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Habitat heterogeneity enables spatial and temporal coexistence of native and invasive macrophytes in shallow lake landscapes

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Abstract

Macrophyte invasive alien species (IAS) fitness is often hypothesised to be associated with beneficial environmental conditions (environmental matching) or species-poor communities. However, positive correlations between macrophyte IAS abundance and native plant richness can also arise, due to habitat heterogeneity (defined here as variation in abiotic and native biotic conditions over space and time). We analysed survey and palaeoecological data for macrophytes in satellite lakes along the Upper Lough Erne (ULE) system (Northern Ireland, UK), covering a gradient of eutrophication and connectivity to partition how environmental conditions, macrophyte diversity and habitat heterogeneity explained the abundance of *Elodea canadensis*, a widely distributed non-native macrophyte in Europe. *E. canadensis* abundance positively correlated with macrophyte richness at both the within- and between-lake scales indicating coexistence of native and invasive species over time. *E. canadensis* was also more prolific in highly connected and macrophyte-rich lakes, but sparser in the more eutrophic-isolated ones. Partial boosted regression trees revealed that in eutrophic-isolated lakes, *E. canadensis* abundances correlated with water clarity (negatively), plant diversity (positively), and plant cover (negatively) whereas in diverse-connected lakes, beta diversity (both positively and negatively) related to most greatly *E. canadensis* abundance. Dense macrophyte cover and unfavourable environmental conditions thus appear to confer invasibility resistance and sufficient habitat heterogeneity to mask any single effect of native biodiversity or environmental matching in controlling *E. canadensis* abundance. Therefore, in shallow lake landscapes, habitat heterogeneity variously enables the coexistence of native macrophytes and *E. canadensis*, reducing the often-described homogenisation effects of invasive macrophytes.

KEYWORDS
boosted regression trees, connectivity, *Elodea canadensis* (Michx.), eutrophication, metacommunities, paleolimnology

1 | INTRODUCTION

Aquatic invasive alien species (IAS), species that have successfully been introduced, established, and spread beyond their native range, are an increasing concern for management and conservation in freshwater ecosystems owing to their potential to cause severe ecological and economic damage (Cuthbert et al., 2021; Strayer, 2010). The ability of aquatic IAS to prosper could depend on resource availability and the physical–chemical environment (Shea & Chesson, 2002; Strayer, 2010). Accordingly, species- and functionally rich communities may limit the abundances of aquatic IAS by reducing access to resources (Levine, Adler, & Yelenik, 2004), whilst beneficial environmental conditions (henceforth referred to as environmental matching) at recipient locations may enhance IAS abundances, irrespective of local native biota (Mack et al., 2000). However, as processes affecting biotic interactions and species distributions are scale-dependent (McGill, 2010), variations in biotic and abiotic conditions within and between sites over space and time (i.e., habitat heterogeneity) may facilitate species coexistence, regardless of their native status (Melbourne et al., 2007). Therefore, habitat heterogeneity could simultaneously increase invasion probability whilst reducing aquatic IAS dominance across a landscape by promoting coexistence in space and time (Clark, Johnston, & Leung, 2013). Landscapes may thus include species that are extirpated at some sites but present at others through spatial and/or temporal storage effects, provided there is sufficient regional connectivity and spatiotemporal habitat heterogeneity (Melbourne et al., 2007).

In lake landscapes, habitat heterogeneity and the distribution of aquatic IAS can be determined by, and correlated to the hydrological network (Salgado et al., 2019a). For example, macrophyte and invertebrate lake communities connected through the hydrological network may be influenced by repeated colonisation events via mass effects, while local environmental factors may dictate community structure through species sorting according to habitat optima in more isolated lakes (Capers, Selsky, & Bugbee, 2010; Padial et al., 2014). Although, there have been attempts to quantify how spatial autocorrelation affects IAS dynamics (Melbourne et al., 2007), disentangling the simultaneous effects of abiotic factors, native biodiversity, and spatially structured dynamics on the abundances of IAS in nature has proved challenging (Nunez-Mir et al., 2017). Available evidence suggests that temporal variation in environmental stress factors and dispersal-related mechanisms promotes co-existence of native and non-native species in freshwater systems (Clark et al., 2013), which could result in a positive relationship between native diversity and aquatic IAS abundance at any one time (Capers, Selsky, Bugbee, & White, 2007). Lake landscapes comprising multiple interconnected lakes that span environmental gradients offer thus, the possibility of more explicitly quantifying how native biodiversity, abiotic factors, and spatial autocorrelation affects aquatic AIS abundances and hence scope to disentangle factors that contribute to regional coexistence.

Among aquatic IAS, macrophyte species are one of the foremost invaders of inland waters across the globe (Bolpagni, 2021). The ecological effects of macrophyte IAS can range from reduced freshwater biodiversity to elevated plant biomass production and altered biogeochemical cycles (Bolpagni, 2021). In Europe, Canadian waterweed (*Elodea canadensis* Michx.) is considered amongst the most widespread non-native plant species (Hussner, 2012; Nentwig, Bacher, Kumschick, Pyšek, & Vilà, 2018). It was first recorded in Great Britain in 1836 (Simpson, 1984). Thereafter it spread rapidly, reaching the maximum extent of its distribution in Great Britain and Ireland by the middle of the twentieth century (Simpson, 1984). The rapid colonization and spread of this species are commonly attributed to a high capacity for vegetative propagation and tolerance of a broad range of physical–chemical conditions, including low illumination, enabling growth at a wide range of water depths and under eutrophication-induced shade (Zehnsdorf, Hussner, Eismann, Rönicke, & Melzer, 2015). Once established *E. canadensis* can quickly replace native submerged macrophytes by forming a dense, closed canopy (Zehnsdorf et al., 2015). Indeed, the propensity for encountering *E. canadensis* in meso-eutrophic isolated temperate lakes has promoted the view that its spread and dominance across Britain and Ireland is attributable to environmental matching (O'Hare, Gunn, Chapman, Dudley, & Purse, 2012). However, few studies have investigated the role of habitat heterogeneity on *E. canadensis* abundance variation over space and time, and the extent to which biotic and/or abiotic factors explain its abundances across invaded landscapes.

Here we examine the drivers of *E. canadensis* abundance in space and time in the Upper Lough Erne (ULE) system, Northern Ireland, a network of interconnected, shallow (<5 m depth), meso-eutrophic (total phosphorus [TP] range = 29–383 μg/L; total nitrogen [TN] range = 0.22–2.25 mg/L), and macrophyte-rich (>40 submerged and floating-leaved species; Table S1) lakes. Present-day and historical data from surveys and sediment core analyses were used to address the following questions:

1. Does habitat heterogeneity (including spatial autocorrelation) per se promote *E. canadensis* coexistence with native macrophyte communities in space and time (decades-centuries)?
2. Which are the main biotic and abiotic factors that contribute to regional coexistence?
3. To what extent does the variation of biotic and/or abiotic factors contribute to variation in *E. canadensis* abundance?

2 | METHODS

2.1 | Site description

The ULE system is composed of a large (surface area 3,450 ha), generally shallow (mean water depth 2.3 m) central lake (ULE), fed by the River Erne, which is linked by winter floods and various channels and tributaries, to a network of over 50 small (<40 ha), shallow satellite lakes (Loughs; Figure 1). *E. canadensis* is thought to have colonized the ULE system in the 1880s (Simpson, 1984). Records from the Botanical Society of Britain and Ireland (BSBI) and more recent macrophyte

monitoring programmes indicate presence of *E. canadensis* in ULE and its satellite lakes from the 1950s (Table 1). The zebra mussel (*Dreissena polymorpha* Pallas) also invaded this system in the 1990s, resulting in strong phytoplankton biomass reductions and increases in water transparency in the central ULE (Minchin, Maguire, & Rosell, 2003).

2.2 | Macrophyte sampling

Macrophytes were sampled in four basins within the central ULE and in 13 satellite lakes representing a gradient of nutrient-enrichment, zebra mussel occurrence and hydrological connectivity to the central ULE (Figure 1). The lakes were grouped into three categories according to Salgado et al. (2019a). *Group 1* included the central ULE and lakes directly connected to it through the River Erne (Castle and Derrykerrib) or via tributaries (Doo and Mill). These lakes are meso-eutrophic (TP = 55.1 ± 11.3 µg/L) with clear waters (Secchi depth = 222 ± 47 cm), are macrophyte rich (M = 17.4 ± 2.7), and zebra mussels commonly occur. *Group 2* lakes are connected to the central ULE by flows through intermediate lakes and associated

FIGURE 1 Map of the Upper Lough Erne (ULE) system showing the geographical location of the system, the studied lakes (loughs) and the recorded abundances of *E. canadensis* during 2008–2009 (circles). The size of the circles represents an abundance scale of 0–5, where 5 is maximum abundances and 0 (red circle) apparent absence. Superscripts numbers indicate a lake group selected according to the water flow direction and degree of connectivity to the Central lake. Water layers obtained from Ordnance Survey Northern Ireland https://www.nidirect.gov.uk/services/osni-online-map-shop and reproduced with the permission of Land & Property Services© Crown Copyright 2018 [Color figure can be viewed at wileyonlinelibrary.com]

tributaries (Killymackan, Cornabrass, and Kilturk). The lakes are eutrophic (TP = 136 ± 54.4 µg/L; Secchi depth = 182.3 ± 55 cm), macrophyte rich (mean = 18.7 ± 4.6), and have sparse occurrences of zebra mussels. *Group 3* lakes (Head, Digh, Derryhowlaght, and Gole) are more isolated than *Group 2* lakes due to intervening small hills, woodlands, and roads (Figure 1). These lakes are highly eutrophic (TP = 176.8 ± 89.3 µg/L) with turbid waters (Secchi depth = 113.3 ± 79.3; zebra mussels rarely occur) and macrophyte richness is low (M = 9 ± 3.5).

Macrophyte sampling was undertaken in 1 m^2 units, approximating to the plant neighbourhood scale (i.e., where individual native plants may compete with *E. canadensis*). The lake percentage volume infested by macrophytes (PVI) method of Canfield and Jones (1984) was used to characterize the distributions and abundances of native macrophytes (including charophytes, bryophytes, and vascular plants) and of *E. canadensis*. Macrophytes were surveyed during the summers of 2008–2009 at individual points separated by approximately 10–15 m of distance from a boat by zig-zagging across the entire lake using grapnel sampling and visual observations with a bathyscope. At each sampling point we recorded latitude/longitude, water depth, average plant height, and species cover (%). Average plant height was estimated by averaging the height of all plant species occurring in each sampling point. PVI was calculated at each point as: (macrophyte cover × average height of macrophyte)/water depth. For comparisons with previous monitoring data (Table 1) and to assess *E. canadensis* abundance patterns at the lake scale, percentage of sample occupancy of *E. canadensis* at each lake was also calculated by dividing the number of sampling points at which *E. canadensis* was observed by the total number of sampling points within the lake X 100.

The total number of macrophyte sampling points per lake varied according to lake size. A minimum of 30 points was sampled for the smaller (<10 ha) lakes (Doo, Gole, Digh, Gole, and Derryhowlaght) and between 60 and 80 points for the remaining larger (12–30 ha) satellite lakes (Figure 1). The ULE was sampled across four separate lake zones (~30 ha) at: Crom State (54°09′42.2″ N 7°26′12.0″ W), Derryad (54°11′40.3″ N 7°28′15.8″ W); Newbridge (54°12′19.7″ N 7°28′48.5″ W), and Trannish (54°13′17.5″ N 7°29′17.9″ W). A total of 20 sampling points per ULE zone were surveyed. The macrophyte sampling strategy across our study lakes covered a total of 540 sampling points. While our sampling approach missed some macrophyte species known to occur in individual lakes (Table S1; Salgado et al., 2019a, 2019b), it nevertheless provides a useful representation of variation in macrophyte distributions and abundances for most species at the plant neighbourhood scale (Salgado, Sayer, Brooks, Davidson, & Okamura, 2018).
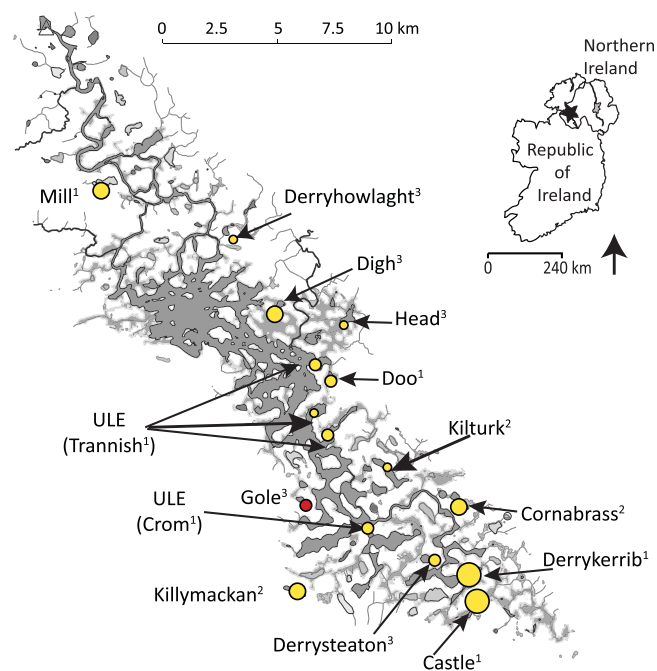
2.3 | Environmental predictors

Our previous studies of the ULE system demonstrate that macrophyte communities are primarily structured by lake water transparency, which is negatively related to nutrient concentrations (TP and TN) and chlorophyll-a and positively related to zebra mussel occurrence

TABLE 1 Historical monitoring records of *Elodea canadensis* at 20 satellite lakes and four basins in the central ULE lake at pre-1930; 1930–1949; 1950–1969; 1970–1986; 1988–1990, 2006–2007 and 2008–2009

Lake (lough)	Pre-1930	1930–1949	1950–1969	1970–1986	1988[a]	2006[a]	2009
Abacon				X	4	2	
Castle[b]				X	3	4	4
Cornabrass[b]				X	3	4	3
Corracoash				X	4	3	
Corraharra				X	1	2	
Derryhowlaght[b]				X	4	2	1
Derrykerrib[b]				X	4	4	4
Derrymacrow	X			X	4	4	
Derrysteaton[b]				X	4	3	2
Drumroosk				X	5	1	
Gole[b]				X	3	1	0
Killymackan[b]				X	4	4	3
Kilmore				X	1	1	
Kilturk[b]	X			X	4	3	1
Digh[b]				X	2	2	3
Doo[b]				X	2	3	2
Head[b]				X	1	3	1
Mill[b]				X	4	4	3
Pound				X	1	4	
Sarah				X	3	3	
Sessiagh east				X	5	0	
US904				X	5	2	
Central ULE[b]	X						
Central ULE (Belleisle)				X	1	2	
Central ULE (Crom)[b]				X	1	3	2
Central ULE (Trannish)[b]				X	1	2	2
Central ULE ULE (Derryad)[b]				X			2
Central ULE (Newbridge)[b]				X			1

Note: Botanical records from the British Society & Ireland (BSBI) Botanical are indicated by an X; Abundance = semi-quantitative scale of 0–5. Lakes showing a decline in *Elodea* abundances over time are highlighted in bold.
[a]Data obtained from Goldsmith et al. (2008).
[b]Lakes included in the present study.

(Figure S1; Salgado et al., 2019a). Thus, we used water clarity at each sampling point, as an indirect predictor of environmental stress across the macrophyte sampling points. An index of water clarity for each sampling point was defined as: lake Secchi depth measured at the deepest point of each lake/water depth at the sampling point.

2.4 | Plant macrofossil data

Previously published plant macrofossil abundance data derived from dated sediment cores were used to represent macrophyte community changes over the last c.120 years (Salgado et al., 2019b). Cores were taken from Castle Lough and the Trannish area of ULE (lake *Group 1*), from Cornabrass and Killymackan (*Group 2*), and from Gole and Head (*Group 3*).

E. canadensis remains preserve poorly in lake sediments and so we inferred temporal changes in its abundance indirectly from a recent macrophyte study in the ULE system (Salgado et al., 2019a) and from available historical monitoring data (Table 1). Salgado et al. (2019a) showed that macrophyte assemblages now found in the central ULE or closely connected lakes (e.g., Castle and Derrykerrib) are similar to those characterised in sediment cores prior to eutrophication (i.e., pre-1950s). However, macrophytes currently found in the more isolated eutrophic sites (e.g., Gole and Head) resembled those characteristics of sediment cores post-eutrophication (i.e., post-1960). Accordingly, we used the current lake sample occupancy of *E. canadensis* (Figure 1) in lakes close to the central ULE as a surrogate of historical abundances prior to 1950, and the current lake sample occupancy of *E. canadensis* in the isolated lakes to infer historical

abundances during the onset of eutrophication from 1960 to 1980. More recent (post-1980) *E. canadensis* abundance data were obtained from macrophyte surveys conducted in 1988, 2006, and 2009 (Table 1). To standardise these various sources of *E. canadensis* occurrence into a single comparable abundance measurement, we assigned the sample occupancy data into a 0–5 abundance scale following (Salgado, Sayer, Brooks, Davidson, & Okamura, 2018) as: 5 (100–80% occupancy of sampled points); 4 (79–60%); 3 (59–40%); 2 (39–20%); 1 (19–1%); 0 (0%).

2.5 | Statistical analysis

Two diversity-related measures were previously shown to influence macrophyte IAS fitness (Capers et al., 2007): *diversity* and *plant cover*. We therefore developed three complementary indicators from the macrophyte PVI data to estimate native macrophyte diversity: species richness, the Shannon–Wiener diversity index (henceforth referred to as native Shannon diversity), and macrophyte beta diversity. These indicators address key elements of native macrophyte community structure at the sampling point and lake scales: the number of native species (richness), their relative abundances (Shannon diversity), and their compositional variation across space and time (beta diversity). The native macrophyte cover data (%) collected during the PVI assessments at each sampling point were assigned to native plant cover (total sum of native macrophyte species cover) and to two functional growth forms (submerged plant cover or floating plant cover). Beta diversity was calculated as the compositional variation in the native macrophyte species' PVI values (excluding *E. canadensis*) across all sampling points as estimated via principal curves analysis (PC; De'ath, 1999). PC analyses were run using the *prcurve* function in the "analogue" package in R (Simpson, Oksanen, & Simpson, 2020), using Canonical Analysis as the starting point. Prior to analysis, the PVI data were square root transformed to normalize the skewed distribution of the data. The plant macrofossil data (Table S1) were similarly grouped into five native diversity predictors: taxon richness, Shannon diversity, native plant cover, submerged plant cover, and floating plant cover.

The relationship between native species richness and *E. canadensis* abundance variation in space and time was assessed using Pearson correlation coefficients. Correlations were assessed at both within- and among-lake scales for the contemporary data and at the within-lake scale for the palaeo-data. Since unvegetated sampling points could produce spurious positive correlations between *E. canadensis* abundance and native macrophytes at the within lake scale (Capers et al., 2007), we removed these (179 in total) from all analyses. Sampling points with native macrophytes but no *E. canadensis* or with only *E. canadensis* were retained. A controlling effect of speciose native assemblage on *E. canadensis* abundance will result in a negative correlation (Beaury, Finn, Corbin, Barr, & Bradley, 2020), whilst positive correlations would suggest that coexistence of native and invasive species in space and time is mediated by habitat heterogeneity (Clark et al., 2013).

To address more specifically the extent to which diversity and abiotic factors alone determine *E. canadensis* abundance, as a second complementary analytical step, we used a combination of boosted regression tree analysis (BRT; Elith, Leathwick, & Hastie, 2008) and random forest analysis (RFA; Breiman, 2001). BRT was used to partition the variation in *E. canadensis* abundance explained by diversity and environmental descriptors alone, and how they might together reflect habitat heterogeneity at the landscape scale (Feld et al., 2016; Feld, Segurado, & Gutiérrez-Cánovas, 2016). BRT constitutes a machine-learning method that combines classical regression tree analysis with boosting (Elith et al., 2008). BRT was ideal for our study as it can accommodate collinear data (e.g., latitude and longitude) and handle linear and non-linear descriptors with missing values. BRT partitioning (pBRT) was assessed through an additive partial regression scheme following Feld, Birk, et al. (2016) and Feld, Segurado, & Gutiérrez-Cánovas (2016). This analysis decomposed each BRT-explained variation into four fractions: (a) pure diversity, (b) pure abiotic, (c) shared diversity/abiotic, and (d) unexplained variation. The shared fraction (c) represents the variation that may be attributed to biological and/or abiotic descriptors together and is obtained additively in partial regression.

To reduce any spatial autocorrelation in the data arising due to the underlying hydrological network and to evaluate whether the importance of diversity and abiotic predictors in explaining *E. canadensis* abundance shifted with degree of lake connectivity and eutrophication, we ran independent pBRTs for each lake group using the "dismo" (Hijmans, Phillips, Leathwick, Elith, & Hijmans, 2017), and "gbm" (Greenwell, Boehmke, Cunningham, Developers, & Greenwell, 2019) packages in R (R Core Team, 2019). For each pBRT we used Gaussian distributions, tree complexity of 2, a learning rate of between 0.005 and 0.001, and a bag fraction of 0.5. The *set. seed* (*123*) argument in R was used for each BRT as a numerical starting point. Between 145 and 250 observations per lake group were analysed for each pBRT to deliver stable and reliable results (Feld, Segurado, & Gutiérrez-Cánovas, 2016).

RFAs were then used to assess the extent to which diversity predictors explain *E. canadensis* abundances through time. Like BRTs, RFA is suited to analysing non-linear relationships by fitting several models (regression trees) to bootstrapped data subsets with the advantage of handling datasets with a low number of observations and predictors, that is, our palaeo-data (Feld, Segurado, & Gutiérrez-Cánovas, 2016). RFAs were run using the function *rfsrc* of the package "randomForestSRC" (Ishwaran & Kogalur, 2016).

3 | RESULTS

Except for Gole Lough, *E. canadensis* was encountered in all study sites (Figure 1). The highest mean sample occupancy of *E. canadensis* per lake was in *Group 1* lakes (48%), followed by *Group 2* lakes (32%), and *Group 3* lakes (28%). Current native macrophyte species richness and *E. canadensis* sample occupancies were positively correlated among lakes ($r = .44$; $p = .08$) (Figure 2a). This positive relationship

became significantly stronger (r = .74; p < .01) after excluding Kilturk Lake, which was identified as an outlier by having 19 native macrophytes species but an *E. canadensis* occupancy of just 9% (Figures 2a and S2).

Positive and significant correlations between current native macrophyte species richness and *E. canadensis* abundance were similarly observed within Castle Lough (R = .44; p < .001), Deryykerrib Lough (R = .42; p < .01), Mill Lough (R = .2; p < .05), Doo Lough (R = .44; p < .01); Cornabrass Lough (R = 0.34; p < .01), and Kilturk Lough (R = .25; p < .05) (Figure 2b,c). A positive but not significant correlation between native macrophyte species richness and *E. canadensis* abundance was also observed for the central ULE (R = .2; p > .05) and Digh Lough (R = .6; p > .05) (Figure 2b,d). No evident associations between native macrophyte species richness and *E. canadensis* were observed for Killymackan Lough (R = .05; p > .05); Derrysteaton Lough (R = .07; p > .05); Derryhowghlaght Lough (R = .14; p > .05); and Head Lough (R = .1; p > .05) (Figure 2c,d).

Positive and significant correlations between lake taxon richness of plant macrofossils and *E. canadensis* abundances were also observed over time for Castle Lough (R = .62; p < .05), Cornabrass Lough (R = .55; p < .05, Gole Lough (R = .63; p < .05), and Head Lough (R = .69; p < .05) (Figure 3a–c). The correlations in Killymackan

Lough and the central ULE were also positive but not significant (R = .23; p > .05, in both cases) (Figure 3a,b).

pBRTs showed that the importance of the pure abiotic fraction in explaining *E. canadensis* abundance variation declined from 30% in *Group 1* to 13% in *Group 3* (Figure 4a). Within the pure abiotic fraction, latitude explained almost half of the variation (48%) in *Group 1*, but just 9% in *Group 3* (Figure 4c). Water clarity in *Group 3* explained 68% of the abundance variation compared with only 24% in *Group 1* (24%). Longitude effects remained relatively constant across the three lake groups, explaining 24% of the abiotic fraction in *Group 1*, 21% in *Group 2*, and 23% in *Group 3*.

The importance of the pure diversity fraction in explaining *E. canadensis* abundance variation in the pBRTs almost doubled from 17% in *Group 1* to 31% in *Groups 2* and *3* (Figure 4a). Native beta diversity emerged as the most important predictor, accounting for almost two thirds of the pure diversity fraction in *Groups 1* and *2* (61 and 62%, respectively), and 40% of the variation in *Group 3* (Figure 4b). The importance of native Shannon diversity showed an increasing trend from relatively low levels of explained variation in *Group 1* (8%) to nearly fourfold higher (31%) in *Group 3*. The explanatory importance of floating plant cover increased from *Group 1* (10%) to *Group 3* (16%), whilst overall plant cover was most influential in
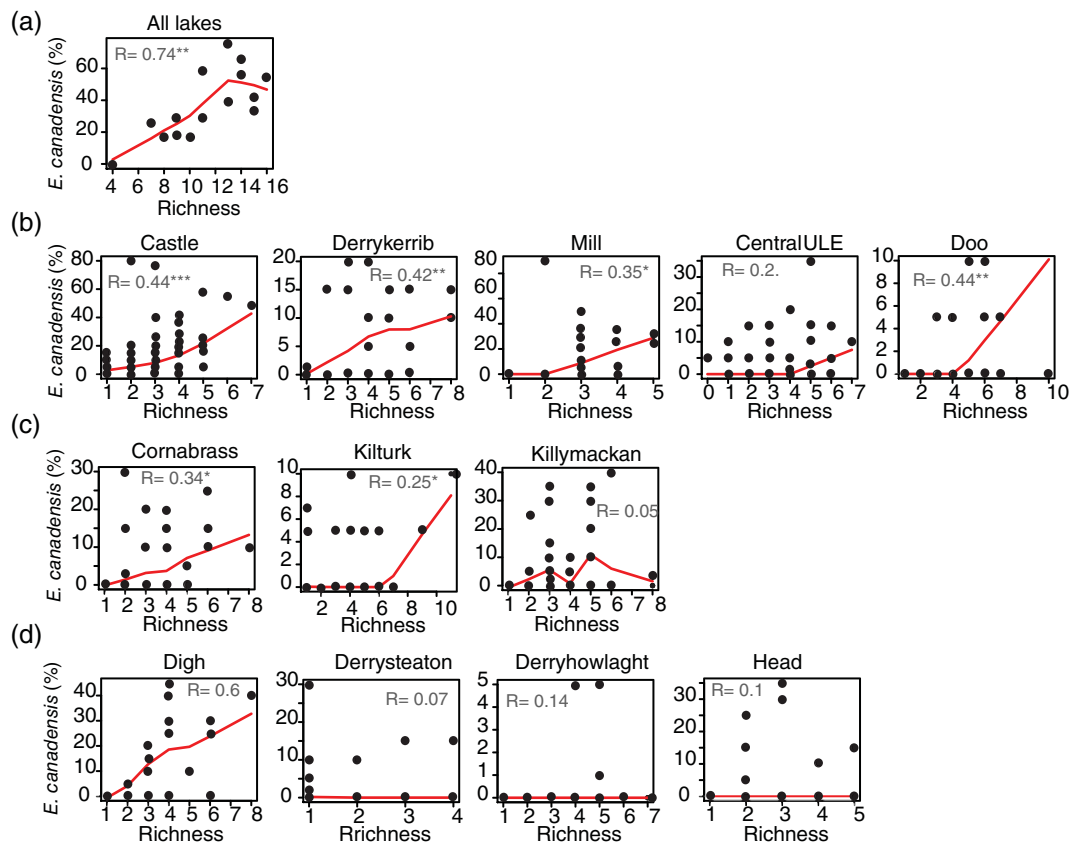

FIGURE 2 The relationship between (a) richness of survey native macrophyte species and *E. canadensis* lake percentage of occurrences at all the study lakes (Loughs). The relationship between native macrophyte species richness and *E. canadensis* abundance at each lake sampling points in lake *Group 1* (b); Lake *Group 2* (c) and (d) lake *Group 3*. Pearson correlation coefficients, LOESS line trend and significance for each analysis are indicated at each plot. *p < .05; **p < .01; ***p < .001 [Color figure can be viewed at wileyonlinelibrary.com]

FIGURE 3 The temporal relationship between native plant macrofossil richness and *E. canadensis* abundance at the within-lake scale in (a) Castle Lough and the central Upper Lough Erne–ULE (*Group 1* of lakes); (b) Cornabrass Lough and Killymackan Lough (*Group 2*); and (c) Gole Lough and Head Lough (*Group 3*). Pearson correlation coefficients and significance for each analysis are indicated on each plot. *p < .05; **p < .01; ***p < .001 [Color figure can be viewed at wileyonlinelibrary.com]
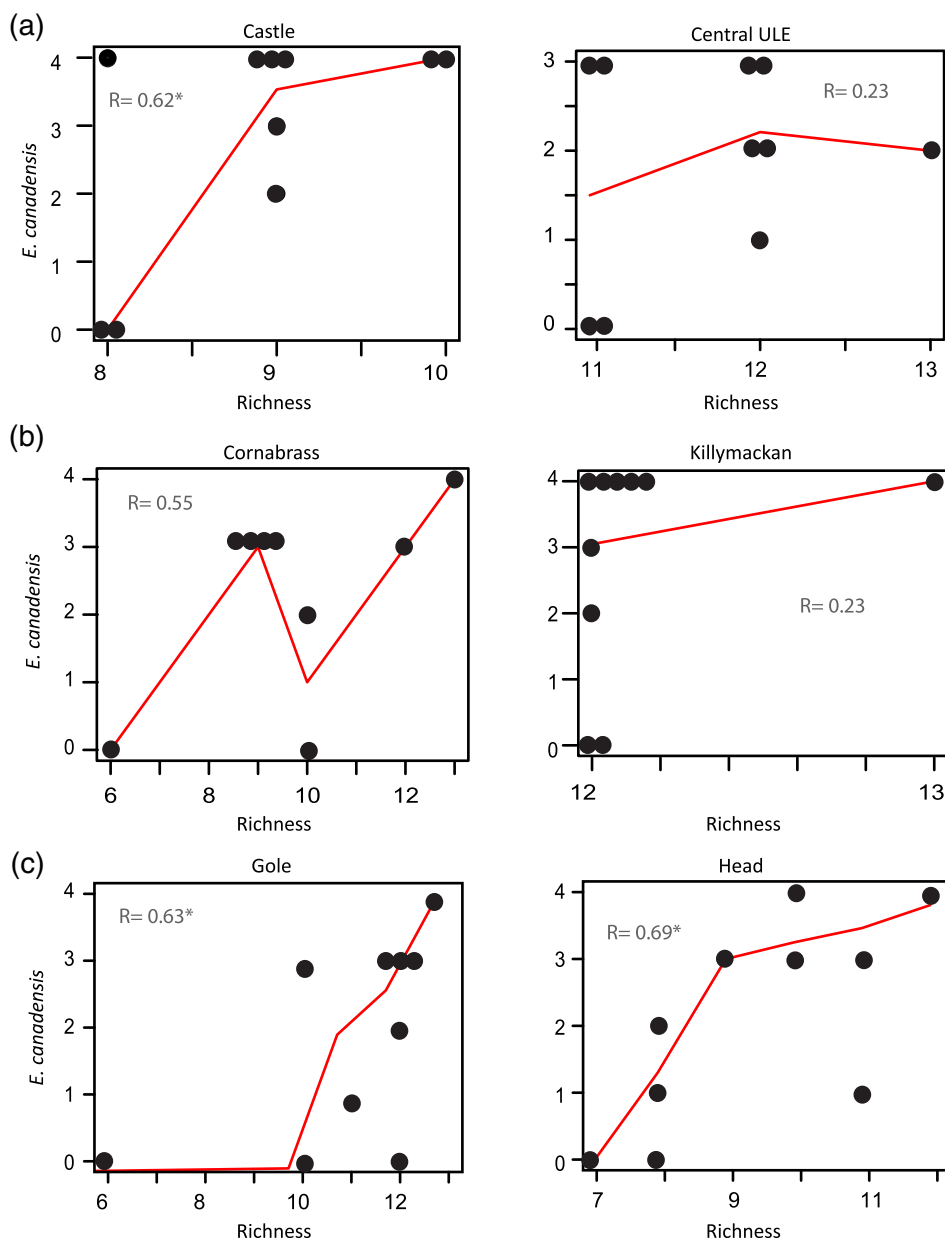
Group 1 (16%) compared to *Group 2* (8%) and *Group 3* (7%). The influence of submerged plant cover was generally low among the three groups, explaining just 5–7% of the pure diversity fraction. The proportion of variance jointly attributable to the fraction of both abiotic and diversity descriptors increased from *Group 1* (37%) to *Group 3* (51%). The proportion of unexplained variation declined from 16% in *Group 1* to 5% in *Group 3*.

The pBRT fitted function plots (Figure 5) show marked reductions in *E. canadensis* abundances with declining water clarity (index values <1.2) and with increases in native plant cover (>60%), in particular for *Groups 2* and *3*. A nonlinear pattern with three distinct phases of *E. canadensis* abundances and native macrophyte beta diversity also emerged, characterised by: (a) abundant *E. canadensis* co-occurring with diverse native macrophyte communities and high submerged plant cover; (b) low abundances or absences of

E. canadensis coupled with high native plant cover and low native macrophyte diversity; and (c) abundant *E. canadensis* co-occurring with diverse native macrophyte communities and high floating plant cover.

RFA on the palaeo-data in *Group 1* lakes identified again beta diversity as the most important predictor in explaining *E. canadensis* abundance variation through time (Figure 6a). Shannon diversity and floating plant cover were also influential. *E. canadensis* abundances were positively related to all three diversity predictors. For *Group 2*, variation in submerged plant cover was the most important driver of *E. canadensis* abundances followed by beta diversity and Shannon diversity, respectively (Figure 6b). Here, *E. canadensis* abundances were positively related to beta diversity and Shannon diversity values, whilst negatively related to submerged plant cover. The analysis of *Group 3* lakes identified plant cover as the most important variable in
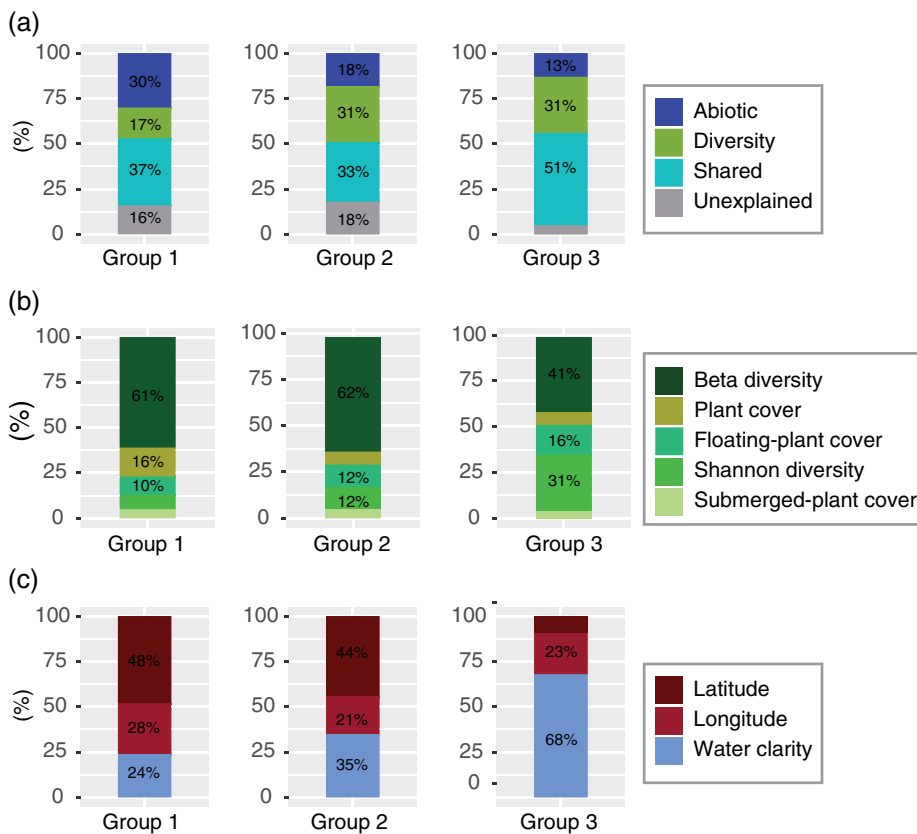
FIGURE 4 (a) Partial boosted regression trees (pBRT) on the three-study lake groups showing the pure and shared proportions of explained and unexplained variance in *E. canadensis* abundance by abiotic metrics and native biodiversity metrics; (b) diversity fraction of the pBRT analysis showing the unique contribution of Shannon diversity, plant cover, submerged plant cover, floating plant cover and beta diversity on *E. canadensis* abundance variation across the three-study lake groups; (c) abiotic fraction of the pBRT analysis showing the unique contribution of water clarity, longitude and latitude on *E. canadensis* abundance variation across the three-study lake groups. Only percentages values of explained variation >10% are presented in the plots [Color figure can be viewed at wileyonlinelibrary.com]

explaining *E. canadensis* abundance variation through time (Figure 6c). Beta diversity, submerged plant cover, and Shannon diversity also positively influenced *E. canadensis* abundances.

4 | DISCUSSION

The results show that the abundance of *E. canadensis* in the ULE system is not determined by the single effects of native diversity or beneficial environmental conditions but rather by habitat heterogeneity. For instance, *E. canadensis* is commonly reported to dominate over native submerged species once well established, and to exert strong negative ecosystem engineering effects (Zehnsdorf et al., 2015). Conditions considered to favour *E. canadensis* include nutrients availability, suitable carbon sources, and silty substrates (Zehnsdorf et al., 2015). Such conditions characterised our study sites (Salgado et al., 2019a) and would support an environmental-matching control effect. However, while *E. canadensis* was present in all but one site, abundances in lakes were generally low to moderate. Moreover, the positive correlation between *E. canadensis* abundance and native speciose communities over space and time further suggests that native species richness alone does not confer invasibility resistance (Capers et al., 2007). In turn, it indicates sufficient habitat heterogeneity over time within and among-lakes to enable coexistence of native and non-native macrophytes (Clark et al., 2013) which differ from the often-described macrophyte IAS homogenisation impacts (Muthukrishnan & Larkin, 2020).

Water clarity and a nested spatial dependence between *E. canadensis* abundance and the location of sampling points in each lake were highlighted as key controlling abiotic factors. Macrophyte species tend to be distributed at certain depths rather than occur across an entire lake (He et al., 2019). Thus, the nested dependence of *E. canadensis* abundance, likely reflects each lake specific water depth profile and the associated zonation patterns of light availability. The influence of water clarity on *E. canadensis* abundance further diminished with lake isolation to the central ULE, which is in line with our previous studies of the ULE system showing that zebra mussels and eutrophication have spread unevenly across the lakes (Salgado et al., 2019a).

Among diversity predictors, much of the spatial and temporal variation in *E. canadensis* abundance was related to native beta diversity and plant cover; plant community attributes that have been found to better capture macrophyte ecological change in human-dominated landscapes than species richness alone (Fu et al., 2019). The relation of beta diversity and *E. canadensis* abundance was greatest in the more connected lakes (*Group 1*), which likely reflects a pronounced influence of source sink dynamics that fosters heterogeneous plant associations under the less stressful environmental conditions (high water clarity and lower nutrients) of this group of lakes (Salgado, Sayer, Brooks, Davidson, Goldsmith, 2018; Salgado, Sayer, Brooks, Davidson, & Okamura, 2018). In turn, high cover may limit *E. canadensis* abundance. This pattern was particularly revealed among those eutrophic lakes with a lower degree of connectivity to the central ULE (*Groups 2* and *3*), and which are dominated by a few
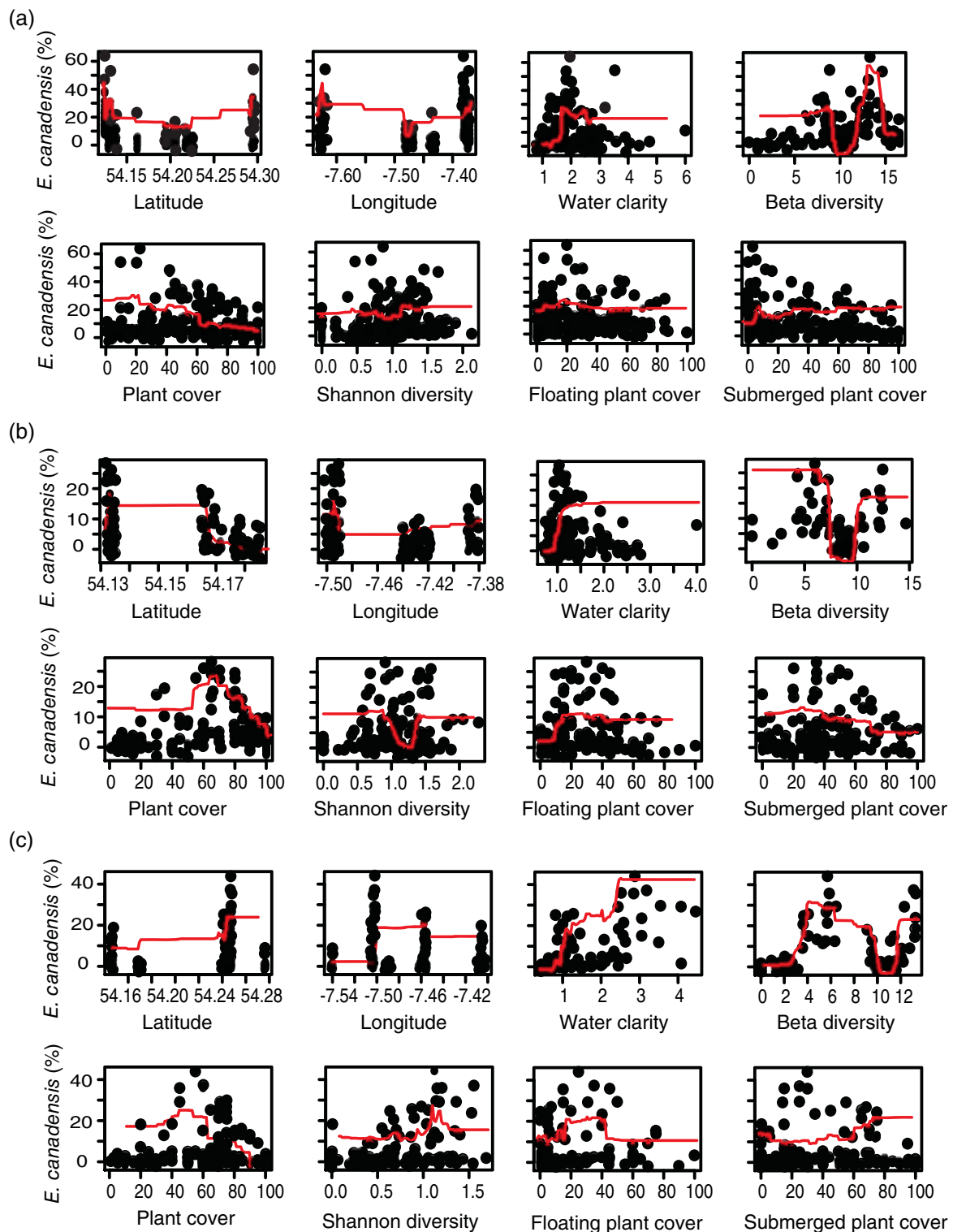
FIGURE 5 pBRT smooth fitted functions plots between *E. canadensis* abundance variation and water clarity, longitude, latitude, Shannon diversity, plant cover, submerged plant cover, floating plant cover, and beta diversity at each lake group (a, b, c) [Color figure can be viewed at wileyonlinelibrary.com]

submerged and floating species (Salgado, Sayer, Brooks, Davidson, Goldsmith, et al., 2018; Salgado, Sayer, Brooks, Davidson, & Okamura, 2018). Negative correlations between plant cover and macrophyte IAS were similarly found by Capers et al. (2007) across a

series of lakes in Connecticut (USA) and in grassland and dessert plants by Cleland et al. (2004), both suggesting that IAS success is diminished by high resource capture by the resident communities. It is thus likely that different processes may control the establishment
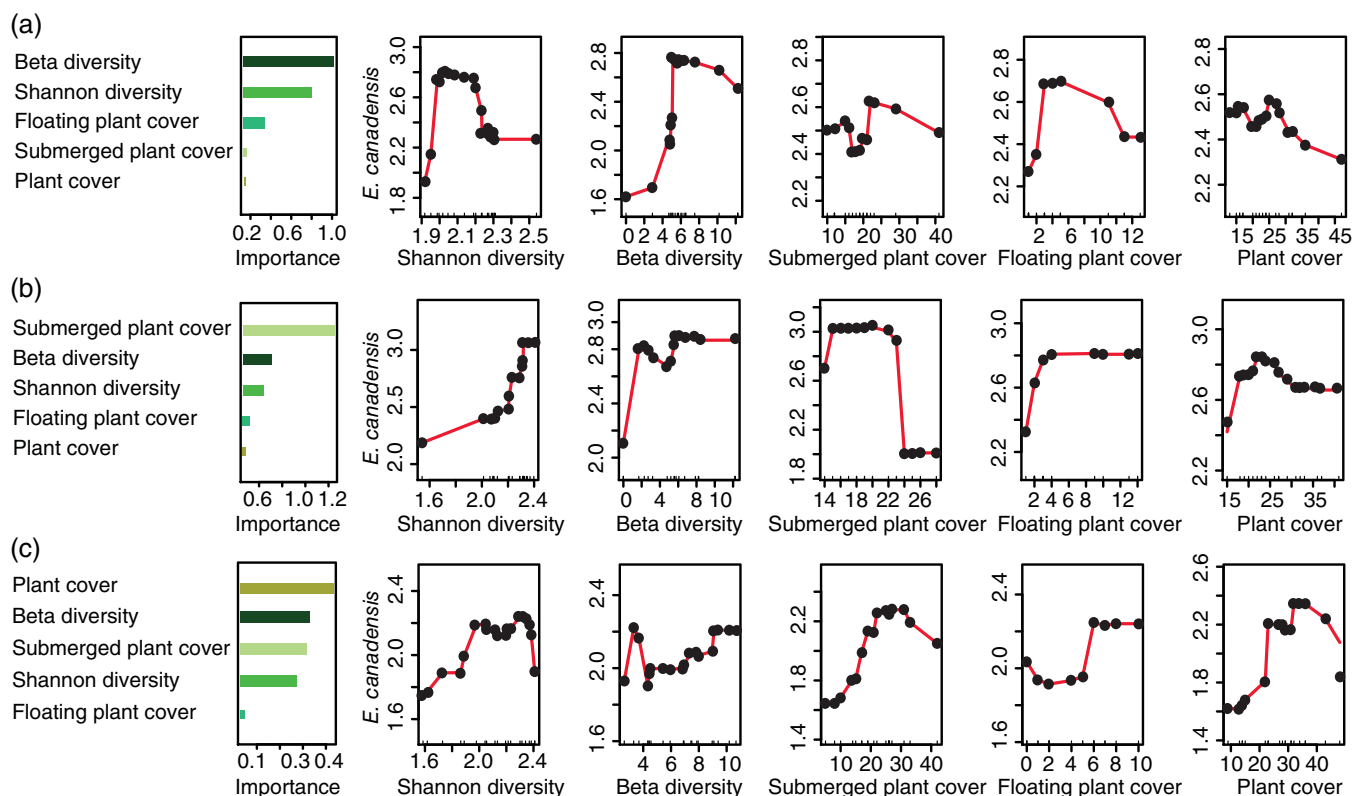
FIGURE 6 Results of Random Forest analysis showing the unique contribution of the native plant macrofossil diversity metrics Shannon diversity, plant cover, submerged plant cover, floating plant cover and beta diversity on *E. canadensis* abundance temporal variation across the three-study (a, b, c) lake groups [Color figure can be viewed at wileyonlinelibrary.com]

vs proliferation of *E. canadensis* in the ULE system. For example, spatial and temporal habitat heterogeneity may facilitate a range of opportunities for *E. canadensis* to establish and coexist (Clark et al., 2013). However, low water clarity and high native plant cover could lower resource availability for *E. canadensis*, thereby reducing opportunities to proliferate (Cleland et al., 2004).

4.1 | Inferring the history of *E. canadensis* in the ULE system

Palaeolimnological data reveal that at the time that *E. canadensis* colonised the ULE system in the late 1800s, macrophyte communities were diverse like those currently observed in *Group 1* lakes (Figure 7; Salgado et al., 2019a). Simpson (1984) reported a cycle of local colonization by *E. canadensis* involving establishment over a three-year period and a subsequent rapid increase in abundance. Given the extensive interconnection by winter flooding *E. canadensis* probably spread rapidly to many sites. Following its widespread establishment, *E. canadensis* possibly therefore persisted at moderate abundances for a long period, co-existing with a reported high diversity of other submerged species across the lakes (Salgado, Sayer, Brooks, Davidson, Goldsmith, et al., 2018; Salgado, Sayer, Brooks, Davidson, & Okamura, 2018). Subsequently, post-1950s, paleoecological data indicate gradual biotic changes associated with more eutrophic conditions

that intensified after the 1980s (Battarbee, 1986) but with differential local nutrient concentrations influencing biota (Salgado et al., 2019a). These post-1950s biotic shifts involved gradual increases in floating plant cover and dominance of fine-leaf *Potamogeton* species, although some sites, such as Castle Lough and Mill Lough, have maintained high macrophyte species diversities and abundances. Reductions in *E. canadensis* abundance in the most degraded lakes of *Group 3* and negative associations with plant cover suggest a gradual decline in abundance across the ULE system over the last three to four decades leading to its current status of being widespread but seldom very abundant.

4.2 | Limitations

Reconstructing *E. canadensis* abundance over time based on survey and sediment core data may have limitations. For instance, some species are likely to have been unrecorded and detection in sediment cores may be biased by preservation issues and under-representation of rare or distantly located macrophyte taxa (Clarke et al., 2014). Our assessments of native macrophyte richness variation over space and time probably favour the more abundant taxa. Unique lake histories could have also introduced some discrepancies between the observed current *E. canadensis* lake occupancies and the inferred past abundance (Salgado et al., 2019a). Nevertheless, analyses of both palaeo- and
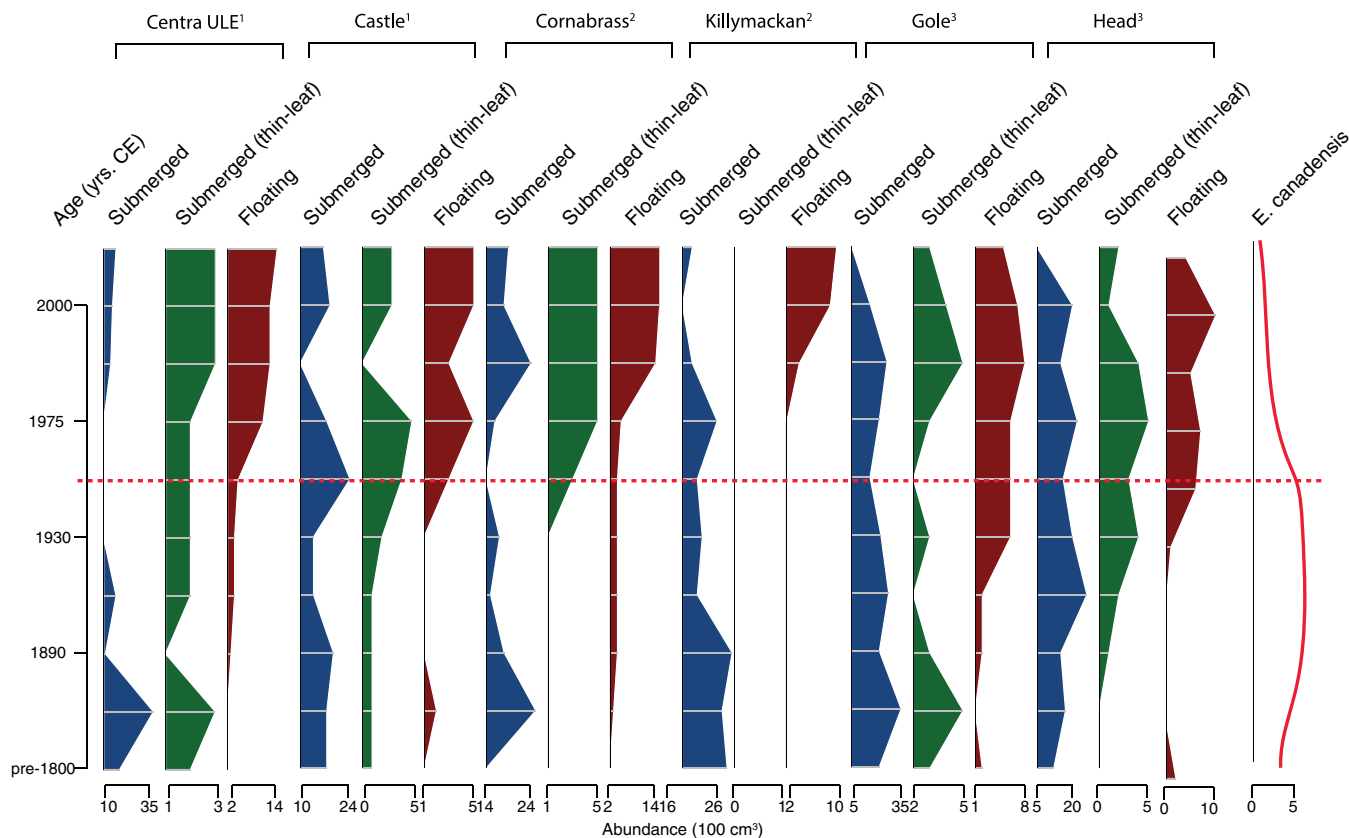
FIGURE 7 Stratigraphic summary of the plant macrofossil data showing the temporal variation in submerged plant cover (separated into thin-leaf taxa and other submerged taxa), and floating plant cover for the central ULE, Castle Lough, Cornabrass Lough, Killymackan Lough, Gole Lough, and Head Lough. Inferred temporal variation of *E. canadensis* abundance is also shown [Color figure can be viewed at wileyonlinelibrary.com]

contemporary data showed a consistent positive relationship between *E. canadensis* abundance and native plant richness in most lakes. Plant cover and beta diversity similarly emerged as the main predictors in explaining the spatial and temporal variation of *E. canadensis* abundance. These lines of evidence coupled with the history of *Elodea* spread in the British Isles (Simpson, 1984) thus allow us to hypothesize what the general long-term patterns of *E. canadensis* spread in the ULE system would have followed the patterns describe above.

5 | CONCLUSIONS AND FUTURE TRAJECTORIES

We demonstrate that in well-connected lake landscapes, habitat heterogeneity can play a defining role in driving macrophyte IAS abundance over space and time by facilitating the coexistence of native and non-native plant species. Water clarity (negatively) and geolocation were the most important abiotic factors explaining *E. canadensis* abundance variation, whereas beta diversity (positive and negative) and native plant cover (negative) emerged as the most important biotic factors. Species coexistence was generally favoured among well-connected lakes, while invasion resistance occurred in stressful environments or when native plant cover was high.

Predicting future trajectories of *E. canadensis* distribution and abundance in the ULE system, and in the United Kingdom in general is, however, challenging. *E. canadensis* has spread in the British Isles by asexual growth, most likely from male clones (Simpson, 1984). It is therefore possible that conditions (e.g., disease) may eventually challenge the persistence of clonal populations due to the lack of genetic variation. Furthermore, with globalization, unexpected and novel invasion dynamics are more probable (Pyšek et al., 2020). Meanwhile, the ULE system is suggested to be declining through advancing eutrophication, which, if unabated, will eventually override positive regional species storage effects (Salgado, Sayer, Brooks, Davidson, Goldsmith, et al., 2018; Salgado, Sayer, Brooks, Davidson, & Okamura, 2018). In addition, the sibling invasive species, *Elodea nuttallii* Planch., is rapidly spreading across the lower part of the ULE system and outcompeting *E. canadensis* under high nutrient conditions (Kelly, Harrod, Maggs, & Reid, 2015). Quantifying the dynamics of these two invasive species at both landscape and temporal scales is critical, therefore, if invasion processes are to be better understood.

DATA AVAILABILITY STATEMENT

The data that support the findings of this study area openly available in Figshare at https://doi.org/10.6084/m9.figshare.14828211.v1.

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SUPPORTING INFORMATION

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

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