatial patterning was irregular, with considerable variation in nearest neighbour distances, averting the reduced statistical power associated with regular sampling design (Bauman et al., 2018). For determining a spatial weighting matrix, we used every combination of connectivity and weighting to perform the variable selection process, as recommended by Bauman et al., (2018), and used the single combination that produced the best (i.e. highest r^2) spatial model (Table S2). The connectivity network based on a minimum spanning tree with linear (distance-based) weighting produced the best overall spatial model. We used forward-selection with a double-stop criterion and a global test of significance (Bauman et al., 2018; Blanchet et al., 2008) to determine the most important eigenvectors for representing spatial attributes. We used this form of variable selection because it has the highest power and accuracy, while maintaining acceptable Type I error rates (Bauman et al., 2018).

2.2.1 | Analysis 1: Spatial versus environmental attributes

We first included 12 environmental attributes (Table 2), equally apportioned among abiotic, biotic, and anthropogenic subcategories. The spatial category included the first 12 predictors (eigenvectors) from MEMs. Although the forward selection process determined 14 eigenvectors for inclusion in the model, we only used the first 12 eigenvectors so that there was an equal number of variables in each subcategory. Each of these eigenvectors had eigenvalues with positive autocorrelation. We used a classical variation partitioning approach in conjunction with a refined variation partitioning analysis that adjusts for spurious contributions due to spatial autocorrelation among environmental attributes

TABLE 2 Three subcategories of environmental attributes used in variation partitioning

Water quality
Alkalinity (mg/L)
Conductivity (μS/cm)
pH
Total phosphorus (ppb)
Invasive species
Invasive species PCA score 1
Invasive species PCA score 2
Invasive species PCA score 3
Invasive species PCA score 4
Land use
Agriculture (%)
Buildings (%)
Grass and turf (%)
Other impervious cover (%)

The spatial category of attributes (not shown) included either 12 or four eigenvectors derived from MEMs, depending on the analysis (see text for details).

(Clappe et al., 2018). This correction enables a more accurate assessment of the importance of environmental heterogeneity among sites (and therefore species sorting as a mechanism) in driving metacommunity structure (Clappe et al., 2018).

2.2.2 | Analysis 2: Spatial versus abiotic versus biotic versus anthropogenic attributes

We used variation partitioning to more finely discriminate among the effects of each of three environmental subcategories (i.e. abiotic, biotic, and anthropogenic; Table 2) and a spatial subcategory on differences among lakes in species composition. We reduced the number of spatial attributes to four to maintain a number of variables as in each environmental subcategory. Furthermore, including the first four spatial attributes excluded variables with relatively small (<0.06) values of r^2. This reduced the cumulative adjusted r^2 of the overall spatial model from 0.62 (using 12 variables) to 0.38 (using four variables). Because the refined variation partitioning analysis (Clappe et al., 2018) can only assess two categories of attributes (e.g. spatial vs. environmental), only classical variation partitioning was used in the second analysis involving the four subcategories.

2.2.3 | Analysis 3: Within subcategory assessments

We used hierarchical partitioning (Chevan & Sutherland, 1991) to explore the unique and interactive contributions of each attribute within each of the four subcategories. When considering the

relative contribution of particular attributes within subcategories, we used untransformed variables instead of PCA scores (invasive species) or MEM scores (geographic coordinates) because untransformed characteristics provide insights that are more directly applicable for conservation. For example, converting invasive species incidence into logistic PCA scores is important for variation partitioning, as it reduces the number of variables and transforms them into continuous data. However, when considering particular invasive species within the biotic subcategory, the relative contribution of each PCA axis is less informative to conservation and management than is the relative contribution of each invasive species, which needs to be targeted in such efforts. Finally, because hierarchical partitioning does not capture directional associations between predictor and response variables, we performed correlations between individual attributes and the latent environmental gradient (RA 1). Associations between RA 1 and the incidence of each invasive species were determined using Spearman rank correlations; all others were determined using Pearson product–moment correlations.

3 | RESULTS

3.1 | Elements of metacommunity structure

Regardless of underlying null model, the native plant metacommunity displayed positive coherence ($p < 0.001$), positive turnover ($p < 0.001$), and positive boundary clumping ($p < 0.001$), indicating a Clementsian structure (Table 3). Consequently, only the results of the most conservative null model (fixed–fixed) form the basis for subsequent consideration. Such consistency enhanced confidence that RA 1 represented the latent environmental gradient to which most species respond, that they did so as compartments of species, and that those compartments replace one another along the environmental gradient (Figure 3). The latent environmental gradient is positively correlated with each of the four attributes of water quality and each of the four attributes of land use (Table 4). Distinctive groups of functionally and phylogenetically related species occurred

at opposite ends of the latent environmental gradient (Figure 3). Functionally, species with emergent leaves (e.g. sedges and rushes), floating-rooted leaves (e.g. water lilies), or submersed-rosulate leaves (e.g. quillworts) are almost entirely on the portion of the gradient that is negatively correlated with water quality and land use attributes, whereas species with heterophyllus leaves (i.e. both floating and submersed leaves) as well as species with submersed–vittate leaves are on the positively correlated end of the gradient. Similarly, the order Alismatales comprises the majority of species on the more positively correlated terminus of the gradient, whereas almost all of the species on the negatively correlated terminus of the gradient belong to other orders.

3.2 | Spatial versus environmental attributes

Spatially structured environmental attributes accounted for 52.2% of variation in species composition among lakes (RA 1), non-spatially structured environmental variation accounted for 16.4% ($p < 0.001$), and non-environmentally related spatial variation accounted for 10.0% ($p < 0.001$) based on a classical variation partitioning analysis (Figure 4). Overall, 78.7% ($p < 0.001$) of variation among lakes in species composition (RA 1) was related to spatial and environmental variables. Model significance and general patterns of adjusted r^2 from the refined analysis did not differ from those of the classical approach (Table S3), with 13.1% ($p < 0.001$) of variation due to non-spatially structured environmental attributes after adjusting for spurious autocorrelation.

3.3 | Spatial versus water quality versus invasive species versus land use

Variation in species composition among lakes (RA 1) was uniquely influenced by space (3.0%; $0.001 < p \leq 0.01$), water quality (4.5%; $0.001 < p \leq 0.01$), invasive species (3.2%; $0.001 < p \leq 0.01$), and land use (2.6%; $0.01 < p \leq 0.05$) (Figure 4; Table S4). The overall effects (unique plus interactive) of space (38.3%), water quality (60.7%), invasive species (40.0%), and land use (28.7%) each

TABLE 3 Results of metacommunity analyses of native aquatic macrophytes in Connecticut lakes

Coherence					Species turnover				Boundary clumping		Metacommunity structure
Null Model	Abs	Mean	Var	*p*	Rep	Mean	Var	*p*	Morisita's index	*p*	
Fixed-fixed (conservative)											
	3,426	4,238	151	<0.001	873,781	533,170	70,527	<0.001	2.01	<0.001	Clementsian
Equiprobable-equiprobable (liberal)											
	3,426	5,052	77	<0.001	873,781	532,965	70,723	<0.001	2.01	<0.001	Clementsian
Fixed-marginal (balanced)											
	3,426	4,350	141	<0.001	873,781	532,685	70,627	<0.001	2.01	<0.001	Clementsian

Abbreviations: Abs, number of empirical absences; Mean, simulated mean; Rep, empirical replacements; Var, simulated variance.
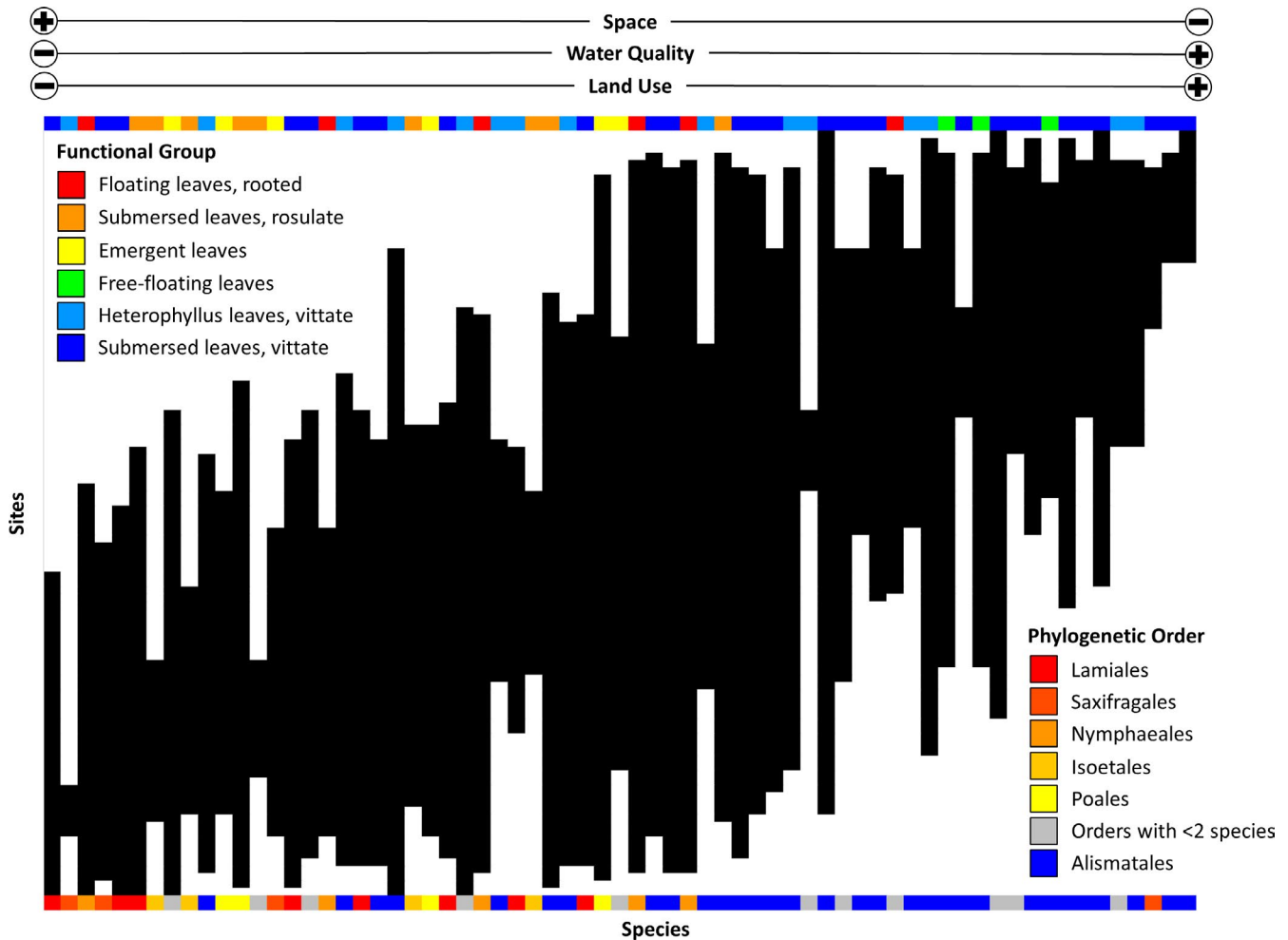
–WILEY⊥

FIGURE 3 Site-by-species matrix based on Axis 1 of reciprocal averaging. Species (black vertical bars) with similar environmental distributions are in close proximity and sites with similar species compositions are in close proximity. Space, water quality, and land use are denoted at the top of the figure, with + indicating a positive association and − indicating a negative association, when consistent with all of the variables within each subcategory. The colours of the horizontal bars are based on functional (top bar) or phylogenetic (bottom bar) characteristics of species. Functional characteristics are primarily grouped based on leaf form and branching pattern, whereas phylogenetic characteristics are grouped based on taxonomic classification at the ordinal level

explained significant amounts of variation ($p < 0.001$), with the total model accounting for 71.6% of variation ($p < 0.001$).

3.4 | Within subcategory assessments

The significant unique ($p < 0.05$) effect on variation in species composition among lakes (RA 1) within the spatial subcategory (Table 5) was greatest for longitude (32.0%), followed by elevation (13.3%), and latitude (4.4%). Alkalinity (20.2%), conductivity (17.8%), and pH (18.2%) had comparable and significant ($p < 0.05$) unique contributions within the water quality subcategory (Table 5), followed by a small but significant contribution by total phosphorus (6.2%). Within the invasive species subcategory (Table 5), *M. spicatum* had a moderate (24.7%) significant effect ($p < 0.05$) along with small but significant ($p < 0.05$) contributions by *P. crispus* (6.0%), *M. heterophyllum* (4.4%), *M. quadrifolia* (3.0%), and *N. minor* (3.6%). Grass and turf explained the most variation (11.8%) within the anthropogenic

subcategory, followed by non-building impervious cover (10.3%) and buildings (6.6%). Agriculture did not have a significant unique effect.

4 | DISCUSSION

4.1 | Metacommunity structure

The majority of species responded to the same latent gradient, species distributions replaced one another along that gradient, and those replacements occurred as compartments (i.e. Clementsian structure). Although several species in the center of the ordinated matrix have distributions that include all sites, a distinctive set of lakes characterises each end of the gradient, with each set of lakes containing unique sets of species. Each compartment, one at each end of the latent environmental gradient, represents species with similar functional or phylogenetic affinities that differ from those at the opposite end of the gradient. The strong positive correlations for

TABLE 4 Correlation coefficient (*r*) and significance (*p*) for associations between Axis 1 of reciprocal averaging and constituents of each of the four subcategories of attributes

Attribute	r	p
Spatial		
Elevation (m)	−0.221	0.024
Latitude (decimal degrees)	−0.131	0.185
Longitude (decimal degrees)	−0.484	<0.001
Environmental (water quality)		
Alkalinity (mg/L)	0.703	<0.001
Conductivity (µg/L)	0.657	<0.001
pH	0.625	<0.001
Total phosphorus (ppb)	0.313	0.001
Environmental (invasive species)		
Presence of *Cabomba caroliniana*	−0.290	0.003
Presence of *Eichhornia crassipes*	0.071	0.477
Presence of *Glossostigma cleistanthum*	−0.146	0.138
Presence of *Marsilea quadrifolia*	0.166	0.093
Presence of *Myriophyllum heterophyllum*	−0.296	0.002
Presence of *Myriophyllum spicatum*	0.584	<0.001
Presence of *Najas minor*	0.304	0.002
Presence of *Potamogeton crispus*	0.344	<0.001
Environmental (land use)		
Agriculture (%)	0.147	0.135
Buildings (%)	0.419	<0.001
Grass and turf (%)	0.491	<0.001
Other impervious cover (%)	0.473	<0.001

Note: Correlation coefficients for biotic attributes were determined using Spearman rank, all others were determined using Pearson product-moment.

all attributes of water quality and land use indicate that one end of the gradient is associated with less disturbed lakes and the other end of the gradient is associated with more disturbed lakes (i.e. higher alkalinity, conductivity, phosphorus concentration, and pH, as well as higher percentages of all four types of human land use). The separation of different functional or phylogenetic groups to opposing ends of the gradient indicates that species within these groups share similar environmental distributions that are not shared by species on the other end of the gradient (i.e. each compartment represents species with similar niche characteristics), and those groups are associated with high or low levels of disturbance. Using a different approach (based on β diversity patterns vs. elements of metacommunity structure), García-Girón et al., (2019) found that species with emergent leaves were associated with the more disturbed end of the

disturbance gradient, and species with floating or submerged leaves occurred in the center to the beginning of the disturbed end of the gradient. Such differences highlight the need to understand the role of functional traits and phylogenetic affiliations in contributing to particular metacommunity structures.

Although dispersal-related functional traits were associated with the geographic distribution of macrophytes (Capers et al., 2010), such associations did not characterise the environmental distribution of macrophytes in these same lakes. Although some form of spatial limitation is associated with dispersal capability (Capers et al., 2010), at the scale of this study, any differences in dispersal capability do not ultimately influence species composition. Instead, composition is strongly influenced by local environmental factors that are spatially patterned.

4.2 | Metacommunity processes

We accounted for a substantial amount (78.7%) of the total variation in species composition among lakes—almost three times that found using the same compositional data in Capers et al., (2010)—by including features of disturbance (i.e. invasive species, land use, and water quality). The large difference between studies may also be related to changes in the approaches used for: (1) characterisation of the metacommunity (elements of metacommunity structure vs. canonical correspondence analysis); (2) generation of spatial predictors (MEMs vs. trend surface analysis); or (3) representation of the environment (water quality from the surface vs. bottom). The considerable variation (68.6%) explained by pure environment and spatially structured environment suggests that environmental heterogeneity is critical in structuring macrophyte metacommunities, in line with conclusions from studies on aquatic plants in other regions (Alahuhta et al., 2015; Alahuhta et al., 2018). Although substantial evidence corroborates the importance of environmental heterogeneity or variability (abiotic, biotic, and anthropogenic) in structuring aquatic plant composition, the significant unique effects of space (10.0%) indicate that dispersal is also important, and the remaining unexplained variation (21.3%) suggests that species equivalence may also play a role in affecting species composition. Of course, the unexplained variation may be due to unmeasured environmental characteristics, and even the unique effects of space could be a consequence of unmeasured spatially structured environmental attributes.

This system of lakes has been in existence long enough for dispersal events to happen sufficiently often so that the boundaries of the environmental distributions of species are delimited accurately. As passive disperses, migration events can happen when individual plant fragments become attached to boats (Johnson et al., 2001; Johnstone et al., 1985) or over thousands of kilometres when attached to waterfowl (Figuerola & Green, 2002). Although aquatic plants can disperse readily throughout the entire region by bird or boat, the frequency of embedded absences along with unexplained variation suggests that dispersal is likely to be infrequent and to some degree stochastic. Additionally, the
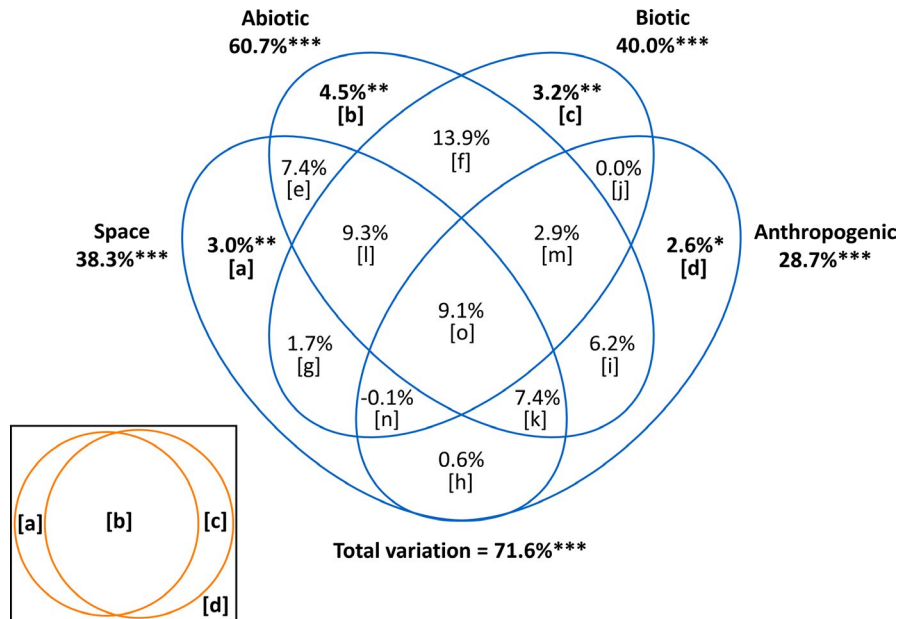
FIGURE 4 Results of variation partitioning illustrate the relative effects of space as well as each of three subcategories (abiotic [water quality], biotic [invasive species], and anthropogenic [land use]) of environmental characteristics on variation in species composition among lakes. Contributions that were testable for significance are in bold text, and significant contributions are indicated with asterisks (i.e. *0.01 < p ≤ 0.05; **0.001 < p ≤ 0.01; ***p ≤ 0.001). Bold contributions within ellipses represent unique (i.e. non-interactive) effects, whereas those outside of ellipses represent overall effects of each subcategory. The inset (bottom left) shows the results of variation partitioning (see Table S3) using two categories. The unique effects of space (10.0%, p < 0.001) are indicated by [a], the unique effects of the environment (16.4%, p < 0.001) are indicated by [c], the effects of spatially structured environment (52.2%) are indicated by [b], and unexplained variation is represented by [d]. After adjustment for possible confounding of environmental and spatial partitions via a refined approach, the unique partition ascribed to the environment remains appreciable and significant (13.1%, p < 0.001). The areas of the ellipses in the main portion of the figure are not proportional to their relative contributions based on the four subcategories, whereas the areas of the circles in the inset are proportional to their relative contributions

significant independent effect of space and its component attributes supports that dispersal is limiting at some spatial extents and for some species (Capers et al., 2010). Nevertheless, pattern detection may be biased towards medium and broad spatial scales, potentially underrepresenting fine scale patterns characterising the cluster of lakes in south-eastern Connecticut that are in close proximity to one another.

Each of three non-transformed spatial attributes (i.e. latitude, longitude, elevation) had significant unique effects on variation in species composition. Geology affects water quality of lakes and the geological provinces of Connecticut change along a longitudinal gradient. Unsurprisingly, longitude had the strongest effect, which is probably due to such spatially structured geological variation. Iversen et al., (2019) found that aquatic plants are distributed globally and regionally based on geological catchment characteristics that determined carbon availability and not based on climate factors. Our results support their findings at a smaller regional extent.

Substantial evidence suggests that species sorting is a primary driver of variation in species composition among lakes. Species sorting is characterised by heterogeneous habitat, niche differences among species, and moderate dispersal. We found evidence for all three. Importantly, species sorting of aquatic plants arises in response to abiotic, biotic, and anthropogenic variability in the landscape.

4.3 | The effects of local environment

Water quality had a stronger total (60.7%, p < 0.001) and unique (4.5%, 0.001 < p ≤ 0.01) effect on species composition compared to biotic or anthropogenic attributes, although the unique factors for both were quite small. More specifically, alkalinity, conductivity, and pH explained the most variation in species composition. These findings corroborate other studies that have found water quality to be an important driver of the composition of aquatic plant species (Alahuhta et al., 2018; Iversen et al., 2019). Each species of aquatic plant has a particular range of pH values within which it persists, and these ranges differ substantially among species (Madsen & Sand-Jensen, 1991). The predominant form of carbon available in the water is determined by pH and alkalinity, and carbon dioxide diffuses slowly in the water when it is available. Aquatic plants are often limited by carbon and differ in their ability to uptake alternative forms such as bicarbonate or carbonate. Salinity also presents a strong abiotic filter, as each aquatic plant species can survive within a particular range of salinity. Salinity is increasing throughout the U.S.A. (Kaushal et al., 2018), which is a challenge for aquatic plants that will result in rapid adaptation or local extirpation. Although significant, phosphorus was of least importance in driving species composition. Phosphorus availability in the water column is the main limiting nutrient for algal growth in lake ecosystems, but not necessarily for

TABLE 5 Hierarchical partitioning results for each of the constituent attributes associated with space, water quality, invasive species, and land use

Variable	*i*	*j*	Total	Significance
Spatial				
Elevation (m)	0.133	−0.085	0.049	*
Latitude (decimal degrees)	0.044	−0.027	0.017	*
Longitude (decimal degrees)	0.320	−0.086	0.234	*
Environmental (water quality)				
Alkalinity (mg/L)	0.202	0.293	0.495	*
Conductivity (μg/L)	0.178	0.255	0.432	*
pH	0.182	0.210	0.391	*
Total phosphorus (ppb)	0.062	0.036	0.098	*
Environmental (invasive species)				
Cabomba caroliniana	0.024	0.037	0.060	
Eichhornia crassipes	0.002	0.001	0.003	
Glossostigma cleistanthum	0.006	0.011	0.017	
Marsilea quadrifolia	0.030	0.020	0.049	*
Myriophyllum heterophyllum	0.044	0.047	0.091	*
Myriophyllum spicatum	0.247	0.112	0.359	*
Najas minor	0.036	0.057	0.093	*
Potamogeton crispus	0.060	0.058	0.118	*
Environmental (anthropogenic)				
Agriculture (%)	0.027	−0.006	0.022	
Buildings (%)	0.066	0.109	0.175	*
Grass and turf (%)	0.118	0.122	0.241	*
Other impervious cover (%)	0.103	0.121	0.224	*

Note: The independent (*i*), joint (*j*), and total contribution of each variable is indicated with respect to variation among lakes in species composition (Axis 1 of reciprocal averaging). An attribute with a significant ($p < 0.05$) independent effect is indicated by an asterisk.

macrophytes. Macrophytes can obtain phosphorus from the sediment, where concentrations are typically higher than in the water column. Increasing phosphorus typically affects macrophytes negatively as a consequence of increasing algal abundance in surface waters, which limits light availability to the macrophytes below, and induces an algae-dominated stable state (Folke et al., 2004).

Invasive species had a weak unique effect (3.2%), but stronger interactive effect with water quality (13.9%), in affecting variation in species composition among lakes. This may transpire if invasive species become competitively dominant under certain abiotic conditions. Invasive and native aquatic plant species that dominate communities display a wide range of tolerance to abiotic conditions. These adaptations may make it easier for such dominant species to outcompete and exclude particular groups of species that do not cope well in stressful or fluctuating abiotic environments. The unique effect of invasive species is probably due to their competitive abilities, which influence native species composition by excluding competitively inferior species, regardless of abiotic conditions. Five of the eight invasive aquatic plant species that occur in Connecticut modulate species composition of native aquatic plants via unique effects. The four most frequently occurring and historically established invasive aquatic plants are included and of particular concern. *Myriophyllum spicatum* (Eurasian watermilfoil) had the strongest total effect of the invasive species and is the most widespread invasive aquatic plant in the U.S.A. (Sheldon, 2019). It disperses easily and proliferates rapidly, competitively excluding native aquatic plants from local communities (Madsen et al., 1991; Smith & Barko, 1990). Lakes with invasive aquatic plants like *M. spicatum* are more likely to contain fewer native species and only those that are better competitors (i.e. tall species that grow rapidly to the water surface).

Land use had the weakest total effect (28.7%) of the four subcategories of environmental factors, but a comparable independent effect (2.6%) to other subcategories. Similar to invasive species, the effects of land use were almost entirely associated with water quality. Because land use occurs around the periphery of a lake, it does not directly affect species composition. Instead, it indirectly influences species composition through variation in water quality and by affecting dispersal via access for boat traffic. Alkalinity, conductivity, pH, and phosphorus are increasing throughout the U.S.A. as a result of anthropogenic land uses in catchments (Kaushal et al., 2018). Although those attributes naturally increase with lake age, drastic increases generally do not occur without considerable anthropogenic inputs, which may enhance species sorting by creating amplified environmental heterogeneity or variability. The unique effect of land use may be related to anthropogenic development that occurs around the shoreline of a lake, which essentially has a direct effect on aquatic plants via alteration or loss of habitat (Elias & Meyer, 2003; Radomski & Goeman, 2001) or via addition of physical structures such as docks or shoreline walls. Three of four land use attributes (buildings, other impervious cover, and grass and turf) had a unique effect, whereas agriculture did not have a significant unique effect, despite being important in other regions (Egertson et al., 2004; Heegaard et al., 2001). Buildings are indicative of the number of septic systems, people, and pets in a catchment, which can act as sources of pollutants to lakes that affect water quality attributes. Buildings in close proximity to a lake are also indicative of modifications to the lake shoreline that can influence littoral processes such as erosion and sedimentation. The effects of other impervious cover (roads, sidewalks, driveways, parking lots) may

manifest by increasing conductivity and sedimentation of lakes via transport of salts and sands that are commonly applied to such surfaces in the winter. Of the land use attributes, grass and turf had the strongest unique and total effects on species composition of native aquatic plants. Grass and turf include small lawns or gardens, as well as large golf courses or sports fields. Grass and turf may be important sources of fertiliser (associated with phosphorus), lime (associated with pH and alkalinity), or other pollutants (e.g. herbicides and pesticides). Moreover, grass and turf commonly occur around lake shorelines because homeowners create lawns that directly extend to the shore. Lawns around the shoreline replace natural vegetative buffers (e.g. forest) that are often crucial for mitigating the influx of nutrients into lakes.

The environmental attributes that drive Clementsian metacommunity structure appear to vary by region (García-Girón et al., 2020). Furthermore, there is often a large amount of unexplained variation that is attributed to stochastic events or priority effects (Capers et al., 2010; García-Girón et al., 2019). This may arise because most studies do not consider all aspects of local environment (abiotic, biotic, and anthropogenic), leading to an inability to comprehensively identify the attributes that drive metacommunity structure and distinguish their unique and joint effects.

4.4 | Caveats and limitations

Studies of biodiversity that reflect variation in the abundance of species provide considerable insight regarding metacommunity structure (Willig & Presley, 2016) or the linkage of biodiversity to ecosystem stability in metacommunities (Wang & Loreau, 2016), especially when decomposing γ components of metrics of biodiversity (e.g. diversity, evenness, dominance) into their constituent α and β components. Studies at broad to intermediate scales, such as this, are limited by their inability to obtain accurate estimates of the abundances of species, and thus provide only partial insights into spatial dynamics. Because we do not capture variation in composition among lakes based on abundance, we cannot explore more nuanced hypotheses that distinguish among sites where few versus many individuals characterise resident species and then link such variation to ecosystem processes. From conceptual and methodological perspectives, the study of ecology would be advanced by integration of variation in species abundances into the framework for quantifying latent environmental gradients and evaluating elements of metacommunity structure (sensu Leibold & Mikkelson, 2002).

5 | CONCLUSIONS

Our research is unique and important in assessing the role of invasive species on structuring a native species metacommunity, as well as in simultaneously assessing the roles of a comprehensive suite of abiotic, biotic, and anthropogenic attributes. Consequently, we are able to distinguish unique effects of each suite of attributes, the interactive effects of all combinations of suites of attributes, and the total effects of each suite of attributes. In doing so, we accounted for a substantial amount of variability among lakes (78.7%), further distinguishing our work from that of many other studies with less explanatory power. Finally, we are able to identify functional and phylogenetic indicators of the compartments that lead to a Clementsian structure and associate them with particular levels of anthropogenic disturbance. Metacommunity research would benefit by consistently considering the anthropogenic and biotic factors that play important roles in shaping variation in species composition, and by including phylogenetic and functional ways of characterising species.

DATA AVAILABILITY STATEMENT

Plant survey and water quality data are available from the Connecticut Agricultural Experiment Station (https://portal.ct.gov/caes). GIS data are available from the Connecticut Department of Energy & Environmental Protection (https://www.ct.gov/deep) and Center for Land Use Education & Research (https://clear.uconn.edu). Other data are available from the corresponding author upon reasonable request.

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SUPPORTING INFORMATION

Additional supporting information may be found online in the Supporting Information section.