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RESEARCH ARTICLE

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Assessing the conservation priority of freshwater lake sites based on taxonomic, functional and environmental uniqueness

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Abstract

Aim: We propose a novel approach that considers taxonomic uniqueness, functional uniqueness and environmental uniqueness and show how it can be used in guiding conservation planning. We illustrate the approach using data for lake biota and environment.

Location: Lake Puruvesi, Finland.

Methods: We sampled macrophytes and macroinvertebrates from the same 18 littoral sites. By adapting the original "ecological uniqueness" approach, we used distance-based methods to calculate measures of taxonomic (LCBD–*t*), functional (LCBD–*f*) and environmental (LCEH) uniqueness for each site. We also considered the numbers and locations of the sites needed to protect up to 70% of total variation in taxonomic, functional or environmental features in the studied part of the lake.

Results: Relationships between taxonomic (LCBD–*t*), functional (LCBD–*f*) and environmental (LCEH) uniqueness were generally weak, and only the relationship between macrophyte LCBD–*t* and LCBD–*f* was statistically significant. Overall, however, if the whole biotic dataset was considered, macroinvertebrate LCBD–*f* values showed a consistent positive relationship with macrophyte LCBD–*f*. Depending on the measure of site uniqueness, between one-third to one half of the sites could help protect up to 70% of the ecological uniqueness of the studied part of Lake Puruvesi.

Main conclusions: Although the dataset examined originated from a large lake system, the approach we proposed here can be applied in different ecosystems and at various spatial scales. An important consideration is that a set of sites has been sampled using the same methods, resulting in species and environmental matrices that can be analysed using the methodological approach proposed here. This framework can be easily applied to grid-based data, sets of islands or sets of forest fragments. We suggest that the approach based on taxonomic, functional and environmental uniqueness will be a useful tool in guiding nature conservation and ecosystem management, especially if associated with meta-system ideas or network thinking.

KEYWORDS
biodiversity, conservation assessment, ecological uniqueness, environmental heterogeneity, freshwaters, lakes, macroinvertebrates, macrophytes

1 | INTRODUCTION

Prioritization for nature conservation can be based on non-living (i.e., abiotic) or living (i.e., biotic) features of the environment (Whittaker & Ladle, 2011). Typically, conservation research has focused on biotic diversity, where the underlying basis is measuring the diversity and composition of ecological assemblages (Gaston, 1996a). However, all nature conservation frameworks should ideally consider both biotic and abiotic environmental characteristics (Astudillo–Scalia et al., 2021; Faith & Walker, 1996). This is important for two main reasons. First, biotic diversity builds on information on the species occurrences, yet one of its main drawbacks is that species presences are often temporally variable. Second, one cannot typically detect all species present at a site owing to a limited sampling effort (e.g., Beck et al., 2018), which is especially true for small, cryptic and rare species (e.g., McCabe, 2011). Abiotic diversity instead provides information on the physical and chemical habitat conditions for a set of different species, is typically temporally more stable than species occurrences at a site and can thus be used as a surrogate for biotic diversity (e.g., Beier & Albuquerque, 2015). For example, physical landforms are likely to remain relatively unchanged compared with distributions of species occurrences over the same period. Hence, conservation planning, in general, should contrast the compositional, functional and environmental basis of conservation (Cadotte & Tucker, 2018; Gillson et al., 2011).

The measures used to describe biotic diversity range from (1) simple counts of the numbers of taxa (e.g., Gaston, 1996b) to (2) those considering the relative levels of species rarity (e.g., Rabinowitz, 1981) and (3) to more recent indices measuring the degree of ecological uniqueness (e.g., Legendre & De Cáceres, 2013). The measure of the ecological uniqueness of a site is compared with other sites in a study area (i.e., local contribution to beta diversity, LCBD). In other words, LCBD measures the contribution of each site to the total compositional variation among assemblages in the area under study and, therefore, it can be used in ranking sites based on their compositional uniqueness (Legendre & De Cáceres, 2013). The set of compositionally most unique sites representative of the natural state of ecosystems should thus be prioritized for nature conservation. This measure can be considered particularly useful for guiding biodiversity assessment, conservation and restoration schemes because it helps distinguish the sites that differ most from other sites in assemblage composition (Legendre & De Cáceres, 2013). Therefore, it is not surprising that the use of this approach has recently come to the fore in biodiversity assessment and conservation research (e.g., Benito et al., 2020; Heino & Grönroos, 2017; Hill et al., 2021; Tan et al., 2019).

Most studies using the LCBD approach for evaluating ecological uniqueness have been based on taxonomic data (e.g., Vilmi et al., 2017). However, a few recent studies have also expanded the original approach to include phylogenetic (e.g., Shooner et al., 2018) and environmental information (e.g., Castro et al., 2019), which could provide further insights into different aspects of ecological uniqueness. In addition, one could also extend the LCBD approach to analysing functional trait composition because functional traits can be considered proxies for ecosystem functions (e.g., McGill et al., 2006). In this sense, the traditional ecological uniqueness (LCBD) approach provides information about *taxonomic uniqueness of ecological assemblages*, whereas the approach we suggest here also includes *functional uniqueness of ecological assemblages* and *environmental uniqueness of sites*. To our knowledge, however, no study to date has simultaneously assessed ecological uniqueness based on taxonomic, functional and environmental features and used resulting information in guiding freshwater conservation planning. Our approach could thus be an important addition to the existing tools that aim at freshwater conservation prioritization based on different facets of biotic and abiotic diversity (e.g., Brumm et al., 2021).

Freshwater biodiversity is declining faster than that in the marine or terrestrial realms (Wiens, 2015), which has been attributed to the small areal extent, high degrees of isolation and vulnerability of freshwater ecosystems (Dudgeon et al., 2006). They are severely threatened by environmental impacts at different spatial and temporal scales (Birk et al., 2020; Reid et al., 2019). Recent accounts have emphasized that the situation is dire, as extinction rates and ecosystem degradation are increasing in freshwater ecosystems due to anthropogenic development and overuse of natural resources (Albert et al., 2021; Jähnig et al., 2021). For example, lakes have suffered from anthropogenic development in recent decades because of land-use change (e.g., Anderson et al., 2013), nutrient enrichment (e.g., Downing et al., 2021; Zhang et al., 2019) and introduction of exotic species (e.g., Hall & Mills, 2000), to name a few major anthropogenic factors acting at local and landscape levels (for a review, see Heino et al., 2021). At the same time, lakes are also important for recreation and provide supplies of drinking water and fish, as well as harbour rare species of particular conservation concern (e.g., Schallenberg et al., 2013). This background of conflicting pressures and values underscores the importance of assessing freshwater lake sites based on different measures of biotic and abiotic nature, which should in turn be used in guiding the conservation and restoration of the structure, function and biota of lakes.

Here, we expand upon contemporary approaches to measure a site's ecological uniqueness based on its taxonomic, functional and environmental features. We apply the approach to a primary producer group in lakes (here, macrophytes) and a taxonomically and functionally highly diverse group of consumers (here, macroinvertebrates). Macrophytes are key players that contribute to nutrient cycling and primary production (e.g., Carpenter &

Lodge, 1986), and provide multiple habitats that other organisms, such as fish (e.g., Quirino et al., 2021) and macroinvertebrates (e.g., Tolonen et al., 2001), can use for foraging and shelter (e.g., Heino & Tolonen, 2017). Macroinvertebrates, in turn, contribute to various ecosystem processes through herbivory, detritivory and predation, acting as key links from autochthonous and allochthonous production to secondary and primary consumers, such as benthivorous fish (Wallace & Webster, 1996).

By focusing on macrophytes and macroinvertebrates sampled at the same sites in a large boreal lake system, we addressed two main questions in this study. (1) How do taxonomic, functional and environmental uniqueness of sites correspond to each other? To answer this question, we calculated taxonomic (LCBD–*t*), functional (LCBD–*f*) and environmental (i.e., local contribution to environmental heterogeneity, LCEH) uniqueness of sites. We assumed that these three measures of site uniqueness should be positively correlated because environmental conditions affect the distributions of both macrophytes (e.g., Alahuhta et al., 2021) and macroinvertebrates (e.g., Heino & Tolonen, 2017), which are also connected via direct and indirect interactions (e.g., García–Girón et al., 2020). (2) Will the same subsets of sites be most valuable for conservation of lake nature based on taxonomic, functional and environmental uniqueness? We addressed this question by testing the congruence between different uniqueness measures and by ranking the sites based on their taxonomic, functional and environmental uniqueness values. Subsequently, we examined how the total beta diversity in the focal lake system was covered by 1, 2, 3… *n* sites with highest uniqueness values in our dataset. This simple and heuristic process to select a set of sites for strict conservation was done separately for macrophytes and macroinvertebrates as well as environmental uniqueness, which is also one of the main novelties of our study (Figure 1). To examine these questions, we used survey data from littoral areas of Lake Puruvesi, Finland. This lake is an important location for boreal freshwater biodiversity and conservation, as most of the lake area is covered by the protected areas belonging to Natura 2000 network.

2 | MATERIALS AND METHODS

2.1 | Study area

Lake Puruvesi is one of the large sub-basins of the large Lake Saimaa system (4400 km^2), the largest lake in Finland. Lake Puruvesi is an oligotrophic and transparent lake with low phytoplankton productivity and high diversity of littoral habitats (Table 1). The lake is a highly important site from a conservation point of view for several reasons. First, Lake Puruvesi harbours diverse fauna and flora with many threatened species. For example, the endangered Saimaa ringed seal (*Pusa hispida saimensis*) has started to re-colonize sites in the lake, from where it disappeared in the 1950s. Second, in a national classification, Lake Puruvesi is classified to belong to a near-threatened habitat type of large humus–poor lakes and designated a Natura 2000 site as a representative example for the lake habitat type "Oligotrophic waters containing very few minerals of sandy plains" (type "*Littorelletalia uniflorae*"). Third, altogether 320 km^2 of the 420 km^2 total surface area of the lake is thus protected as part of the EU's Natura 2000 network (Evans, 2012). As an important location for recreational and inland professional fisheries, multiple water-related recreational activities and tourism, Lake Puruvesi is locally important for regional economy and employment. Our study area (the Hummonselkä subbasin) is situated in the north-eastern part of Lake Puruvesi, where we surveyed macrophytes, macroinvertebrates and environmental features at the same 18 sites in 2017 (Supplementary Information Appendix S1, Figure S1). Most of these 18 sites are near-natural, but five of them were affected by summer cottages or agricultural fields close to the shore.

2.2 | Field sampling and laboratory analyses

Biological samples were collected within 100-m-wide, pre-selected strips of the shoreline (hereafter, referred to as "sites") at depths from 0 to 7 m for macrophytes and from 0 to 3 m for macroinvertebrates between August and September in 2017. Sites for macrophyte mapping were selected using systematic sampling for the mainland shoreline to distribute sites evenly along the shoreline of the study area. Also, the sampling was supplemented with a few sites with underrepresented habitat type (i.e., sandy and soft bottom types) to match the numbers of sites representing main littoral habitat types (i.e., stony, sandy and soft bottom shores). A few additional sites located along the shorelines of islands were selected based on a stratified random sampling scheme. In practice, some of the study sites were randomized to be located on islands classified into five groups based on surface area (0.1–1, 1–5, 5–10, 10–40 and >40 ha).

Macrophyte records were pooled at each site to include 15 × 4 m^2 squares, that is, 60 m^2 in total area. Five squares were investigated at each depth zone: 0–0.5 m, 0.5–2 m and >2 m. At each site, four macrophyte mapping transects with the minimum distance of 20 m were established from the shoreline to the depth of seven metres (maximum colonization depth of macrophytes in Lake Puruvesi). The transects were marked with a sinking rope with markings at 1-m intervals, and weights and buoys attached to each end. Mapping plots of 2 × 2 m were assigned along the transects based on criteria presented below. Macrophyte species covers were mapped by wading from the shoreline to the depth of approximately 1.3 m using an aquascope, placing the first plot at the shoreline (0 m). The deeper plots from the depth of 1.3 m to 7 m were surveyed by scuba-diving. Diving was started from the deep end of the transect, placing the first square at the deep end. A new plot was assigned when the following criteria were met: (a) the depth change from the beginning of the previous plot was 0.5 m, (b) the distance from the beginning of the previous plot was 20 m, and none of the other criteria were met (c) after a non-vegetated plot was met again, and (d) when *Littorella uniflora*, the key indicator plant species for the oligotrophic lake habitat

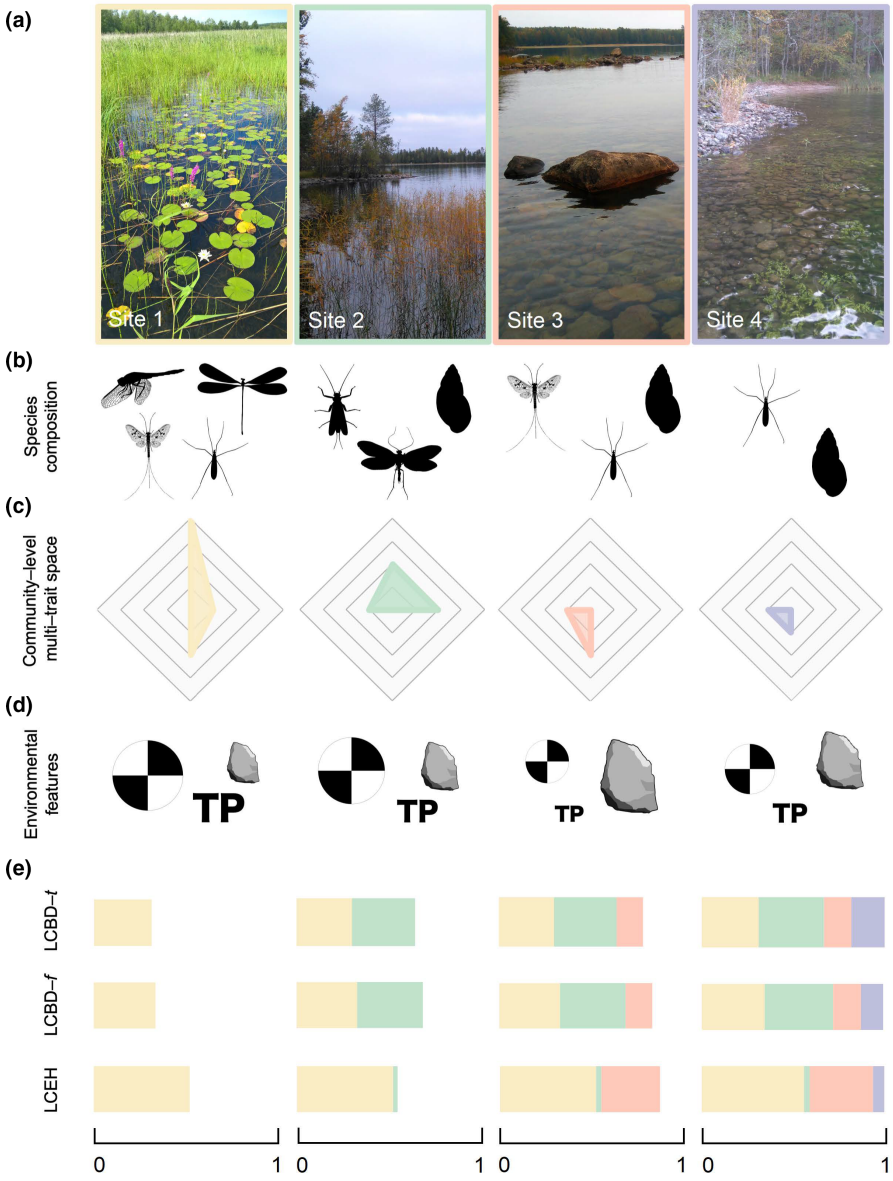

FIGURE 1 Conceptual illustration of our novel approach to guide freshwater conservation planning by joint evaluations of each site's ecological uniqueness based on taxonomic, functional and environmental measures. In this example, (a) four near-natural littoral sites from Lake Puruvesi were surveyed focusing on their biotic and abiotic components. For clarity, we only included (b) taxonomic (a site-by-species matrix synthesizing community composition) and (c) functional features (charts representing community-level functions; Mori et al., 2018) of benthic macroinvertebrate communities, as well as the (d) environmental conditions of the sites (here, Secchi depth, total phosphorous [TP] and substratum size). Based on taxonomic, functional and standardized environmental data (see Figure 2 for details), we obtained (e) taxonomic (LCBD–*t*), functional (LCBD–*f*) and environmental (LCEH) uniqueness values for each site (0–1 range). In our illustrative example, protecting both "site 1" and "site 2" would contribute towards protecting up to three quarters of the biotic uniqueness of Lake Puruvesi. However, the environmental component expanded the number of potential conservation sites to "site 3," emphasizing that different sets of uniqueness indices could provide complementary information for guiding conservation planning

type, was found in the transect. However, at least 1-m distance was always left between two subsequent plots to avoid overlap between the plots. The species that remained unidentified in the field were preserved in plastic bags for later identification. The total number of squares investigated within a site varied from 25 to 74, depending on the bathymetric profile and abundance of vegetation. For further analyses, a total of 15 squares, that is, five squares from each depth zone: 0–0.5 m, 0.5–2 m and >2 m, were randomly drawn from each site to harmonize sample schemes of macrophyte and macroinvertebrate data and to standardize sample sizes among depth zones. The data from each site were pooled for the data analysis.

A pooled sample of macroinvertebrates included an area of $9 \times 1590\,cm^2$ (=$1.431\,m^2$) sampled from each site. In other words, three macroinvertebrate samples were taken at each of the following depth zones: 0–0.5 m, 0.5–2 m and >2 m. Macroinvertebrates were sampled using a centrifugal pump with a combustion engine as a power source. Each sampled area was outlined with a 20-cm-high oblong metal frame ($1590\,cm^2$). On stony bottoms, the stones were brushed with a dish brush to detach attached macroinvertebrates, and invertebrates were drawn into the pump through metal funnel attached to the inlet hose of the pump. Samples were drained to a 0.5-mm sieve through the outlet hose of the pump. After sieving, samples were preserved in ethanol. At sandy and soft bottom vegetated areas, a stiff fibreglass pipe with a $143\,cm^2$ metal funnel at the end of pipe was attached to the end of inlet hose of the pump. The sampled area was closed from surface to bottom by a 0.45-mm mesh net fixed to the metal frame. Each sample was taken from surface to bottom by stirring the water column with a pipe to detach invertebrates attached to macrophytes and to draw them to the pump through the funnel. In the end, sediment was sampled through the funnel. As such, the sampling methods described here are a slightly modified version of the methods described in Tolonen et al. (2001, 2003). Macroinvertebrates were sorted, identified usually to species or genus, and individuals were later counted under the microscope.

TABLE 1 Information on the selected whole-lake and site-level morphometric and water chemistry parameters of Lake Puruvesi

Whole-lake parameters	Value
Surface area (km^2)	420
Shoreline length (km)	962
Mean depth (m)	8.76
Maximum depth (m)	61
Site-level parameters	**Mean (range)**
Bottom slope (%, 0–2 m)	9.7 (0.7–32.8)
Wind fetch (m)	1253 (85–3623)
Stony substrate (%)	37.6 (0.0–87.3)
Sandy–gravelly substrate (%)	29.2 (0.0–75.0)
Fine or organic substrate	32.4 (1.3–98.0)
Secchi depth (m)	6.4 (3.8–8.3)
Total phosphorus ($\mu g\,L^{-1}$)	3.6 (1.5–7.0)
Total nitrogen ($\mu g\,L^{-1}$)	199 (170–240)
Chl-*a* ($\mu g\,L^{-1}$)	1.4 (1.0–3.0)
Turbidity (FNU)	0.45 (0.27–0.70)
pH	7.3 (7.0–7.4)
Colour (mg Pt L^{-1})	6.8 (2–10)

Note: Means and ranges (in parentheses) of water chemistry parameters are given for summer (June–August) values in 2007–2017. Here, only near-natural sites of Lake Puruvesi were studied, referring to site-level parameters. Abbreviation: Chl-*a* refers to chlorophyll-*a* of water.

However, some taxa were identified to a higher level (Oligochaeta, Hydracarina, Chironomidae and Ceratopogonidae).

We estimated coverages (%) of different substratum sizes from each sampling frame based on Wentworth (1922) classes, including rock, boulders, cobbles, pebbles, gravel, sand, fine inorganic sediment, mud and peat. These original classes were subsequently summed into three different categories, including (1) rock, boulders, cobbles and pebbles as stony bottom (%), (2) gravel and sand as gravelly–sandy bottom (%), and (3) fine sediment, mud and peat as fine–organic sediment (%). Wind fetch (m), as a site-specific variable representing whole 100-m-wide littoral strip, was measured from the middle point of each strip using Fetch Model (Finlayson, 2005) in ArcGIS Desktop 10 (Environmental Systems Research Institute [ESRI], 2015). Specifically, this variable refers to effective wind fetch weighted with local wind conditions (method "SPM," see Rohweder et al., 2012). Bottom slope (%) was another site-specific variable that was measured from the shoreline to the depth of 2 m. Because the water chemistry of the study lake is temporally and spatially fairly homogenic, we measured only two water chemistry parameters, that is, turbidity and water colour, at each sampling site.

To obtain data for values of average and maximum current velocity (m/s) and bottom shear stress (N m^2) at the sampling sites, we used a 3-D hydrodynamic model of Lake Puruvesi based on the COHERENS V2.11.2 code (Luyten, 2013). COHERENS solves the 3-D equations using the finite difference method, assumes vertical hydrostatic equilibrium and uses the Boussinesq buoyancy approximation. The rectangular model grid resolution was 50 m × 50 m with 16 vertical variable thickness layers. The model has a minimum depth of 0.5 m and maintains a constant 0.5-m surface and bottom layer thickness in areas deeper than 8 m. The model input data included lake bathymetry, open boundary data (lake surface height at northern and southern boundaries) and weather (temperature, precipitation, wind speed and direction, humidity, air pressure and cloudiness). Measurement data used to create the depth grid for the computational model were a combination of open data retrieved from TrafiCom (https://www.traficom.fi/en/news/open–data) and new data measured by Geological Survey of Finland. Open boundary data were obtained from the Finnish Environment Institute (https://www.syke.fi/en–US/Open_information) and weather data from the Finnish Meteorological Institute (https://en.ilmatieteenlaitos.fi/open–data). The model was run for the time period between May 2017 and November 2017. Current velocity and bottom shear stress values were extracted for each macrophyte vegetation plot from spatial raster layers using custom code adapted from rSDM R package functions developed by Francisco Rodriquez-Sanchez (Species distribution and niche modelling in R, rSDM; pakillo.github.io). For sites with macrophyte plots not covered by cells of the layers, a macrophyte grid cell was assigned the value of the nearest raster cell containing data. Current velocity and bottom shear stress values were finally averaged at each site.

2.3 | Functional traits of macrophytes and macroinvertebrates

We selected three functional trait groups representing features of aquatic macrophytes that are directly related to key ecosystem functions, that is, growth form, perennation and potential size. These functional trait groups are associated with light interception, plant architecture, organ turnover and use of niche space in canopy (Willby et al., 2000). They are important functional features of aquatic macrophytes (Göthe et al., 2017), including those inhabiting boreal lakes (Lindholm et al., 2020). We followed Toivonen and Huttunen (1995) and Schmidt-Kloiber and Hering (2015) to classify species into six different growth form categories: ceratophyllids, elodeids, helophytes, isoetids, lemnids and nymphaeids. Perennation (annual, biennial/short-lived perennial and perennial) was based on information available from the attribute-based classification of Willby et al. (2000), whereas potential size information (cm; i.e., the potential length of an individual omitting the root or rhizome length; Dolédec & Statzner, 1994) was based on Hämet Ahti et al. (1998), complemented by information derived from Mossberg and Stenberg (2012) and other public repositories (e.g., Online Atlas of the British and Irish Flora; https://www.brc.ac.uk/plantatlas/).

We also selected three functional trait groups for macroinvertebrates, including functional feeding habits (i.e., scrapers, gatherers, filterers, shredders and predators), substratum associations (i.e., burrowers, crawlers, sprawlers, sessiles, semi-sessile and swimmers) and body size (i.e., dry mass). The individual traits in these three

functional trait groups are directly associated with ecosystem functions, such as decomposition and recycling of organic material, habitat use and sensitivity of macroinvertebrates to fish predation in lakes (Heino & Tolonen, 2017; Tolonen et al., 2003). The information for functional feeding habits, substratum associations and body size was derived from the literature. Estimates of dry mass were further based on body–length regressions. The lists of original literature sources have largely been reported in Tolonen et al. (2017) and Rocha et al. (2018).

2.4 | Uniqueness measures

We applied the local contribution to beta diversity (LCBD) approach (Legendre & De Cáceres, 2013) to calculate a measure describing the ecological uniqueness of each site in our lake system. This method was originally used for taxonomic site-by-species data, but it can be extended to applications based on functional (this study) and phylogenetic features (e.g., Shooner et al., 2018) of biotic assemblages or abiotic environmental conditions (e.g., Castro et al., 2019). For taxonomic data, we used Jaccard index to calculate each site's contribution to taxonomic beta diversity (LCBD–*t*) in the focal lake system.

For functional data, we used two different frameworks, that is, a standard one inspired by the original approach of Villéger et al. (2013) and a modified approach that explicitly controls for the optimal number of dimensions of species trait space (Mouillot et al., 2021). This latter framework is slightly more demanding than various well-established methods proposed to measure species trait dissimilarity and functional diversity (e.g., Laliberté & Legendre, 2010; Villéger et al., 2013). Yet, this framework has the merit that it can be adapted to any data types, and it can provide comparable trait space features across datasets, especially when functional reconstructions differ among different organismal groups (see Mouillot et al., 2021). In brief, both frameworks require a metric that measures trait differences between species, resulting in subsequent calculation of a functional tree to produce the functional site-by-site community dissimilarity matrix and associated functional LCBD values (LCBD–*f*). Overall, our standard data analysis routine comprised four steps (Figure 2): (i) computing a species-by-species distance matrix, (ii) using a hierarchical clustering analysis on the resulting species-by-species distance matrix for obtaining the functional tree, (iii) using this functional tree along with the site-by-species matrix to calculate the functional community distance matrix based on the Jaccard index, and (iv) computing the LCBD–*f* values based on the resulting functional site-by-site community dissimilarity matrix.

Several measures of multi-trait dissimilarity have been proposed over the years (e.g., Gower, 1971; Laliberté & Legendre, 2010). Here, we chose a novel analytical approach (R function "gawdis") devised by de Bello et al. (2021) that shows key properties that solve the problem of unbalanced contribution of different traits when calculating species-by-species distances (see Supplementary Information Appendix S2 for details). More specifically, we applied the "gawdis" function to minimize differences in the correlation between the dissimilarity of each individual trait and the multi-trait matrix (de Bello et al., 2021), thereby making each single trait to have a comparable influence on the final species-by-species distance matrix. Moreover, to investigate the quality and intrinsic dimensionality of multi-trait space under the parsimonious method of Mouillot et al. (2021), we further (i) identified the orthogonal axes along which species-by-species distances are decomposed using principal coordinate analysis (PCoA; Legendre & Legendre, 2012), and (ii) determined the cumulative number of PCoA axes needed to obtain a reasonable position of species in the lower dimensional space through the application of the elbow inflection point method for the area under the curve (AUC) criterion (see Mouillot et al., 2021 for details). Comparing the more standard framework (see above) with the elbow-based AUC optimal dimensionality routine showed consistent results (Supplementary Information Appendix S3). Thus, for simplicity, we focused on findings based on the more standard approach without trait space dimensionality reduction.

For environmental data, we first calculated standardized (i.e., each environmental variable was standardized to zero mean and unit variance) between-site Euclidean distance to obtain a site-by-site environmental distance matrix (see also Castro et al., 2019). To calculate local contributions to environmental heterogeneity (LCEH), this distance matrix was submitted to the "LCBD.comp" function available from "adespatial" R package (Dray et al., 2021). The main steps of our statistical approach are shown as a flow diagram in Figure 2.

2.5 | Correlation between taxonomic, functional and environmental uniqueness

Since tests based on Moran's I coefficients found no spatial autocorrelation for the different measures of site uniqueness (Supplementary Information Appendix S4), we tested for the correlations between LCBD–*t*, LCBD–*f* and LCEH using Spearman's rank correlation. For significant relationships, we further evaluated the importance of linear vs. non-linear trends with Akaike's Information Criterion (AIC) and visualized the presence and location of breakpoints using a combination of Davies tests (Davies, 2002) and segmented linear regressions (Muggeo, 2003).

2.6 | How many and which sites to conserve?

To determine how many and which sites to conserve based on single and combined evaluations of LCBD–*t*, LCBD–*f* and LCEH, we used two different approaches: (i) a cumulative uniqueness threshold of 0.7 (70% of cumulative uniqueness covered by *n* sites), and (ii) an inflection point criterion based on the elbow-based method (Thorndike, 1953). The idea behind the elbow-based method is to maximize cumulative uniqueness gains while reducing the cost (here, the number of sites to be conserved). In other words, this algorithm calculates an inflection point that corresponds to the cumulative uniqueness value above which the conservation benefit becomes lower than the cost (Nguyen

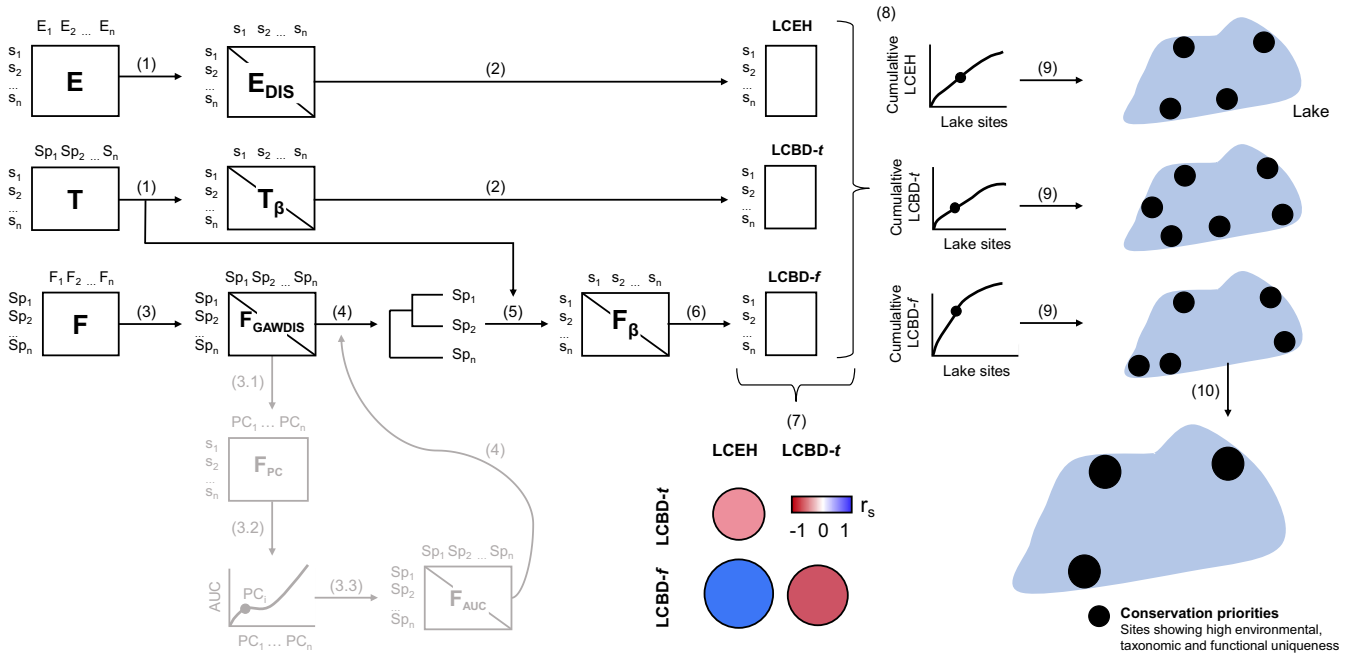

FIGURE 2 Schematic diagram showing the different steps of our modelling framework from environmental (E), site-by-species (i.e., taxonomic; T) and species multi-trait (i.e., functional; F) matrices to the identification of potential conservation areas (10) after calculating site-by-site distance matrices for obtaining the uniqueness measures (LCEH, LCBD–*t*, LCBD–*f*; 2–6), and extracting correlations among ecological uniqueness measures (7) and the number of sites significantly contributing to LCEH, LCBD–*t* and LCBD–*f* (8–9). For taxonomic and standardized environmental data, we calculated (1) between-site Jaccard and Euclidean distances (T_β and E_{DIS}), respectively, and obtained (2) local contributions to beta diversity (LCBD–*t*) and environmental heterogeneity (LCEH). For functional measures, a species-by-species dissimilarity matrix with uniform contributions for each individual trait (F_{GAWDIS}) is produced (3) with the "gawdis" routine (de Bello et al., 2021), and a functional tree from hierarchical clustering analysis (4) is then used along with the site-by-species community matrix to compute (5) the functional community distance matrix (F_β). The resulting site-by-site functional dissimilarity matrix is used (6) to calculate the local contributions to functional beta diversity (LCBD–*f*). Alternatively (in grey), functional species pairwise dissimilarities (F_{GAWDIS}) are synthesized (3.1) using principal coordinate analyses (F_{PC}). Then, the elbow-based AUC optimal dimensionality routine (Mouillot et al., 2021) is applied (3.2) to determine the new species coordinates in a low-dimensional orthogonal space. These reduced synthetic axes will provide (3.3) the basis for a new ecologically meaningful species trait space (F_{AUC}) from which to compute (4) the functional tree (Supplementary Information Appendix S3). Spearman's rank correlation coefficients are used to calculate (7) pairwise correlations among different ecological uniqueness measures. Finally, "cumulative ecological uniqueness profiles" are plotted (8) to determine arbitrary thresholds in the sequences (e.g., up to 0.7) or the more objective elbow inflection points (Thorndike, 1953) from which to decipher the number and identity of potential lake areas for conservation. This is based both on single (9) and combined (10) evaluations of LCBD–*t*, LCBD–*f* and LCEH

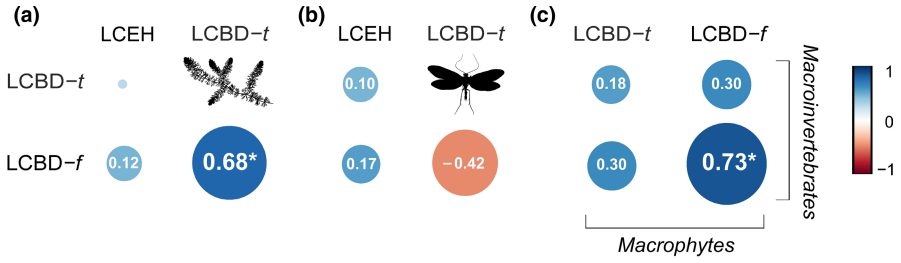

FIGURE 3 Graphical representation of the correlations between different measures of site uniqueness for macrophytes (a) and macroinvertebrates (b), including local contribution to beta diversity based on taxonomic data (LCBD–*t*) and functional data (LCBD–*f*), as well as local contribution to environmental heterogeneity (LCEH). The correlations between different uniqueness measures between macrophytes and macroinvertebrates are also shown (c). The size of the circle denotes the strength of the correlation, and the colours represent the sign of the correlation along a range from positive (blue) to negative (red). Values inside each circle denote the correlation coefficient (r_S) and asterisks indicate statistical significance (*$p < .05$). Circles with no values if $r_S \leq 0.01$

& Holmes, 2019). The first approach is not very objective, but it has the merit of providing a comparable and standardized cumulative uniqueness value across measurements and organismal groups.

All statistical analyses were run in R version 4.0 (R Development Core Team, 2020). The list of R packages and computational routines are available in Supplementary Information Appendix S5.

3 | RESULTS

Associations between taxonomic (LCBD–*t*), functional (LCBD–*f*) and environmental (LCEH) uniqueness were relatively weak (Figure 3). For macrophytes, only the relationship between LCBD–*t* and LCBD–*f* was statistically significant (r_s = 0.68, p = .002), whereas no significant association was recorded between any site uniqueness measure of benthic macroinvertebrate communities. However, when the entire biotic dataset was considered (i.e., macrophyte LCBD–*t* or LCBD–*f* values vs. macroinvertebrate LCBD–*t* or LCBD–*f* values), macroinvertebrate LCBD–*f* values showed a consistent linear trend in response to increasing macrophyte LCBD–*f* (r_s = 0.73, p = .001; Figure 4b). The relationship between macrophyte LCBD–*t* and LCBD–*f* was quadratic, however, and seemed to be virtually independent of LCEH (Figure 4a). Davies tests suggested a statistically significant (p = .04) inflection point at LCBD–*t* = 0.067 (Figure 4a), with a 95% confidence interval ranging between 0.063 and 0.071, and the slopes being positive and negative below and above the inflection point, respectively (1.2 vs. −2.6). This suggests reduced diversity of trait combinations and concomitant increase in species similarity in macrophyte communities that showed highly unique species combinations.

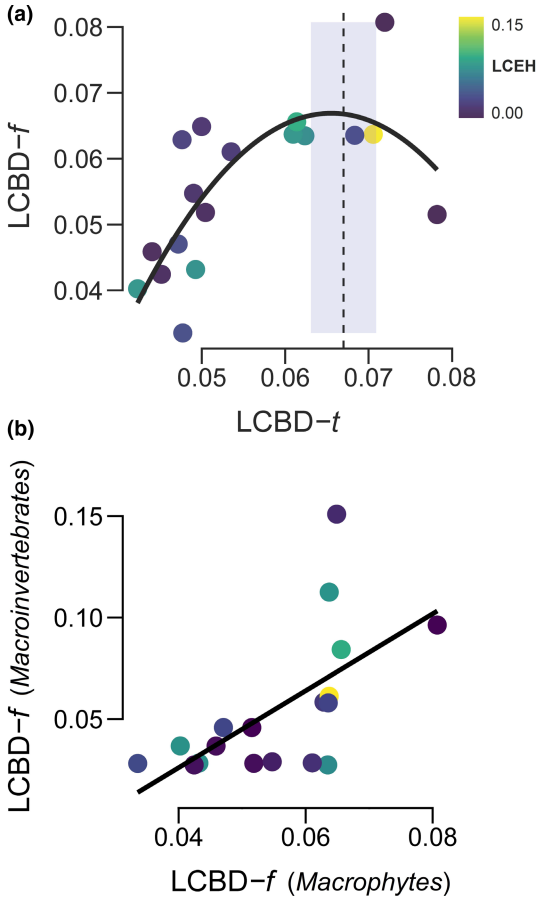

FIGURE 4 Scatter plots showing the non-linear relationship between LCBD–*t* and LCBD–*f* for macrophytes (a), and the linear relationship between macrophyte LCBD–*f* and macroinvertebrate LCBD–*f* (b)

Based on our dataset, between one-third to one half of the sites studied could help protect up to three quarters of the ecological uniqueness of the studied part of Lake Puruvesi, accounting for more than 90% of observed macrophyte (n = 36) and macroinvertebrate (n = 143) species. Of the five site uniqueness measurements (i.e., macrophyte LCBD–*t*, macrophyte LCBD–*f*, macroinvertebrate LCBD–*t*, macroinvertebrate LCBD–*f* and LCEH), we obtained the number of lake sites studied with high conservation potential ranging between six and nine using the elbow-based approach and between nine and 12 using the cumulative threshold of 0.7 (Figure 5a–e). For all site uniqueness measures, the more objective elbow-based inflection points were within the limits of the 0.7 cumulative uniqueness threshold (Figure 5a–e), thereby reducing the number of lake sites to be included in explicit conservation schemes (Figure 5f–i vs. Figure 5j–m). For instance, selecting only relatively few areas (Figure 5f–i) would contribute efforts towards protecting more than 50% of the ecological uniqueness of Lake Puruvesi littoral area (Figure 5a–e). More specifically, a certain degree of congruence was found when it comes to identifying potential sites to be prioritized based on macrophyte (Figure 5f,j) and macroinvertebrate (Figure 5g,k) uniqueness measures. However, incorporating the abiotic environmental component in the analyses (i.e., LCEH; Figure 5h,l) impaired the spatial correspondence among the three dimensions of ecological uniqueness by half (Figure 5i,m), constraining the number of potential conservation sites that consider all site uniqueness measures combined to three to five sites (based on the elbow-based and threshold-based approaches, respectively).

4 | DISCUSSION

Here, we proposed an approach that exemplifies how taxonomic uniqueness, functional uniqueness and environmental uniqueness can be used in guiding conservation planning. This approach was illustrated using data for lake biota and littoral environment. The novelty of this study, therefore, lies in the joint assessment of a site's ecological uniqueness (sensu Legendre & De Cáceres, 2013) based on the taxonomic and functional features of macrophyte and macroinvertebrate communities, as well as environmental features. We found that although the correlations between the different measures of site uniqueness were typically not significant, the numbers of sites required for the conservation of ecological uniqueness and hence most of total beta diversity were relatively low. In practice, protecting one-third to half of the sites could help accounting for about 70% of the total beta diversity and apparently more than 90% of species of macrophytes and macroinvertebrates in the focal lake ecosystem. However, while this finding is promising, the sets of sites to be prioritized varied depending on the measured ecological uniqueness considered. This obstacle could be overcome if conservation of lake sites was based on a combined measure of the biotic uniqueness of organisms and abiotic uniqueness of the environment. Below, we will consider the lack of match between the ecological uniqueness of sites based on different measures and discuss

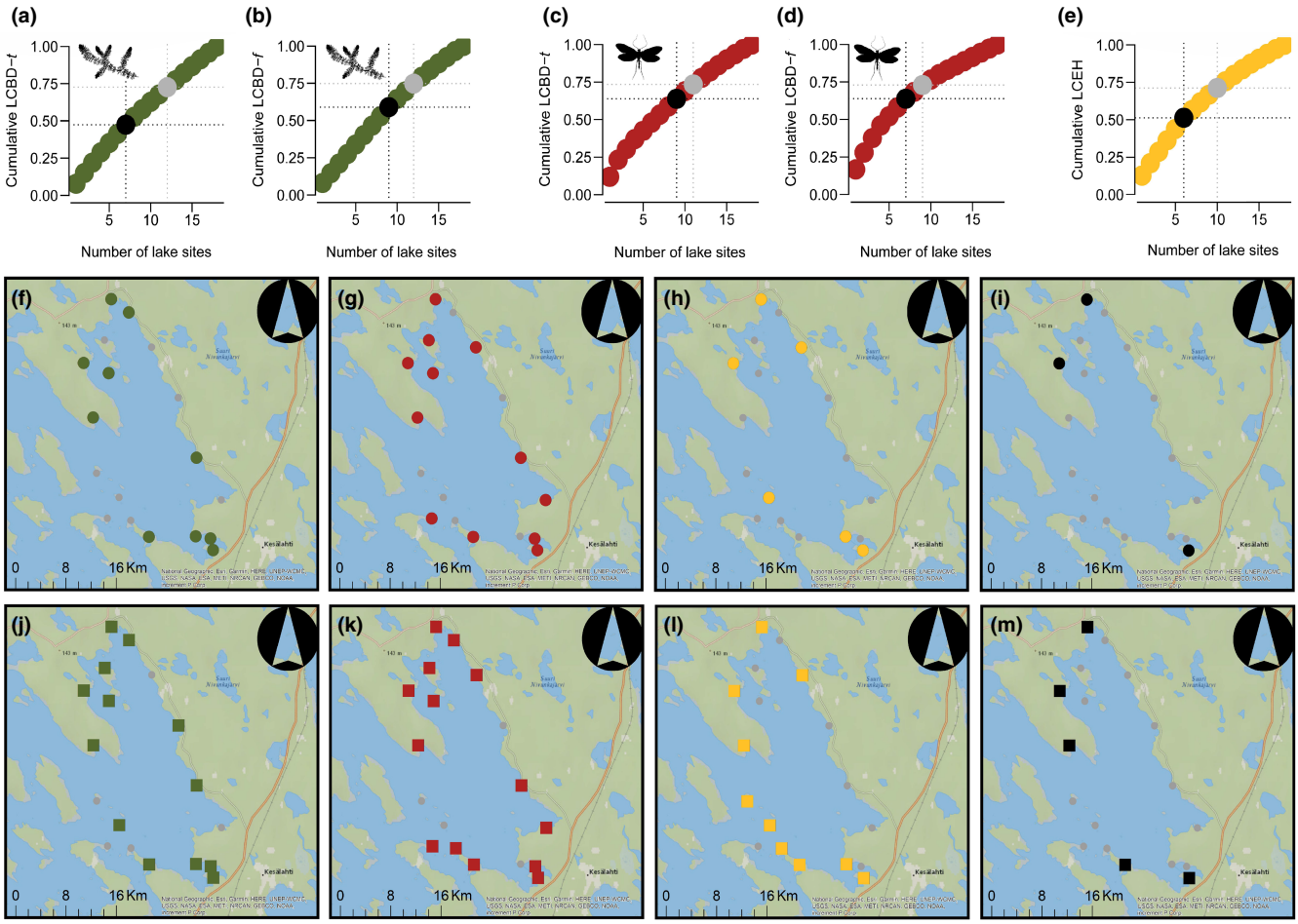

FIGURE 5 (a–e) Cumulative ecological uniqueness profiles for taxonomic (LCBD–*t*) and functional (LCBD–*f*) features of (a, b) macrophytes and (c, d) macroinvertebrates, as well as for (e) the environmental conditions of lake sites. Black and grey dots and dotted lines represent the elbow-based and threshold-based breakpoints for each ecological uniqueness measure, respectively. (f–m) Locations of potential sites for conservation in Lake Puruvesi considering the following: facets of taxonomic and functional uniqueness of (f, j) macrophytes and (g, k) macroinvertebrates, (h, l) local contributions to environmental heterogeneity (LCHE), and (i, m) combined evaluations of LCBD–*t*, LCBD–*f* and LCEH (only lake sites showing high conservation value for *all* measures combined, that is, high local contributions to taxonomic, functional and environmental uniqueness). Coloured circles in (f to i) indicate potential sites for conservation based on the elbow-based approach, whereas coloured squares (j to m) represent lake sites with high conservation value based on the threshold-based analysis

alternative avenues to improve the use of ecological uniqueness measures in conservation planning. We will specifically focus on correlations among macrophytes, macroinvertebrates and the environment, as they were generally higher and more ecologically meaningful than LCBD–*t* and LCBD–*f* correlations within macrophytes or macroinvertebrates only.

The match between the uniqueness values of macrophytes and macroinvertebrates was variable and generally low. While macrophytes obviously are important for macroinvertebrates by providing habitats (e.g., Tolonen et al., 2003) and through mediating spatially explicit biotic interactions (e.g., García–Girón et al., 2020), we could also have expected stronger correlation between their uniqueness measures. Cross-taxon congruence between taxonomic uniqueness measures was especially weak, which may be due to problems in detecting all species occurring at a site or that strong spatial dynamics within a large lake obscured species–environment associations (e.g., Tolonen et al., 2017). Only one correlation, that is, LCBD–*f* of macrophytes and LCBD–*f* of macroinvertebrates, provided evidence of strong enough cross-taxon congruency (Caro, 2010) potentially useful for conservation applications ($r > 0.7$; Heino, 2010). This finding suggests that LCBD–*f* could potentially be a suitable proxy for lake biodiversity, especially if functional diversity and maintenance of ecosystem functions is the main target of conservation. This is particularly relevant considering that the relationship between LCBD–*t* and LCBD–*f* was statistically significant for macrophytes, although seemingly non-linear (Figure 4a), suggesting that maintaining sites with species combinations that have relatively high uniqueness should protect most plant forms and functions. This could also have repercussions for protecting other organisms relying on macrophyte beds during parts of their life cycles, such as many species of invertebrates (e.g., Tolonen et al., 2003), fish (e.g., Cowx & Welcomme, 1998) and waterfowl (e.g., Elmberg et al., 1993).

Degree of match between biotic and abiotic measures of uniqueness was surprisingly weak. It is possible that the environmental

variables used did not effectively capture the biologically relevant dimensions of the environmental uniqueness. However, as already proposed above, the lack of strong correlations may also be related to strong effects of dispersal on the composition of littoral macroinvertebrate communities, which has been noticed in large lakes previously (Tolonen et al., 2017). Dispersal-related mass effects (Leibold et al., 2004) may result in seemingly weaker species–environment associations than expected because some species may occur at sites where they cannot have self-sustaining populations (Pulliam, 1988). This may be a particularly important consideration in large lake systems where dispersal is not strongly prevented by physical barriers (Heino et al., 2021). In our current scenario, it is possible that mass effects via high dispersal rates homogenize species composition among sites, thereby weakening the LCBD and LCEH relationship. This may also hinder selecting sites based on LCBD because sites are not independent of each other but rather there is a continuous exchange of organisms between nearby sites. While such metacommunity dynamics may be considered as a nuisance factor when selecting a set of sites, it also underscores the importance to protect certain sites for strict conservation. These sites, if comprising a network of "stepping-stones," could act as havens for organisms and facilitate colonization of other sites in a lake (Heino et al., 2021). In practice, a set of sites selected using cumulative LCBD values could serve well because it helps maintain and protect beta diversity, that is, the variation of assemblage compositional variation across sites (Anderson et al., 2011).

Given that single measures of uniqueness suggested different sets of sites for strict protection, we also considered an overall measure of ecological uniqueness. The benefits of this combined approach include that it is not based on a single organism group nor biotic or abiotic diversity alone. A general drawback may be that the selected sites may be too far from each other considering the dispersal distances of a focal organism group, for example, when it comes to frequency of dispersal of macroinvertebrates between sites (see also Heino et al., 2017). This consideration is important if the aim is to protect sites to account for as much total beta diversity and guarantee a suitable network of sites facilitating natural meta-system dynamics. In practice, also the matrix, that is, the intervening areas surrounding the littoral sites to be protected, should be evaluated because large expanses of non-natural littoral areas preventing dispersal may result in a set of isolated sites. Such isolated sites may, in the long term, act as extinction traps for species if anthropogenic impacts in the matrix are not regulated. Specifically, for lakes, strictly protected sites could also provide dispersing organisms via "spill-over" effects to the matrix areas, where biodiversity, fish stocks and other ecosystem services would benefit from the vicinity of strictly protected unique littoral sites, as has been suggested in marine systems (Russ & Alcala, 2011).

While the present study illustrated the use of LCBD and LCEH as the basis of selecting sites for conservation, the practical applications of the approach need to be fully considered in further studies. First, one needs to be sure that the number of sites considered is large enough to allow trustworthy propositions for conservation planning. In the present case, we had data from only 18 sites where intensive mapping of macrophytes was done and large-sized macroinvertebrate samples were taken. This number of sites is obviously too low to facilitate conservation planning in practice, and more sites should be surveyed, scaled with the extent of the study area. Second, the presentation of habitat types in the surveys should correspond to that occurring in nature. In the current case, the sampling was stratified to incorporate the main littoral habitat types in Lake Puruvesi, that is, vegetated, stony and sandy shores. While there are significant differences in macroinvertebrate assemblages among these habitats (Tolonen et al., 2001, 2003), environmental variation is continuous and no strictly compartmentalized habitats really exist. This makes it important to consider LCBD and LCEH as continuous variables describing biotic and abiotic uniqueness, respectively, rather than assume a priori that a given habitat type always shows high ecological uniqueness. Third, in practical conservation planning, the matrix intervening the sites presumably in close-to-natural conditions should be considered because the biotic assemblage at a site may be strongly affected by nearby sites. This is especially plausible in open systems, such as large lakes, where dispersal is not prevented by obvious physical barriers (Heino et al., 2021). Finally, when beginning to survey sites for nature conservation, it is of utmost importance to focus on pristine or near-natural sites. In the case of randomly sampling large numbers of sites, the naturalness of sites should be carefully considered because sites that have suffered from moderate-to-high levels of anthropogenic impacts may show "unique" assemblages when compared to more natural sites. If so, those impacted yet unique sites could be instead considered candidates for ecological restoration (Legendre & De Cáceres, 2013).

Five of the 18 sites studied had rather intensive land use close to the shoreline, such as near-shore farming, summer cottages and a holiday village. However, only one of these sites, with near-shore farming, was included in the subsets of potential conservation sites for LCBD–*t*, LCBD–*f* and LCEH. This site was the same in all three cases, but its littoral habitat was seemingly not much affected by the surrounding agricultural fields. Whether such a site should be included in the subset of sites for conservation planning is an open question. It depends on deciding if near-natural littoral habitats harbouring unique biota and environmental conditions are the target or if land use adjacent to the littoral site should also be considered. Nature conservation typically focuses on pristine and near-pristine sites and targets at preservation of natural ecosystems per se. However, freshwater ecosystems in urban and rural landscapes may also harbour highly valuable biotas, which requires ranking of sites based on their conservation value (e.g., Hill et al., 2021). It might thus be advisable to prioritize sites in natural and human-affected landscapes using separate data analyses.

To conclude, we proposed an approach to select a set of sites based on their ecological uniqueness. We suggest that rather than focusing only on taxonomic uniqueness, we should also consider functional uniqueness and environmental uniqueness because they provide information about different features of nature that are

important in guiding conservation planning (e.g., Gillson et al., 2011). While our exemplary dataset originated from a large lake system, the data analysis approach we proposed here is highly amenable for applications in different ecosystems and at various spatial scales. However, a key consideration is that a set of sites (or a set of areas) have been sampled using the same methods, resulting in species and environmental matrices that can be analysed using the data analysis routines detailed in this paper. For example, the approach can be easily applied to grid-based data, sets of islands or sets of forest fragments, whereby the sets of sites needed to account for a specific amount of total beta diversity in the focal study region can be identified. We anticipate that the approach based on ecological uniqueness can be a useful conservation tool (Legendre & De Cáceres, 2013), especially if associated with meta-system ideas or network thinking in guiding nature conservation and ecosystem management (Heino et al., 2021). Our hope is thus that the proposed approach be used widely in different ecological and geographical settings to prove its suitability in practice.

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CONFLICT OF INTEREST

The authors declare no conflict of interest.

DATA AVAILABILITY STATEMENT

List of computational routines and essential statistical functions are in Supplementary Material Appendix S5, where open code, vignettes and detailed manuals can be found freely using citations. The biological and environmental datasets used in the analyses are available on Dryad: https://doi.org/10.5061/dryad.tqjq2bw2k.

PEER REVIEW

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BIOSKETCH

The group of authors is broadly interested in biological, environmental and anthropogenic phenomena associated with aquatic ecosystems.

Author Contributions: J.H. devised the original study idea and led the writing. J.H. and J.G.G. planned the flow of the data analyses. J.G.G. ran the analyses and drew the figures. A.T. and K.T.T. prepared the data for the analysis and combined the abiotic and species data. J.G.G. and K.T.T. compiled macrophyte and macroinvertebrate trait information, respectively. J.K., K.N., K.T.T., J.I. and H.H. planned the field sampling, J.K. and J.I. led the fieldwork, and S.H. trained the macrophyte survey team. T.M. identified most of the macroinvertebrate samples, supported by K.T.T.. J.R. built the hydrodynamic model for current data. All authors commented on the drafts of the manuscript and gave final approval for publication.

SUPPORTING INFORMATION

Additional supporting information can be found online in the Supporting Information section at the end of this article.

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