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ORIGINAL PAPER

Effects of *Elodea nuttallii* on temperate freshwater plants, microalgae and invertebrates: small differences between invaded and uninvaded areas

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Abstract The invasive aquatic plant species *Elodea nuttallii* could pose a considerable risk to European freshwater ecosystems based on its current distribution, rate of spread and potential for high biomass. However, little research has been conducted on the impacts of this species on native biota. This study takes an ecosystem-wide approach and examines the impact of *E. nuttallii* on selected physicochemical parameters (dissolved oxygen and pH), algae, invertebrate and macrophyte communities. *Elodea nuttallii* had small but significant impacts on plant, invertebrate and algal species. The richness of algal periphyton was lower on *E. nuttallii* than on native macrophytes. The taxonomic composition of invertebrate communities associated with *E. nuttallii* differed from that associated with similar native plant species, but did not differ in terms of total biomass or species richness. Macrophyte species richness and total cover were positively correlated with percentage cover of *E. nuttallii*. Not all macrophyte species responded in the same way to *E. nuttallii* invasion; cover of the low-growing species, *Elodea canadensis* and charophytes were negatively correlated with *E. nuttallii* cover, whilst floating-rooted plants were positively correlated with *E. nuttallii* cover. All observed differences in the macrophyte community were small relative to other factors such as nutrient levels, inter-annual variation and differences between sites. Despite this, the observed negative association between *E. nuttallii* and charophytes is a key concern due to the rarity and endangered status of many charophyte species.

Keywords Algae · Aquatic · Invasion · Limnology · Macroinvertebrate · Macrophyte

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Introduction

Freshwater systems have been shown to be at particularly high risk from biological invasions (Sala et al. 2000) and invasive aquatic plants are widely considered to be a major threat to both species diversity and ecosystem functioning (Strayer 2010).

The assessment of potential impacts of invasive species on ecosystems is essential for the effective prioritisation of resources (Leung et al. 2012), and traits associated with successful naturalisation cannot be reliably used to infer potential impact (Hulme 2012). Despite this, in Europe there is a lack of studies directly assessing the impacts of aquatic species on natural ecosystems across trophic levels (Caffrey et al. 2014).

Invasive macrophytes can be 'ecosystem engineers', fundamentally altering ecosystems through alterations to habitat structure and water chemistry (Strayer 2010). The impacts of invasive macrophytes on native macrophytes are more frequently studied than their impacts on algae or invertebrates (Evangelista et al. 2014). Invasive macrophytes are frequently observed to be dominant in plant assemblages. They may reduce overall macrophyte richness (Carniatto et al. 2013; Michelan et al. 2010; Stiers et al. 2011) and native seed banks (deWinton and Clayton 1996), and alter plant community composition (Mjelde et al. 2012; O'Hare et al. 2012). However, invasive macrophytes may also benefit native plant species by altering the physical environment (e.g. stabilisation of sediment, reduction of turbidity or altering water clarity, Rybicki and Landwehr 2007; Thomaz et al. 2012). Previous laboratory experiments conducted with *Elodea nuttallii* have shown that it can outcompete other submerged species (Barrat-Segretain 2005) and floating species when nutrient concentrations are not limiting (Szabo et al. 2010). However, floating species are likely to out-compete *E. nuttallii* in high nutrient conditions due to their superior ability to compete for light (Netten et al. 2010; Szabo et al. 2010).

Algal periphyton is a key link between macrophytes and aquatic invertebrate species (Hamilton et al. 1992). Algal periphyton communities differ between plant hosts (Toporowska et al. 2008) both as a result of plant architecture (Declerck et al. 2007; Warfe and Barmuta 2006) and chemical exudates (Erhard and Gross 2006). Suppression of algal taxa by macrophyte exudates has been observed for several submersed species, including *E. nuttallii* and its congener *Elodea canadensis* (van Donk and van de Bund 2002; Wu et al. 2009). As competition with periphyton and phytoplankton is a major limiting factor for aquatic macrophytes, such allelopathy could constitute a substantial competitive advantage for these species.

Allelopathic exudates may also affect zooplankton and macroinvertebrates, e.g. negative effects of *Elodea* spp. on growth and development of *Daphnia* spp. (Burks et al. 2000) and lepidopteran larvae in the family Pyralidae (Erhard et al. 2007). Many macrophyte species contain chemicals that deter grazing, and invertebrates and fish may preferentially select native macrophyte species as food (Burks and Lodge 2002; Schultz and Dibble 2012). Furthermore, the physical structure of different macrophytes provides varying amounts of predator-free refuge space (Kovalenko and Dibble 2014; Valinoti et al. 2011). In some cases, the increase in plant biomass associated with invasive macrophytes may increase the overall productivity of the invaded system, resulting in an increase in biomass and diversity of invertebrate species and changes in invertebrate community composition (Schultz and Dibble 2012).

Elodea nuttallii is a submerged freshwater plant species which occurs in lakes and slow moving rivers, and which could pose a significant risk to European waterbodies based on its rapid spread and high abundance (Champion et al. 2010) and the observed impacts of *E. canadensis*. Whilst spread rates and suitability of European waterbodies for the establishment of *E. nuttallii* have been studied (Hussner 2012; Kelly et al. 2014a, b), little research has been conducted on the impacts of this species in invaded waterbodies.

Elodea nuttallii was first introduced to Europe in 1939 and has spread rapidly, replacing the ecologically similar *E. canadensis* in many locations (Thiébaut et al. 2008). *E. canadensis* is considered to be one of the '100 worst' invasive species in Europe (DAISIE 2015) and has impacts on macrophyte communities and aquatic food webs (e.g. deWinton and Clayton 1996; Kelly and Hawes 2005; Kornijow et al. 2005). *E. nuttallii* and *E. canadensis* are so similar that they may be ecologically and functionally redundant (Herault et al. 2008), in which case their distribution and impacts could be expected to be similar. Both *E. canadensis* and *E. nuttallii* have high photosynthetic rates, show strong effects on pH, dissolved oxygen and CO_2 levels within plant stands (James et al. 1999) and may play an important role in phosphorus cycling in eutrophic systems (Angelstein and Schubert 2008). Field evidence suggests that *E. nuttallii* is replacing *E. canadensis* (Barrat-Segretain 2001; Barrat-Segretain et al. 2002) and laboratory experiments have shown that *E. nuttallii* is more competitive than *E. candensis*

(Barrat-Segretain 2005). Hence, the impacts of *E. nuttallii* could be more severe than those of *E. canadensis*.

According to the "invasional meltdown" hypothesis (Simberloff 2006) invasive species may facilitate the establishment or growth of other invasive species leading to accelerating rates of invasion; however, there are few empirical examples of this (Montgomery et al. 2012). Recent research on invasive macrophytes found evidence of facilitation of *Egeria densa* by *Ludwigia grandiflora,* but mutual inhibition between *L. grandiflora* and *Myriophyllum aquaticum* (Thouvenot et al. 2013), suggesting that such interactions may be species- and/or context-specific. Therefore, it is important to examine the potential interactions between *E. canadensis* and *E. nuttallii* where they co-occur in order to ascertain whether impacts on native biota are amplified by the interaction of these species.

Here, we describe two correlational studies which provide insights into the potential impacts of *Elodea*. Firstly, we used historical data on the macrophyte communities in two large lakes over the course of an invasion to examine the impact of *E. nuttallii* on other macrophyte species, and to examine interactions between *E. nuttallii* and *E. canadensis*. Secondly, we used a paired survey design to examine differences in microalgae and invertebrates associated with native macrophytes and invasive *E. nuttallii* within six waterbodies. We used a combination of standard community metrics (e.g. biomass and species richness) and multivariate analyses of communities, both in terms of taxonomic groups and broader functional or structural groups, to examine impacts at different trophic levels.

Methods

Macrophyte study sites

Lough Erne in County Fermanagh, Northern Ireland, comprises Upper Lough Erne (ca. 29 km^2) and Lower Lough Erne (ca. 104 km^2). Lough Erne is a naturally eutrophic lake system with high alkalinity due to the underlying geology of the area. Upper Lough Erne is the shallower of the two lakes with a mean depth of 2.9 m; Lower Lough Erne has a mean depth of 11.9 m. Over the period of this study pH in these lakes ranged from 6.2 to 9.3, total phosphorus from 10 to 780 $\mu g\ l^{-1}$ and nitrates from 20 to 1,080 $\mu g\ l^{-1}$ [data provided by Northern Ireland Environment Agency (NIEA), based on monthly measurements at ten monitoring points from 2006 to 2010]. Lough Erne is notable for its conservation value, being designated as a Special Area of Conservation (SAC) and Ramsar site and containing many Irish Red Data List species, including the pointed stonewort (*Nitella mucronata*) and aquatic invertebrates such as the pond skater (*Limnoporus rufoscutellatus*), water beetles (*Donacia aquatica, D. bicolora, Gyrinus distinctus, G. natator* and *Hydroporus glabriusculus*) and white-clawed crayfish (*Austropotabius pallipes*). *E. nuttallii* was first recorded in Lough Erne in 2006.

Macrophyte field and laboratory methods

Data on macrophyte community composition were obtained for both Upper and Lower Lough Erne from the Water Management Unit of the NIEA. These data represent a total of 15 transects in Upper Lough Erne during 2007 and 2010 and 18 transects in Lower Lough Erne during 2006 and 2009. Surveys were carried out by wading and by boat depending on water depth. Macrophyte species and percentage cover were recorded within 5 m^2 quadrats positioned every 5 m along each transect perpendicular to the shoreline until the edge of the macrophyte zone was reached. Nitrogen and phosphorus (NO_3N, NO_2N, NH_4N, total organic nitrogen, soluble P, and total P) were measured in surface waters in late July or August for each survey year at a central point in Upper Lough Erne and two points in Lower Lough Erne (Fig. 1). These chemistry data are included to account for differences between lakes and over time, rather than smaller scale differences between transects. Unfortunately, it was not possible to obtain more detailed information on water chemistry due to the historical nature of the dataset. We have also accounted for this issue by using a paired statistical design which means that we are not comparing between quadrats from different parts of the lakes. Only quadrats which were surveyed in both years were used in the analysis ($n = 728$ quadrats).

In order to determine whether the presence of *E. nuttallii* affected the structure of macrophyte beds, each macrophyte species was allocated to one of eight groups based on its structural characteristics: emergent, free-floating, floating rooted, submerged (canopy forming), submerged (low growing), bryophytes, filamentous algae and charophytes.

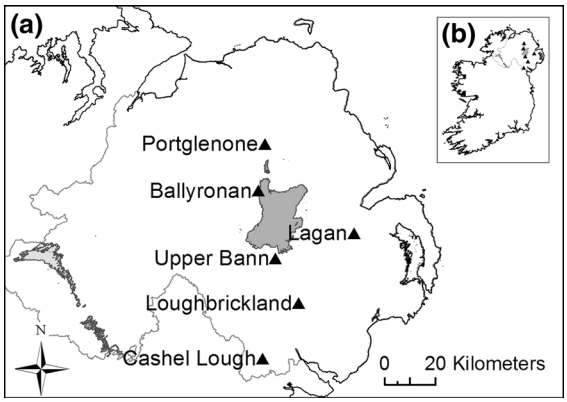

Fig. 1 **a** Field sites for study of impacts of *E. nuttallii* on dissolved oxygen, chorophyll *a*, pH, algae and invertebrates. Samples were paired within sites such that samples were taken from a stand of *E. nuttallii* and a stand of native plants within each site, **b** *inset map* of Ireland showing field site locations

Dissolved oxygen, pH, algae and invertebrate study sites

A paired survey design of six sites in Northern Ireland was used to examine the associations between *E. nuttallii*, dissolved oxygen, pH, and algal and invertebrate communities, between July and September 2010 (Fig. 2). At each site a native macrophyte stand and a stand of the invader were chosen within the same water body (distance between macrophyte stands <500 m). Native species differed between sites, but all had a predominantly submerged habit. Native species and sites were as follows: *Potamogeton pectinatus* (Lagan), *Potamogeton perfoliatus/Myriophyllum spicatum* (Ballyronan), *Potamogeton natans* (Lough Cashel), *Ceratophyllum demersum* (Loughbrickland and Upper Bann), *Sagittaria sagittifolia* (Lower Bann). Waterbodies were selected to represent the most common site conditions in which *E. nuttallii* was found and included three lake sites and three slow-flowing river sites. All samples were taken in shallow water between 0.45 m and 1.05 m in depth. There was no consistent pattern as to whether *E. nuttallii* or native plants occurred in deeper water (the mean difference in depth between *E. nuttallii* and native plants within sites was 14 cm). Sites covered a range of nutrient levels from mesotrophic to hypereutrophic (measured total phosphorus ranging from 18 to 1168 μg l^{-1} and total dissolved nitrogen between 4.61 and 530 μg l^{-1}).

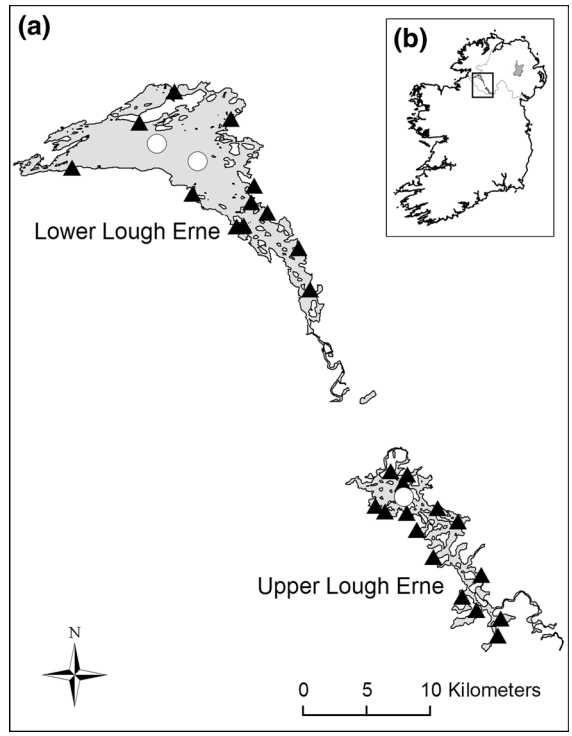

Fig. 2 **a** Study sites for macrophytes in Lough Erne. Black triangles show the locations of survey transects. *White circles* show locations where water chemistry parameters were measured, **b** *inset map* of Ireland showing location of Lough Erne

Dissolved oxygen, pH, algae and invertebrate field and laboratory methods

Water chemistry, environmental data and algal sampling took place monthly for 3 months from July to September 2010. The pH and dissolved oxygen were recorded at each site using a Hanna pHep 4 pH meter and a portable dissolved oxygen meter (VWR DO200). Two litres of water was collected within each macrophyte bed for chlorophyll *a* analysis, filtered using a 0.45 μm Metricel® membrane filter and stored at −20 °C. Chlorophyll *a* analysis was conducted using methanol-based pigment extraction and spectrophotometry readings (Hamilton 2010). A further two litres of water was collected for nutrient analyses: soluble reactive phosphorus (SRP), total phosphorus (TP), total soluble phosphorus (TSP), total organic nitrogen (TON), ammonium (NH_4), nitrogen dioxide (NO_2), nitrates (NO_3) and total dissolved nitrogen (TDN). Nutrient analyses were conducted by the Agri-Food and Biosciences Institute, Newforge Lane, Belfast, Northern Ireland.

Algal periphyton was collected by taking approximately 10 cm length of plant material from both the tip and the base of the macrophyte with approximately 15 ml of water immediately surrounding the macrophyte leaves. Care was taken to carry out this procedure slowly and carefully in situ to minimise loss of periphyton. Water samples were filtered through a 250 μm mesh within 10 min of sampling to remove zooplankton and preserved using Lugol's Iodine solution (5 g iodine (I_2), 10 g potassium iodide (KI), 85 ml distilled H_2O). One algal sample was taken in each invaded and each uninvaded macrophyte bed in each of July, August and September. Algal samples were kept in the dark at 5–7 °C before processing.

Algal periphyton was separated from plant samples by vigorous shaking for 60 s. The algal sample was then transferred into a sterile 20 ml tube. Plant material was dried at 60 °C for 72 h and the dry mass was recorded. The algal sample was placed in a Lund chamber. Five horizontal transects of the chamber were carried out at 100× magnification and larger species were identified and counted. A further 20 random fields of view (450 μm^2) were examined at 400× magnification and all species were identified and counted. Taxa were identified to genus level where possible, or to the lowest practical taxonomic level (Bellinger and Sigee 2010; Cox 1996; John et al. 2002). It was not possible to accurately identify all cells under 10 μm; those which could not be identified were measured for biovolume and recorded as "unidentified genera" (1.9 % of total algal biovolume). For unicellular and colonial algae, the first 10 cells or colonies of each genus or species were measured. For filamentous algae, the first 30 filaments were measured as there was greater variation observed in filament length than in cell or colony size. Mean cell biovolumes were calculated using the 'WISER phytoplankton counter spreadsheet' (Carvalho et al. 2007) and biovolume formulae were added for new taxa as defined in Hillebrand et al. (1999).

Algal species were categorised into seven functional groups based on Kruk et al. (2010) plus an eighth group of 'uncategorised genera' (Supplementary Material, Table S1). These groups have been proposed to be useful predictors of algal responses to environmental variables as they are closely linked with functional characteristics such as prey avoidance, *K* and *r* strategies and sinking rates (Kruk et al. 2010).

Invertebrates were sampled during July and late September/early October using two methods at each sampling date. Firstly, at each site, four replicate core samples of sediment were taken from each macrophyte bed using a KC Denmark Kayak core sampler 45 mm in diameter (hereafter, referred to as 'sediment invertebrate samples'). Secondly, invertebrates present in macrophyte material were collected using a bespoke bucket and mesh trap of 379 cm^2 surface area and 300 μm mesh size (hereafter, referred to as 'macrophyte invertebrate samples').

Invertebrates were separated from samples using a 250 μm sieve and stored in 70 % ethanol. Plant material was dried at 60° C for 72 h and its dry mass recorded for calculation of macrophyte stand density. All invertebrates were identified to the lowest possible taxonomic level (Edington and Hildrew 1995; Elliott and Mann 1998; Fitter and Manuel 1986; Friday 1998; Gledhill et al. 1993; Savage 1989; Wallace et al. 1990). For sediment invertebrate samples, specimen length, width and dry mass were measured ($n = 523$). Linear regressions based on the length or width and biomass (transformed by Log_{10} or a natural logarithm depending on best fit described by the adjusted R^2 value) were conducted using SigmaPlot 10 to describe the relationship between individual length/width and biomass for each common invertebrate family or genus (Supplementary Material, Table S2). In taxa that exhibited a significant relationship between length/width and body mass these regression formulae were used to calculate the biomass of individuals of that taxa in the macrophyte invertebrate samples. For all other species dry mass was measured directly. Invertebrate species were further categorised into six functional feeding guilds: collector filterers, collector gatherers, herbivore piercers, predators, scraper grazers and shredders following (Chaloner et al. 2009; Compin and Cereghino 2007; Cummins and Klug 1979; Heino 2008) (Supplementary Material, Table S3).

Statistical analyses

Macrophytes

In Lough Erne, the impact of *Elodea* spp. on total macrophyte cover, non-*Elodea* macrophyte cover and species richness (i.e. of native plants) was examined using a Generalized Linear Mixed Model (GLMM)

approach. Explanatory variables in the models were year (fitted as a factor with four levels: 2006, 2007, 2009 or 2010), water depth, nutrient concentration, the percentage cover of *E. nuttallii*, the percentage cover of *E. canadensis*, and the interaction of *E. nuttallii* and *E. canadensis*. Nutrient concentration was expressed as the first axis of a PCA analysis of nitrogen and phosphorus values, which explained 62.7 % of the variance with a positive relationship with nitrogen variables ($r = 0.95$) and a negative relationship with phosphorus variables ($r = -0.67$). Quadrat nested within lake was included as a random factor.

All GLMMs were first fitted with a Gaussian distribution and identity link function. Model residuals were tested for normality using a Shapiro–Wilk test. Models for which residuals were not normally distributed were refitted using alternative distributions more suited to the response data. Specifically, gamma distributions with a log-link function were used for continuous response data and a Poisson distribution with a log link function was used for count data (i.e. species richness). In each GLMM, all possible subsets of explanatory variables were ranked using the Akaike Information Criterion adjusted for small sample sizes (AICc), and the most optimal model was taken as that with the lowest AICc value.

Multivariate responses in macrophyte communities were assessed using partial Canonical Correspondence Analysis (pCCA). Two pCCAs were conducted, the first with a response matrix of percentage cover of macrophyte structural groups and a second with percentage cover of macrophyte genera. The associated environmental matrix included the percentage cover of *E. nuttallii*, *E. canadensis*, Year (as a factor), water depth and nutrient content. Quadrat was fitted as a random factor. The optimal model was obtained following stepwise forward selection followed by backward stepwise elimination. Explanatory variables were sequentially added to a null model (with site fitted as a random factor) where these variables significantly improved model AICc values based on a permutation test ($P < 0.05$ for inclusion), and then successively dropped from the model based on the same inclusion criteria. As *E. canadensis* was not included in the final pCCA model, it was then added to the response matrices (i.e. plant genera and structural datasets).

In order to assess whether species communities where *E. nuttallii* was present were more similar to each other than those without *E. nuttallii*, an analysis was carried out on multivariate homogeneity of group dispersion using the function "betadisper" in R. This was conducted based on a Jaccard dissimilarity distance between species communities (i.e. the proportion of species which differed between quadrats where *E. nuttallii* was present vs. the proportion of species which differed between quadrats where *E. nuttallii* was not present).

Dissolved oxygen, pH, algae and invertebrates

GLMMs were used to examine all univariate dependent variables in relation to the presence of *E. nuttallii*. Water chemistry response variables (dissolved O_2 saturation, pH and chlorophyll *a*) were tested for correlation prior to GLMM analysis using Spearman's rank correlation test. There was no significant correlation between these variables (dissolved O_2–chlorophyll *a* (rho = 0.168, $P = 0.327$), dissolved O_2–pH (rho = 0.286, $P = 0.091$) and chlorophyll *a* and pH (rho = 0.086, $P = 0.617$). Explanatory variables for these physiochemical variables were the presence or absence of *E. nuttallii* and month (July, August or September), waterbody type (i.e. two level factor "Lake" or "River") and the interaction between *E. nuttallii* presence and waterbody type. Site was fitted as a random factor.

Explanatory variables for GLMMs of algal biovolume, algal species richness and macrophyte bed density were the presence and absence of *E. nuttallii*, month, waterbody type (i.e. a two level factor "Lake" or "River") and the interaction between *E. nuttallii* presence and waterbody type, nutrient concentration and the interaction of *E. nuttallii* and nutrient concentration. Nutrient concentration was expressed as the first axis of a PCA analysis of nitrogen and phosphorus values which explained 64.1 % of the total variance and had a positive relationship with both nitrogen ($r = 0.83$) and phosphorus variables ($r = 0.73$). Site was fitted as a random factor.

Invertebrate richness and biomass in both macrophyte samples and sediment core samples were examined as above for algae. However, macrophyte bed density was added as an explanatory variable to each model. Model selection was as above for previous GLMMs.

Multivariate community responses were assessed using pCCA. Response matrices for algae were

biovolume of each algal functional group and biovolume of each algal taxon (per unit of plant dry mass). Response matrices for invertebrate species were the biomass of invertebrate feeding guilds and biomass of invertebrate taxa. The associated explanatory environmental matrix included the same factors and covariates as those used in univariate analyses i.e. the presence/absence of *E. nuttallii*, month and nutrient concentrations, waterbody type and the interaction between *E. nuttallii* presence and waterbody type, with the addition of plant density in invertebrate models only. Site was fitted as a random factor. Model optimisation was conducted as previously described for pCCAs of macrophyte communities.

In order to assess whether algal and invertebrate communities on *E. nuttallii* were more similar to each other than those on native plants were to each other we conducted an analysis of multivariate homogeneity of group dispersion using the function "betadisper" in R (as per macrophyte community data).

Unless otherwise stated all analyses were performed using R 3.0.2 (R Core Development Team 2012) and the packages glmmADMB (Fournier et al. 2012), MuMIn (Barton 2013) and vegan (Oksanen et al. 2013).

Results

Macrophytes

Elodea nuttallii was present in 2 % of the 728 quadrats in the initial survey in 2006–2007 and increased to presence in 70 % of quadrats in 2009–2010. Over the same period, the percentage cover of *E. nuttallii* within each quadrat increased from a mean of 0.03 (0–4 %) to 21.3 (0–100 %) on resurvey in 2009–2010. *E. canadensis* declined in presence from 33 to 9 % of quadrats and in mean cover per quadrat from 1.1 (0–70 %) to 0.5 (0–30 %) over the same period. A total of 71 other macrophyte species were recorded. *E. canadensis* and *E. nuttallii* were the only invasive species recorded in these surveys.

Total macrophyte cover within quadrats was positively associated with cover of both *E. nuttallii* ($\beta = 0.013 \pm 0.003$, $\chi^2 = 20.24$, $P < 0.001$) and *E. canadensis* ($\beta = 0.029 \pm 0.012$, $\chi^2 = 5.53$, $P = 0.019$). Excluding both *Elodea* species from the total macrophyte cover, the cover of remaining species was not significantly associated with the cover of either *E. nuttallii* or *E. canadensis*, but declined with water depth and differed between years. Both total macrophyte cover and the cover of non-*Elodea* species were negatively associated with water depth, the PCA axis of nutrient concentration and differed between years (see Supplementary Material, Table S5).

Species richness of macrophytes other than *E. nuttallii* and *E. canadensis* (i.e. native species) was positively associated with percentage cover of both *E. nuttallii* ($\beta = 0.002 \pm 0.001$, $\chi^2 = 3.85$, $P = 0.050$) and *E. canadensis* ($\beta = 0.013 \pm 0.004$, $\chi^2 = 11.58$, $P < 0.001$) and with the PCA axis of nutrient concentrations and negatively associated with water depth and differed between years (see Supplementary Material, Table S5). There was no evidence of an interaction between *E. canadensis* and *E. nuttallii* in any model.

The pCCA of macrophyte structural groups showed that year and percentage cover of *E. nuttallii* influenced structural composition and explained 4.6 % of the variation in plant structure after variation between quadrats (69 %) was accounted for ($P = 0.005$; Fig. 3). The pCCA of macrophyte genera showed that

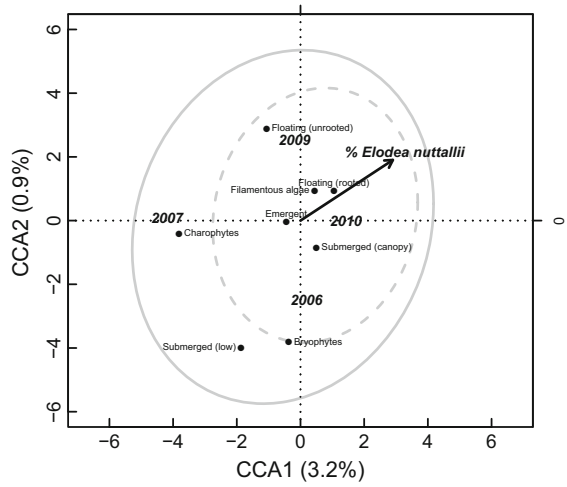

Fig. 3 Plot of partial Canonical Correspondence Analysis showing relationships between *E. nuttallii* and plant functional groups, when year is also fitted an explanatory factor and quadrat ID is accounted for as a random factor. Species scores are unscaled. Axis labels show % of total variation in macrophyte communities explained by each CCA axis. *Grey ellipse* shows 95 % confidence interval around sites where *E. nuttallii* is present, *dashed grey ellipse* shows 95 % confidence interval around sites where *E. nuttallii* is not present

Table 1 Results of partial Canonical Correspondence Analysis (pCCA) of macrophyte structural groups, showing orthogonal species scores when *E. nuttallii* is fitted as the explanatory variable and quadrat and year are accounted for by partial CCA; variance explained by percentage cover of *E. nuttallii*, variance explained by year and the variance explained by the full model (i.e. *E. nuttallii*, year and quadrat)

	CCA scores against only *Elodea nuttallii*	Variance explained by *Elodea nuttallii* (%)	Variance explained by year (%)	Variance explained by full model (%)
Submersed low-growing	−0.60	0.25	0.45	52.70
Charophytes	−0.28	0.50	10.55	63.50
Emergent	−0.16	1.12	0.67	87.12
Filamentous algae	0.04	0.13	3.80	88.26
Submersed canopy-forming	0.04	0.15	4.57	89.21
Bryophytes	0.17	0.06	1.41	74.78
Floating-rooted species	0.43	0.96	0.41	48.18
Free-floating	0.47	1.77	2.98	79.45

water depth, year and percentage cover of *E. nuttallii* influenced composition of genera significantly and explained 3.9 % of the variation after between-quadrat variation (53.9 %) was accounted for ($P = 0.005$). The percentage cover of *E. nuttallii* alone (with the other factors accounted for by pCCA) explained only 0.6 and 0.5 % of the variation in structural groups and genera respectively ($P = 0.033$ and $P = 0.005$, respectively; Supplementary Material, Table S6). The cover of submersed low-growing species and charophytes was negatively associated with the cover of *E. nuttallii*, whilst the surface-growing plants (both free-floating and rooted) were positively associated with *E. nuttallii* (Table 1). At a taxonomic level, the most negatively affected species was *E. canadensis* whilst *Nuphar lutea* and *Stratiotes aloides* were the most positively associated (Table 2). However, variance in plant community explained by *E. nuttallii* was very low relative to variance between quadrats and between years (Tables 1, 2).

Analysis of multivariate homogeneity of group dispersion showed that quadrats containing *E. nuttallii* were more homogeneous (mean Jaccard dissimilarity = 0.43, SE <0.01) than those that did not contain *E. nuttallii* (mean Jaccard dissimilarity = 0.49, SE <0.01) ($F = 24.34$, $P < 0.01$.

Dissolved oxygen, pH, algae and invertebrates

Dissolved O_2 saturation differed between lakes and rivers being higher in lakes than in rivers. The presence of *E. nuttallii* was included in the best model of dissolved O_2 saturation ($\chi^2 = 3.21, P = 0.073$), being higher in *E. nuttallii* stands (mean ± SE = 93.97 % ± 5.46) than in native plant stands (85.13 ± 3.86 %). Chlorophyll *a* showed no significant association with rivers or lakes, months or the presence of *E. nuttallii*. The pH varied significantly between months, but was not significantly associated with the presence of *E. nuttallii* (Supplementary Material, Table S7).

Macrophyte bed density did not differ between *E. nuttallii* and native macrophyte beds and was not associated with any of the other variables tested. The optimal model for algal species richness contained *E. nuttallii* with marginal significance ($\chi^2 = 3.67$, $P = 0.055$) and month, but not nutrient concentration. Algal biovolume per gram of plant dry mass varied significantly between months. Algal biovolume was not affected by either the presence of *E. nuttallii* or nutrient concentration (Supplementary Material, Table S8).

The pCCA of algal community data showed no significant effect of *E. nuttallii* on algal community composition in terms of either functional groups or taxa. The community composition in terms of algal functional groups was not significantly associated with any of the explanatory variables tested. However, nutrient concentration and month significantly affected community composition in terms of algal taxa ($P = 0.015$). Analysis of multivariate homogeneity of group dispersion did not show any significant difference in the variance between algal communities on *E. nuttallii* and those on native plants ($F = 0.42$, $P = 0.521$).

Table 2 Results of partial Canonical Correspondence Analysis (pCCA) for the genera most strongly associated with *E. nuttallii*

Genus/family	Species	CCA scores against only *Elodea nuttallii*	Variance explained by *Elodea nuttallii* (%)	Variance explained by depth and year (%)	Variance explained by full model (%)
Elodea	*E. canadensis*	−0.77	3.01	4.12	74.99
Juncus	*J. bulbosus*	−0.65	0.80	4.08	61.64
Sparganium	*S. emersum*	−0.32	0.54	0.57	69.87
	S. erectum				
Characeae[a]	*Chara globularis*	−0.32	0.65	10.68	63.77
	Chara vulgaris				
	Nitella flexilis agg.				
	Nitella translucens				
Equisetum	*E. fluviatile*	−0.30	0.68	5.55	77.02
	E. palustre				
Potamogeton	*P. alpina*	0.10	0.67	2.16	89.54
	P. crispus				
	P. filiformis				
	P. friesii				
	P. lucens				
	P. natans				
	P. obtusifolius				
	P. pectinatus				
	P. perfoliatus				
	P. praelongus				
	P. pusillus				
	P. trichoides				
	P. zizii				
Nuphar	*N. lutea*	0.44	0.94	1.25	47.75
Nymphaea	*N. alba*	0.94	0.54	2.63	45.54
Stratiotes	*S. aloides*	1.60	4.75	8.16	73.69

Genera with greater than 0.5 % of variation explained by *E. nuttallii* are shown. Table shows species from each genus present in the dataset, species scores when *E. nuttallii* is fitted as the explanatory variable and depth, quadrat location and year are accounted for by partial CCA, variance explained by percentage cover of *E. nuttallii,* variance explained by depth and year, and the variance explained by the full model

[a] Characeae were analysed at a family level as 2006 and 2007 surveys did not record at a species level within this family

None of the community metrics of invertebrate species on macrophytes or in the sediment differed between *E. nuttallii* and native macrophyte samples. Invertebrate species richness (derived from macrophyte samples) varied significantly between months. Invertebrate biomass in macrophyte samples also varied significantly between months and was positively correlated with plant density and nutrient concentration. Invertebrate species richness in sediment cores was not significantly associated with any of the environmental parameters. Invertebrate biomass in the sediment cores was positively associated with nutrient, but not with any of the other environmental parameters (Supplementary Material, Table S9).

The pCCAs of invertebrate taxonomic communities sampled from macrophytes showed a significant effect of the interaction of waterbody type and the presence of *E. nuttallii*, suggesting that the impact of *E. nuttallii* on invertebrate communities differed between lakes and rivers. This interaction explained 10 % of the variation in invertebrate communities ($P = 0.043$) after variation between sites (45 %) was

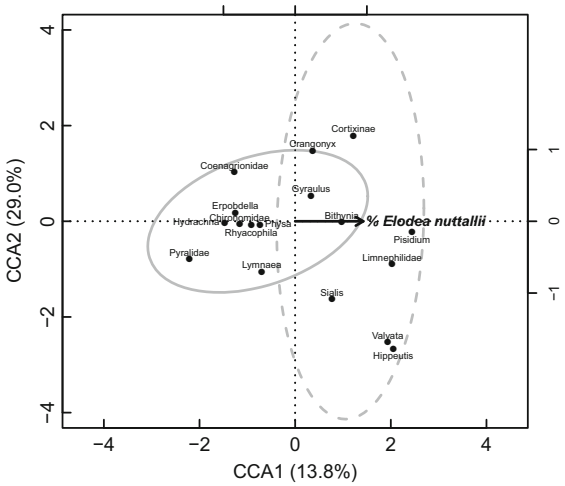

Fig. 4 Plot of partial Canonical Correspondence Analysis showing relationships between *E. nuttallii* and invertebrate taxa in lakes, when site is accounted for as a random factor. Species scores are unscaled. Taxonomic groups which were present in more than one sample and for which > 0.5 % of variation is explained by *E. nuttallii* are shown. Axis labels show % of total variation in macrophyte communities explained by each CCA axis. *Grey ellipse* shows 95 % confidence interval around sites where *E. nuttallii* is present, *dashed grey ellipse* shows 95 % confidence interval around sites where *E. nuttallii* is absent

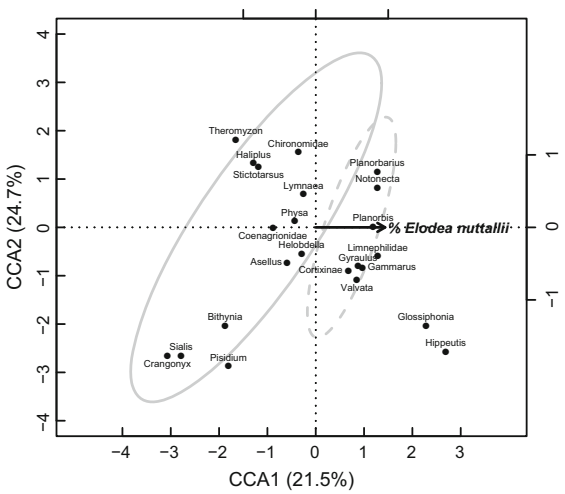

Fig. 5 Plot of partial Canonical Correspondence Analysis showing relationships between *E. nuttallii* and invertebrate taxa in rivers, when site is accounted for as a random factor. Species scores are unscaled. Taxonomic groups which were present in more than one sample and for which > 0.5 % of variation is explained by *E. nuttallii* are shown. Axis labels show % of total variation in macrophyte communities explained by each CCA axis. *Grey ellipse* shows 95 % confidence interval around sites where *E. nuttallii* is present, *dashed grey ellipse* shows 95 % confidence interval around sites where *E. nuttallii* is absent

accounted for ($P = 0.005$). When rivers and lakes were examined separately, *E. nuttallii* was found to explain 9 % of variation in invertebrate communities in lakes and 13 % of the variation in rivers, after accounting for variation between sites (41 and 33 % respectively; Tables 3, 4; Figs. 4, 5). The pCCAs of invertebrate functional groups from the macrophyte invertebrate samples and the pCCAs of invertebrate community in sediment core samples showed no association with any of the tested variables after accounting for variation between sites (Supplementary Material, Table S10). In addition, analysis of multivariate homogeneity of group dispersion did not show any significant difference in the variance between invertebrate communities associated with *E. nuttallii* stands and those associated with native plant stands in either macrophyte ($F = 0.15$, $P = 0.702$) or sediment samples ($F = 1.92$, $P = 0.179$).

Discussion

Freshwater communities associated with *E. nuttallii* differed in small but significant ways from uninvaded communities. Specifically, we observed differences in oxygen saturation, plant and algal richness, and invertebrate and macrophyte species composition. However, observed differences were small relative to other factors such as nutrient levels, inter-annual variation and differences between sites. Furthermore, there was no evidence of any effect of *E. nuttallii* on the biovolume of periphytic algae, biomass of invertebrate species or the cover of native macrophyte species. In addition, whilst plant communities in quadrats containing *E. nuttallii* were more similar to each other than quadrats in which *E. nuttallii* was not present, no similar effect was observed on algal or invertebrate communities.

The effects of *E. nuttallii* on species communities could be seen as both positive and negative, for example, the increased species richness of macrophyte species may be contrasted with the lower richness of algal taxa. Increases in floating plants associated with *E. nuttallii* can be contrasted with declines in submerged species. The association between floating plant species and *E. nuttallii* may arise as a result of structural complexity where *E. nuttallii* reaches the water surface, which reduces surface turbidity and provides anchorage for floating species. In addition,

Table 3 Results of partial Canonical Correspondence Analysis (pCCA) of invertebrate taxa living on macrophytes in lakes

Taxa	Species present	Order	CCA scores against *Elodea nuttallii* only	Variance explained by *Elodea nuttallii* (%)	Variance explained by full model (%)
Pyralidae	Spp.	Lepidoptera	−2.21	27.29	32.27
Hydrachna	Spp.	Trombidiformes	−1.47	17.93	57.90
Coenagrionidae	Spp.	Odonata	−1.27	5.47	9.03
Erpobdella	*E. octoculata*	Rhynchobdellida	−1.25	20.00	55.60
	E. testacea				
Chironomidae	Spp.	Diptera	−1.16	38.42	45.23
Rhyacophila	Spp.	Trichoptera	−0.92	0.65	37.26
Physa	*P. fontinalis*	Planorboidea[a]	−0.74	5.01	17.72
Lymnaea	*L. auricularia*	Lymnaea	−0.70	6.23	33.01
	L. palustris				
	L. peregra				
Gyraulus	*G. albus*	Planorboidea[a]	0.34	1.25	24.87
Crangonyx	*C. pseudogracilis*	Amphipoda	0.37	1.70	17.04
Sialis	*S. lutaria*	Megaloptera	0.77	2.56	46.89
Bithynia	*B. tentaculata*	Truncatelloidea[a]	0.98	8.56	49.57
Cortixinae	Spp.	Hemiptera	1.22	9.30	49.01
Valvata	*V. cristata,*	Valvatoidea[a]	1.94	11.46	33.69
	V. piscinalis				
Limnephilidae	Spp.	Trichoptera	2.03	26.19	45.12
Hippeutis	*H. complanatus*	Gastropoda	2.05	11.73	31.97
Pisidium	*P. casertanum*	Planorboidea[a]	2.44	23.66	54.02
	P. subtruncatum				

Taxanomic groups which were present in more than one sample and for which > 0.5 % of variation is explained by *E. nuttallii* are shown. Table details taxa scores when *E. nuttallii* is fitted as the explanatory variable, variance explained by percentage cover of *E. nuttallii,* and the variance explained by the full model

[a] Within the class Gastropoda, superfamily is given instead of Order as Orders are not defined for these taxa

floating species are most likely to out-compete *E. nuttallii* for light and have been shown to out-compete *E. nuttallii* in high nutrient conditions (Netten et al. 2010; Szabo et al. 2010). Submerged species which are negatively associated include low-growing species which are likely to be shaded by *E. nuttallii* (such as *Eleocharis acicularis, Isoetes spp., Littorella uniflora*), canopy-forming submerged species occupying a similar niche space to *E. nuttallii* (including *E. canadensis*) and charophyte species.

Although the observed negative association between *E. nuttallii* and charophytes is small, this is of concern due to the rarity and conservation status of charophyte species. Charophytes are usually low-growing (<0.5 m in height) and are likely to be out-competed for light by *E. nuttallii*. While this negative association could arise in this study from charophytes reducing the likelihood of establishment of *E. nuttallii*, this seems unlikely as charophytes have been previously shown to be out-competed by structurally similar invaders from the same plant family (e.g. *Lagarosiphon major* (Barrs et al. 2008) and *E. canadensis* (Mjelde et al. 2012)).

The observed negative association between the cover of *E. nuttallii* and *E. canadensis* suggests a competitive interaction between these two closely related invasive species. We did not find any indication that *E. nuttallii* or *E. canadensis* interact to increase impacts on native macrophyte cover or richness. Therefore, our findings do not support the invasional meltdown hypothesis in the case of *E. nuttallii* and *E. canadensis*. In addition, the observed rapid increase range and abundance of *E. nuttallii* in Lough Erne (such that it is much now much more

Table 4 Results of partial Canonical Correspondence Analysis (pCCA) of invertebrate taxa living on macrophytes in rivers

Taxa	Species present	Order	CCA scores against *Elodea nuttallii* only	Variance explained by *Elodea nuttallii* (%)	Variance explained by full model (%)
Crangonyx	*C. pseudogracilis*	Amphipoda	−3.07	40.46	55.82
Sialis	*S. lutaria*	Megaloptera	−2.78	37.99	52.11
Bithynia	*B. tentaculata*	Truncatelloidea[a]	−1.88	29.44	55.33
Pisidium	*P. amnicum*	Veneroida	−1.81	6.49	13.26
	P. casertanum				
Theromyzon	*T. tessulatum*	Rhynchobdellida	−1.66	9.72	52.30
Haliplus	*H. confinis*	Coleoptera	−1.29	7.74	59.27
Stictotarsus	*S. duodecimpustulatus*	Coleoptera	−1.18	6.94	61.61
Coenagrionidae	Spp.	Odonata	−0.89	1.12	16.89
Asellus	*A. aquaticus*	Isopoda	−0.59	14.33	57.41
Physa	*P. fontinalis*	Planorboidea[a]	−0.44	3.23	57.12
Chironomidae	spp.	Diptera	−0.36	1.24	13.24
Helobdella	*H. stagnalis*	Rhynchobdellida	−0.29	3.75	64.28
Lymnaea	*L. palustris*	Lymnaeoidea[a]	−0.26	1.32	81.69
	L. stagnalis				
	L. peregra				
	L. trunculata				
Cortixinae	Spp.	Hemiptera	0.67	1.89	32.35
Valvata	*V. piscinalis*	Valvatoidea[a]	0.85	1.91	28.78
Gyraulus	*G. albus*	Planorboidea[a]	0.87	5.58	72.10
Gammarus	*G. pulex*	Amphipoda	0.97	5.26	25.61
Planorbis	*P. carinatus*	Planorboidea[a]	1.19	22.78	60.58
Planorbarius	*P. corneus*	Planorboidea[a]	1.28	20.42	75.93
Notonecta	Spp.	Hemiptera	1.28	9.16	17.87
Limnephilidae	Spp.	Trichoptera	1.28	8.45	64.97
Glossiphonia	*G. complanata*	Rhynchobdellida	2.28	20.12	40.63
	G. heteroclite				
Hippeutis	*H. complanatus*	Planorboidea[a]	2.69	14.39	38.29

Taxonomic groups which were present in more than one sample and for which > 0.5 % of variation is explained by *E. nuttallii* are shown. Table details taxa scores when *E. nuttallii* is fitted as the explanatory variable, variance explained by percentage cover of *E. nuttallii,* and the variance explained by the full model

[a] Within the class Gastropoda, superfamily is given instead of Order as Order is not defined for these taxa

frequently observed than *E. canadensis*), supports the suggestion that *E. nuttallii* may be replacing *E. canadensis* in parts of its invaded range (Barrat-Segretain 2001; Barrat-Segretain et al. 2002).

It is perhaps surprising that species richness of native macrophytes was positively associated with the presence of *E. nuttallii* and *E. canadensis* in Lough Erne, after differences in nutrient levels and between years had been accounted for. Mechanisms for facilitation of native plant species could include alteration of flow rate and turbidity, or increases in primary productivity over time through the release of nutrients from the sediment. However, these alterations could also make conditions suitable for further establishment of *E. nuttallii*, which can absorb nutrients directly from the water column and is adapted to low-light conditions (Angelstein and Schubert 2008, 2009). An alternative explanation for the positive correlation between *E. nuttallii* and species richness of native macrophytes is that some other environmental factor, unaccounted for here, facilitates both an increase in *E. nuttallii* cover (or its establishment)

and macrophyte species richness. Previous studies have suggested that while species richness increases resistance to invasion at small spatial scales (Kennedy et al. 2002), such effects may be overwhelmed by environmental factors which co-vary with species richness, such as propagule pressure, resulting in an apparent positive relationship between invasive species and native species richness (Levine 2000; Lonsdale 1999). Furthermore, a recent large-scale study of invasive species in macrophyte communities found no clear relationship between native species richness and exotic species richness (Capers et al. 2007).

In common with previous authors we found that plant density was significantly correlated with the biomass of invertebrate species living on macrophytes (Schultz and Dibble 2012). However, in our study plant density and invertebrate biomass did not differ between *E. nuttallii* and native plants, reflecting an explicit decision to examine differences between similar native and invasive plant beds. Whilst *E. nuttallii* may not alter the biomass of invertebrate species relative to similar-sized plants, results from our macrophyte dataset suggest that *E. nuttallii* may be replacing low-growing species and increasing overall macrophyte cover. Hence, by altering the relative regional abundance of different plant functional groups, *E. nuttallii* may produce corresponding changes in invertebrate biomass at larger spatial scales.

Differences in invertebrate assemblages associated with macrophytes have also been shown previously for similar submerged invasive species (Hogsden et al. 2007; Kelly and Hawes 2005; Stiers et al. 2011). The reasons for the observed differences in invertebrate species composition may be varied and complex, and are likely to relate to differences in plant architecture, plant palatability, chemical exudates, water chemistry and water flow rates. Oxygen saturation is an important factor in determining invertebrate communities in freshwater environments. Higher oxygen saturation levels associated with *E. nuttallii* may have influenced species composition here: there was a lower abundance of some species groups associated with low oxygen saturation levels such as true fly larvae in the family Chironomidae, Alderflies (*Sialis lutaria*), leeches in the genera *Erpobdella* and *Theromyzon*, and *Asellus* isopods, and a higher abundance of some species associated with higher oxygen saturation such as caddisflies in the family Linephiidae. However, several species behaved contrary to expectation based on oxygen saturation alone, suggesting that other factors influence their distributions, for example damselflies in the family Coengriidae were negatively associated with *E. nuttallii*, leeches in the family Glossiphonidae were positively associated with *E. nuttallii*, and freshwater snails in the genera *Hippeautis*, *Lymnea*, *Valvata*, *Physa* and *Bithynia*, which have similar oxygen requirements, show a range of different responses. Allelopathy may explain observed negative association between *E. nuttalii* and lepidopteran larvae in the family Pyralidae, as *E. nuttalii* has been previously shown to retard the growth and reduce the survival of the Pyralidae species *Acentria ephemerella* under laboratory conditions (Erhard et al. 2007). Where Pyralidae larvae exist in large numbers they may substantially reduce cover of other macrophyte species providing an indirect advantage to *Elodea* spp. (Gross et al. 2001).

One weakness of the pairing of native and invasive plant beds in this study was that it was not possible to use sites where only *E. nuttallii* was present (i.e. highly invaded sites). Therefore, if native species are required at particular points in invertebrate life cycles (e.g. reproduction), population declines associated with their absence may not have been detected as invertebrate species could move between plant beds if necessary. Additionally, many Northern Irish water bodies, such as those sampled here, have been subject to considerable pressure from eutrophication, pollution and human disturbance, especially in lowland areas (Heegaard et al. 2001) prior to the introduction of invasive species, such as *E. nuttallii*. The algal and invertebrate communities present in these waterbodies differ from those in more pristine sites, especially in the relative lack of rare species. Impacts of invasive macrophytes may also differ depending on trophic status of waterbodies (Strayer 2010) and in some cases the same invasive macrophyte species has opposite effects on invertebrates in different study systems (Schultz and Dibble 2012). Therefore, it is possible that the impact of *E. nuttallii* on invertebrate and algal communities would have been different in oligotrophic sites or more pristine sites which had not been previously impacted by anthropogenic pressures.

Together these field studies provide insights into the potential impacts of the widespread invader *E. nuttallii* on a range of taxa in temperate waterbodies. Due to the correlational nature of these studies it is not

possible to determine cause-and-effect, or to reveal the exact drivers of change in biological communities. Here, where possible, we have used closely paired sites within waterbodies to minimise potentially confounding differences between sites. We suggest that the results of this research may be used to direct further research including both field and laboratory experiments focused on the interaction of *E. nuttallii* with particular species of concern (e.g. the observed negative association of *E. nuttallii* and charophytes).

In conclusion, our findings suggest that whilst *E. nuttallii* significantly altered freshwater communities, observed differences were small relative to other factors such as nutrient levels, inter-annual variation and differences between sites. In addition, we add to a growing body of literature that suggests that the impacts of aquatic invasive plant species are not consistently negative and they may, for example, increase the richness of native plant species or the abundance of invertebrate species if total plant biomass increases as a result of invasion (Schultz and Dibble 2012; Strayer 2010; Thomaz et al. 2012).

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