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

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

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15 **Running title:** Impacts of *Elodea nuttallii*

16

17 **Abstract**

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

36

37 **Introduction**

38 Freshwater systems have been shown to be at particularly high risk from biological invasions
39 (Sala et al. 2000) and invasive aquatic plants are widely considered to be a major threat to
40 both species diversity and ecosystem functioning (Strayer 2010). The assessment of potential
41 impacts of invasive species on ecosystems is essential to the prioritisation of resources
42 (Leung et al. 2012), and traits associated with successful naturalisation cannot be reliably
43 used to infer potential impact (Hulme 2012). Despite this, in Europe there is a lack of studies
44 directly assessing the impacts of aquatic species on natural ecosystems across trophic levels
45 (Caffrey et al. 2014).

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

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

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

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

85 *E. nuttallii* was first introduced to Europe in 1939 and has spread rapidly, replacing the
86 ecologically similar *E. canadensis* in many locations (Thiébaud et al. 2008). *E. canadensis* is
87 considered to be one of the ‘100 worst’ invasive species in Europe (DAISIE, 2015) and has
88 impacts on macrophyte communities and aquatic food webs (e.g. deWinton, Clayton 1996;
89 Kelly, Hawes 2005; Kornijow et al. 2005). *E. nuttallii* and *E. canadensis* are so similar that
90 they may be ecologically and functionally redundant (Hérault et al. 2008), in which case
91 their distribution and impacts could be expected to be similar. Both *E. canadensis* and *E.*
92 *nuttallii* have high photosynthetic rates, show strong effects on pH, dissolved oxygen and
93 CO₂ levels within plant stands (James et al. 1999) and may play an important role in
94 phosphorus cycling in eutrophic systems (Angelstein, Schubert 2008). Field evidence
95 suggests that *E. nuttallii* is replacing *E. canadensis* (Barrat-Segretain et al. 2001; Barrat-
96 Segretain, 2002) and laboratory experiments have shown that *E. nuttallii* is more competitive
97 than *E. canadensis* (Barrat-Segretain 2005). Hence, the impacts of *E. nuttallii* could be more
98 severe than those of *E. canadensis*.

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

108 Here, we describe two correlational studies which provide insights into the potential
109 impacts of *Elodea*. Firstly, we used historical data on the macrophyte communities in two

110 large lakes over the course of an invasion to examine the impact of *E. nuttallii* on other
111 macrophyte species, and to examine interactions between *E. nuttallii* and *E. canadensis*.
112 Secondly, we used a paired survey design to examine differences in micro-algae and
113 invertebrates associated with native macrophytes and invasive *E. nuttallii* within six
114 waterbodies. We used a combination of standard community metrics (e.g. biomass and
115 species richness) and multivariate analysis of communities, both in terms of taxonomic
116 groups and broader functional or structural groups, to examine impacts at different trophic
117 levels.

118

119 **Methods**

120 *Macrophyte study sites*

121 Lough Erne in County Fermanagh, Northern Ireland, comprises Upper Lough Erne (*ca.* 29
122 km²) and Lower Lough Erne (*ca.* 104 km²). Lough Erne is a naturally eutrophic lake system
123 with high alkalinity due to the underlying geology of the area. Upper Lough Erne is the
124 shallower of the two lakes with a mean depth of 2.9 m; Lower Lough Erne has a mean depth
125 of 11.9 m. Over the period of this study pH in these lakes ranged from 6.2 to 9.3, total
126 phosphorus from 10 µg l⁻¹ to 780 µg l⁻¹ and nitrates from 20 µg l⁻¹ to 1,080 µg l⁻¹ (data
127 provided by Northern Ireland Environment Agency (NIEA), based on monthly measurements
128 at ten monitoring points from 2006-2010). Lough Erne is notable for its conservation value,
129 being designated as a Special Area of Conservation (SAC) and Ramsar site and containing
130 many Irish Red Data List species, including the pointed stonewort (*Nitella mucronata*) and
131 aquatic invertebrates such as the pond skater (*Limnoporus rufoscutellatus*), water beetles
132 (*Donacia aquatica*, *D. bicolora*, *Gyrinus distinctus*, *G. natator* and *Hydroporus*
133 *glabriusculus*) and white-clawed crayfish (*Austropotamius pallipes*). *E. nuttallii* was first
134 recorded in Lough Erne in 2006.

135

136 *Field and laboratory methods*

137 Data on macrophyte community composition were obtained for both Upper and Lower Lough
138 Erne from the Water Management Unit (WMU), NIEA. These data represent a total of 15
139 transects in Upper Lough Erne during 2007 and 2010 and 18 transects in Lower Lough Erne
140 during 2006 and 2009. Surveys were carried out by wading and by boat depending on water
141 depth. Macrophyte species and percentage cover were recorded within 5 m² quadrats
142 positioned every 5 m along each transect perpendicular to the shoreline until the edge of the
143 macrophyte zone was reached. Nitrogen and phosphorus (NO₃N, NO₂N, NH₄N, Total
144 Organic Nitrogen, soluble P, and Total P) were measured in surface waters in late July or
145 August for each survey year at a central point in Upper Lough Erne and two points in Lower
146 Lough Erne (Fig 1). These chemistry data are included to account for differences between
147 lakes and over time, rather than smaller scale differences between transects. Unfortunately, it
148 was not possible to obtain more detailed information on water chemistry due to the historical
149 nature of the dataset. We have also accounted for this issue by using a paired statistical design
150 which means that we are not comparing quadrats from different parts of the lakes. Only
151 quadrats which were surveyed in both years were used in the analysis ($n = 728$ quadrats).

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

156

157 *Dissolved oxygen, pH, algae and invertebrate study sites*

158 A paired survey design of six sites in Northern Ireland was used to examine the associations
159 between *E. nuttallii*, dissolved oxygen, pH, and algal and invertebrate communities, between

160 July and September 2010 (Fig 2.). At each site a native macrophyte stand and a stand of the
161 invader were chosen within the same water body (distance between macrophyte stands <500
162 m). Native species differed between sites, but all had a predominantly submerged habit.
163 Native species and sites were as follows: *Potamogeton pectinatus* (Lagan), *Potamogeton*
164 *perfoliatus/Myriophyllum spicatum* (Ballyronan), *Potamogeton natans* (Lough Cashel),
165 *Ceratophyllum demersum* (Loughbrickland and Upper Bann), *Sagittaria sagittifolia* (Lower
166 Bann). Waterbodies were selected to represent the most common site conditions in which
167 *Elodea nuttallii* was found and included three lake sites and three slow-flowing river sites.
168 All samples were taken in shallow water between 0.45 m and 1.05 m in depth. There was no
169 consistent pattern as to whether *E. nuttallii* or native plants occurred in deeper water (the
170 mean difference in depth between *E. nuttallii* and native plants within sites was 14 cm). Sites
171 covered a range of nutrient levels from mesotrophic to hypereutrophic (measured total
172 phosphorus ranging from 18 $\mu\text{g l}^{-1}$ to 1,168 $\mu\text{g l}^{-1}$ and total dissolved nitrogen between 4.61
173 $\mu\text{g l}^{-1}$ and 530 $\mu\text{g l}^{-1}$).

174

175 *Field and laboratory methods*

176 Water chemistry, environmental data and algal sampling took place monthly for 3 months
177 from July to September 2010. The pH and dissolved oxygen were recorded at each site using
178 a Hanna pHep 4 pH meter and a portable dissolved oxygen meter (VWR DO200). Two litres
179 of water was collected within each macrophyte bed for chlorophyll *a* analysis, filtered using a
180 0.45 μm Metrical® membrane filter and stored at -20°C. Chlorophyll *a* analysis was
181 conducted using methanol-based pigment extraction and spectrophotometry readings
182 (Hamilton, 2010). A further two litres of water was collected for nutrient analyses: soluble
183 reactive phosphorus (SRP), total phosphorus (TP), total soluble phosphorus (TSP), total
184 organic nitrogen (TON), ammonium (NH_4), nitrogen dioxide (NO_2), nitrates (NO_3) and total

185 dissolved nitrogen (TDN). Nutrient analyses were conducted by the Agri-Food and
186 Biosciences Institute, Newforge Lane, Belfast, Northern Ireland.

187 Algal periphyton was collected by taking approximately 10 cm length of plant material
188 from both the tip and the base of the macrophyte with approximately 15 ml of water
189 immediately surrounding the macrophyte leaves. Care was taken to carry out this procedure
190 slowly and carefully *in situ* to minimise loss of periphyton. Water samples were filtered
191 through a 250 µm mesh within 10 minutes of sampling to remove zooplankton and preserved
192 using Lugol's Iodine solution (5 g iodine (I₂), 10 g potassium iodide (KI), 85 ml distilled
193 H₂O). One algal sample was taken in each invaded and each uninvaded macrophyte bed in
194 each of July, August and September. Algal samples were kept in the dark at 5-7 °C before
195 processing.

196 Algal periphyton was separated from plant samples by vigorous shaking for 60 seconds.
197 The algal sample was then transferred into a sterile 20 ml tube. Plant material was dried at
198 60°C for 72 hrs and the dry mass was recorded. The algal sample was placed in a Lund
199 chamber. Five horizontal transects of the chamber were carried out at x100 magnification
200 and larger species were identified and counted. A further 20 random fields of view (450 µm²)
201 were examined at x400 magnification and all species were identified and counted. Taxa were
202 identified to genus level where possible, or to the lowest practical taxonomic level
203 (Bellinger, Sigee 2010; Cox 1996; John et al. 2002). It was not possible to accurately identify
204 all cells under 10 µm; those which could not be identified were measured for biovolume and
205 recorded as "unidentified genera" (1.9% of total algal biovolume). For unicellular and
206 colonial algae, the first 10 cells or colonies of each genus or species were measured. For
207 filamentous algae, the first 30 filaments were measured as there was greater variation
208 observed in filament length than in cell or colony size. Mean cell biovolumes were calculated

209 using the 'WISER phytoplankton counter spreadsheet' (Carvalho et al. 2007) and biovolume
210 formulae were added for new taxa as defined in Hillebrand et al. (1999).

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

216 Invertebrates were sampled during July and late September/early October using two
217 methods at each sampling date. Firstly, at each site, four replicate core samples of sediment
218 were taken from each macrophyte bed using a KC Denmark Kayak core sampler 45 mm in
219 diameter (hereafter, referred to as 'sediment invertebrate samples'). Secondly, invertebrates
220 present in macrophyte material were collected using a bespoke bucket and mesh trap of 379
221 cm² surface area and 300 µm mesh size (hereafter, referred to as 'macrophyte invertebrate
222 samples').

223 Invertebrates were separated from samples using a 250 µm sieve and stored in 70%
224 ethanol. Plant material was dried at 60° C for 72 hrs and its dry mass recorded for calculation
225 of macrophyte stand density. All invertebrates were identified to the lowest possible
226 taxonomic level (Edington, Hildrew 1995; Elliott, Mann 1998; Fitter, Manuel 1986; Friday
227 1998; Gledhill et al. 1993; Savage 1989; Wallace et al. 1990). For sediment invertebrate
228 samples, specimen length, width and dry mass were measured ($n = 523$). Linear regressions
229 based on the length or width and biomass (transformed by Log₁₀ or a natural logarithm
230 depending on best fit described by the adjusted R² value) were conducted using SigmaPlot 10
231 to describe the relationship between individual length/width and biomass for each common
232 invertebrate family or genus (Supplementary Material, Table S2). In taxa that exhibited a
233 significant relationship between length/width and body mass these regression formulae were

234 used to calculate the biomass of individuals of that taxa in the macrophyte invertebrate
235 samples. For all other species dry mass was measured directly. Invertebrate species were
236 further categorised into six functional feeding guilds: collector filterers, collector gatherers,
237 herbivore piercers, predators, scraper grazers and shredders following (Chaloner et al. 2009;
238 Compin, Cereghino 2007; Cummins, Klug 1979; Heino 2008) (Supplementary Material,
239 Table S3).

240

241 **Statistical analyses**

242

243 *Macrophytes*

244 In Lough Erne, the impact of *Elodea* spp. on total macrophyte cover, non-*Elodea*
245 macrophyte cover and species richness (i.e. native plants) was examined using a Generalized
246 Linear Mixed Model (GLMM) approach. Explanatory variables in the models were Year
247 (fitted as a factor with four levels: 2006, 2007, 2009 or 2010), water depth and nutrient
248 concentration, the percentage cover of *E. nuttallii*, the percentage cover of *E. canadensis*,
249 and the interaction of *E. nuttallii* and *E. canadensis*. Nutrient concentration was expressed as
250 the first axis of a PCA analysis of nitrogen and phosphorus values, which explained 62.7 %
251 of the variance with a positive relationship with nitrogen variables ($r = 0.95$) and a negative
252 relationship with phosphorus variables ($r = -0.67$). Quadrat nested within lake was included
253 as a random factor.

254 All GLMMs were first fitted with a Gaussian distribution and identity link function.
255 Model residuals were tested for normality using a Shapiro-Wilk test. Models for which
256 residuals were not normally distributed were refitted using alternative distributions more
257 suited to the response data. Specifically, gamma distributions with a log-link function were
258 used for continuous response data and a Poisson distribution with a log link function was

259 used for count data (i.e. species richness). In each GLMM, all possible subsets of
260 explanatory variables were ranked using the Akaike Information Criterion adjusted for small
261 sample sizes (AICc), and the most optimal model was taken as that with the lowest AICc
262 value.

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

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

282

283

284 *Dissolved oxygen, pH, algae and invertebrates*

285 GLMMs were used to examine all univariate dependent variables in relation to the presence
286 of *E. nuttallii*. Water chemistry response variables (dissolved O₂ saturation, pH and
287 chlorophyll *a*) were tested for correlation prior to GLMM analysis using Spearman's rank
288 correlation test. There was no significant correlation between these variables (dissolved O₂ –
289 chlorophyll *a* ($\rho = 0.168$, $P = 0.327$), dissolved O₂ – pH ($\rho = 0.286$, $P = 0.091$) and
290 chlorophyll *a* and pH ($\rho = 0.086$, $P = 0.617$). Explanatory variables for these
291 physiochemical variables were the presence or absence of *E. nuttallii* and month (July,
292 August or September), waterbody type (i.e. two level factor “Lake” or “River”) and the
293 interaction between *E. nuttallii* presence and waterbody type. Site was fitted as a random
294 factor.

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

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

306 Multivariate community responses were assessed using pCCA. Response matrices for
307 algae were biovolume of each algal functional group and biovolume of each algal taxon (per
308 unit of plant dry mass). Response matrices for invertebrate species were the biomass of

309 invertebrate feeding guilds and biomass of invertebrate taxa. The associated explanatory
310 environmental matrix included the same factors and covariates as those used in univariate
311 analyses i.e., the presence/absence of *E. nuttallii*, month and nutrient concentrations,
312 waterbody type and the interaction between *E. nuttallii* presence and waterbody type, with
313 the addition of plant density in invertebrate models only. Site was fitted as a random factor.
314 Model optimisation was conducted as previously described for pCCAs of macrophyte
315 communities.

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

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

323

324 **Results**

325

326 *Macrophytes*

327 *Elodea nuttallii* was present in 2% of the 728 quadrats in the initial survey in 2006-07 and
328 increased to presence in 70% of quadrats in 2009-10. Over the same period, the percentage
329 cover of *E. nuttallii* within each quadrat increased from a mean of 0.03% (0-4%) to 21.3%
330 (0-100%) on resurvey in 2009-10. *E. canadensis* declined in presence from 33% to 9% of
331 quadrats and in mean cover per quadrat from 1.1% (0%-70%) to 0.5% (0%-30%) over the
332 same period. A total of 71 other macrophyte species was recorded. *E. canadensis* and *E.*
333 *nuttallii* were the only invasive species recorded in these surveys.

334 Total macrophyte cover within quadrats was positively associated with cover of both *E.*
335 *nuttallii* ($\beta = 0.013 \pm 0.003$, $\chi^2 = 20.24$, $P < 0.001$) and *E. canadensis* ($\beta = 0.029 \pm 0.012$, χ^2
336 $= 5.53$, $P = 0.019$). Excluding both *Elodea* species from the total macrophyte cover, the
337 cover of remaining species was not significantly associated with the cover of either *E.*
338 *nuttallii* or *E. canadensis*, but declined with water depth and differed between years. Both
339 total macrophyte cover and the cover of non-*Elodea* species were negatively associated with
340 water depth, the PCA axis of nutrient concentration and differed between years (see
341 Supplementary Material, Table S5).

342 Species richness of macrophytes other than *E. nuttallii* and *E. canadensis* (i.e. native
343 species) was positively associated with percentage cover of both *E. nuttallii* ($\beta = 0.002 \pm$
344 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
345 with the PCA axis of nutrient concentrations and negatively associated with water depth and
346 differed between years (see Supplementary Material, Table S5). There was no evidence of an
347 interaction between *E. canadensis* and *E. nuttallii* in any model.

348 The pCCA of macrophyte structural groups showed that year and percentage cover of *E.*
349 *nuttallii* influenced structural composition and explained 4.6% of the variation in plant
350 structure after variation between quadrats (69%) was accounted for ($P < 0.005$; Fig. 3). The
351 pCCA of macrophyte genera showed that water depth, year and percentage cover of *E.*
352 *nuttallii* influenced composition of genera significantly and explained 3.9% of the variation
353 after between-quadrat variation (53.9%) was accounted for ($P < 0.005$). The percentage cover
354 of *E. nuttallii* alone (with the other factors accounted for by pCCA) explained only 0.6% and
355 0.5% of the variation in structural groups and genera respectively ($P < 0.033$ and $P < 0.005$
356 respectively; Supplementary Material, Table S6). The cover of submersed low-growing
357 species and charophytes was negatively associated with the cover of *E. nuttallii*, whilst the
358 surface-growing plants (both free-floating and rooted) were positively associated with *E.*

359 *nutallii* (Table 1). At a taxonomic level, the most negatively affected species was *E.*
360 *canadensis* whilst *Nuphar lutea* and *Stratiotes aloides* were most positively associated (Table
361 2). However, variance in plant community explained by *E. nutallii* was very low relative to
362 variance between quadrats and between years (Tables 1, 2).

363 Analysis of multivariate homogeneity of group dispersion showed that quadrats
364 containing *E. nutallii* were more homogeneous (mean Jaccard dissimilarity = 0.43, s.e. <
365 0.01) than those that did not contain *E. nutallii* (mean Jaccard dissimilarity = 0.49, s.e. <
366 0.01) ($F = 24.34, P < 0.001$).

367

368 *Dissolved oxygen, pH, algae and invertebrates*

369 Dissolved O₂ saturation differed between lakes and rivers being higher in lakes than in rivers.
370 The presence of *E. nutallii* was included in the best model of dissolved O₂ saturation ($\chi^2 =$
371 3.21, $P = 0.073$), being higher in *E. nutallii* stands (mean \pm s.e. = 93.97% \pm 5.46) than in
372 native plant stands (85.13% \pm 3.86). Chlorophyll *a* showed no significant association with
373 rivers or lakes, months or the presence of *E. nutallii*. The pH varied significantly between
374 months, but was not significantly associated with the presence of *E. nutallii* (Supplementary
375 Material, Table S7).

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

382 The pCCA of algal community data showed no significant effect of *E. nutallii* on algal
383 community composition in terms of either functional groups or taxa. The community

384 composition in terms of algal functional groups was not significantly associated with any of
385 the explanatory variables tested. However, nutrient concentration and month significantly
386 affected community composition in terms of algal taxa ($P = 0.015$). Analysis of multivariate
387 homogeneity of group dispersion did not show any significant difference in the variance
388 between algal communities on *E. nuttallii* and those on native plants ($F = 0.42$, $P = 0.521$).

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

397 The pCCAs of invertebrate taxonomic communities sampled from macrophytes showed a
398 significant effect of the interaction of waterbody type and the presence of *E. nuttallii*,
399 suggesting that the impact of *E. nuttallii* on invertebrate communities differed between lakes
400 and rivers. This interaction explained 10% of the variation in invertebrate communities ($P =$
401 0.043) after variation between sites (45%) was accounted for ($P = 0.005$). When rivers and
402 lakes were examined separately, *E. nuttallii* was found to explain 9% of variation in
403 invertebrate communities in lakes and 13% of the variation in rivers, after accounting for
404 variation between sites (41% and 33% respectively; Tables 3 & 4, Fig. 3). The pCCAs of
405 invertebrate functional groups from the macrophyte invertebrate samples and the pCCAs of
406 invertebrate community in sediment core samples showed no association with any of the
407 tested variables after accounting for variation between sites (Supplementary Material, Table
408 S10). In addition, analysis of multivariate homogeneity of group dispersion did not show any

409 significant difference in the variance between invertebrate communities associated with *E.*
410 *nuttallii* stands and those associated with native plant stands in either macrophyte ($F = 0.15$,
411 $P = 0.702$) or sediment samples ($F = 1.92$, $P = 0.179$).

412

413 **Discussion**

414

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

425 The effects of *E. nuttallii* on species communities could be seen as both positive and
426 negative, for example, the increased species richness of macrophyte species may be
427 contrasted with the lower richness of algal taxa. Increases in floating plants associated with
428 *E. nuttallii* can be contrasted with declines in submerged species. The association between
429 floating plant species and *E. nuttallii* may arise as a result of structural complexity where *E.*
430 *nuttallii* reaches the water surface, which reduces surface turbidity and provides anchorage
431 for floating species. In addition, floating species are most likely to out-compete *E. nuttallii*
432 for light and have been shown to out-compete *E. nuttallii* in high nutrient conditions (Netten
433 et al. 2010; Szabo et al. 2010). Submerged species which are negatively associated include

434 low-growing species which are likely to be shaded by *E. nuttallii* (such as *Eleocharis*
435 *acicularis*, *Isoetes* spp., *Littorella uniflora*), canopy-forming submerged species occupying a
436 similar niche space to *E. nuttallii* (including *E. canadensis*) and charophyte species.

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

444 The observed negative association between the cover of *E. nuttallii* and *E. canadensis*
445 suggests a competitive interaction between these two closely related invasive species. We did
446 not find any indication that *E. nuttallii* or *E. canadensis* interact to increase impacts on native
447 macrophyte cover or richness. Therefore, our findings do not support the invasion meltdown
448 hypothesis in the case of *E. nuttallii* and *E. canadensis*. In addition, the observed rapid
449 increase range and abundance of *E. nuttallii* in Lough Erne (such that it is much now much
450 more frequently observed than *E. canadensis*), supports the suggestion that *E. nuttallii* may
451 be replacing *E. canadensis* in parts of its invaded range (Barrat-Segretain et al. 2001; Barrat-
452 Segretain, 2002).

453 It is perhaps surprising that species richness of native macrophytes was positively
454 associated with the presence of *E. nuttallii* and *E. canadensis* in Lough Erne, after differences
455 in nutrient levels and between years had been accounted for. Mechanisms for facilitation of
456 native plant species could include alteration of flow rate and turbidity, or increases in primary
457 productivity over time through the release of nutrients from the sediment. However, these
458 alterations could also make conditions suitable for further establishment of *E. nuttallii*, which

459 can absorb nutrients directly from the water column and is adapted to low-light conditions
460 (Angelstein, Schubert 2008, 2009). An alternative explanation for the positive correlation
461 between *E. nuttallii* and species richness of native macrophytes is that some other
462 environmental factor, unaccounted for here, facilitates both an increase in *E. nuttallii* cover/or
463 its establishment and macrophyte species richness. Previous studies have suggested that while
464 species richness increases resistance to invasion at small spatial scales (Kennedy et al. 2002),
465 such effects may be overwhelmed by environmental factors which co-vary with species
466 richness, such as propagule pressure, resulting in an apparent positive relationship between
467 invasive species and native species richness (Levine 2000; Lonsdale 1999). Furthermore, a
468 recent large-scale study of invasive species in macrophyte communities found no clear
469 relationship between native species richness and exotic species richness (Capers et al. 2007).

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

480 Differences in invertebrate assemblages associated with macrophytes have also been
481 shown previously for similar submerged invasive species (Hogsden et al. 2007; Kelly, Hawes
482 2005; Stiers et al. 2011). The reasons for the observed differences in invertebrate species
483 composition may be varied and complex, and are likely to relate to differences in plant

484 architecture, plant palatability, chemical exudates, water chemistry and water flow rates.
485 Oxygen saturation is an important factor in determining invertebrate communities in
486 freshwater environments. Higher oxygen saturation levels associated with *E. nuttallii* may
487 have influenced species composition here: there was a lower abundance of some species
488 groups associated with low oxygen saturation levels such as true fly larvae in the family
489 Chironomidae, Alderflies (*Sialis lutaria*), leeches in the genera *Erpobdella* and *Theromyzon*,
490 and *Asellus* amphipods, and a higher abundance of some species associated with higher
491 oxygen saturation such as caddisflies in the family Linephiidae. However, several species
492 behaved contrary to expectation based on oxygen saturation alone, suggesting that other
493 factors influence their distributions, for example damselflies in the family Coengriidae were
494 negatively associated with *E. nuttallii*, leeches in the family Glossiphonidae were positively
495 associated with *E. nuttallii*, and freshwater snails in the genera *Hippeautis*, *Lymnea*, *Valvata*,
496 *Physa* and *Bithynia*, which have similar oxygen requirements, show a range of different
497 responses. Allelopathy may explain observed negative association between *E. nuttallii* and
498 lepidopteran larvae in the family Pyralidae, as *E. nuttallii* has been previously shown to retard
499 the growth and reduce the survival of the Pyralidae species *Acentria ephemerella* under
500 laboratory conditions (Erhard et al. 2007). Where Pyralidae larvae exist in large numbers they
501 may substantially reduce cover of other macrophyte species providing an indirect advantage
502 to *Elodea* spp. (Gross et al. 2001).

503 One weakness of the pairing of native and invasive plant beds in this study was that it was
504 not possible to use sites where only *E. nuttallii* was present (i.e. highly invaded sites).
505 Therefore, if native species are required at particular points in invertebrate life cycles (e.g.
506 reproduction), population declines associated with their absence may not have been detected
507 as invertebrate species could move between plant beds if necessary. Additionally, many
508 Northern Irish water bodies, such as those sampled here, have been subject to considerable

509 pressure from eutrophication, pollution and human disturbance, especially in lowland areas
510 (Heegaard et al. 2001) prior to the introduction of invasive species, such as *E. nuttallii*. The
511 algal and invertebrate communities present in these waterbodies differ from those in more
512 pristine sites, especially in the relative lack of rare species. Impacts of invasive macrophytes
513 may also differ depending on trophic status of waterbodies (Strayer 2010) and in some cases
514 the same invasive macrophyte species has opposite effects on invertebrates in different study
515 systems (Schultz, Dibble 2012). Therefore, it is possible that the impact of *E. nuttallii* on
516 invertebrate and algal communities would have been different in oligotrophic sites or more
517 pristine sites which had not been previously impacted by anthropogenic pressures.

518 Together these field studies provide insights into the potential impacts of the widespread
519 invader *Elodea nuttallii* on a range of taxa in temperate waterbodies. Due to the correlational
520 nature of these studies it is not possible to determine cause-and-effect or to reveal the exact
521 drivers of change in biological communities. Here, where possible we have used closely
522 paired sites within waterbodies to minimise potentially confounding differences between
523 sites. We suggest that the results of this research may be used to direct further research
524 including both field and laboratory experiments focused on the interaction of *E. nuttallii* with
525 particular species of concern (e.g. the observed negative association of *E. nuttallii* and
526 charophytes).

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

534

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544

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784 **Tables**

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

790

	CCA scores against only <i>Elodea nuttallii</i>	Variance explained by <i>Elodea nuttallii</i> (%)	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

791

792 **Table 2.** Results of partial Canonical Correspondence Analysis (pCCA) for the genera most
 793 strongly associated with *Elodea nuttallii*. Genera with greater than 0.5% of variation
 794 explained by *Elodea nuttallii* are shown. Table shows species from each genus present in the
 795 dataset, species scores when *Elodea nuttallii* is fitted as the explanatory variable and depth,
 796 quadrat location and year are accounted for by partial CCA, variance explained by percentage
 797 cover of *Elodea nuttallii*, variance explained by depth and year, and the variance explained
 798 by the full model.

799

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

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

800 **Table 3.** Results of partial Canonical Correspondence Analysis (pCCA) of invertebrate taxa
 801 living on macrophytes in lakes. Taxonomic groups which were present in more than one
 802 sample and for which > 0.5% of variation is explained by *Elodea nuttallii* are shown. Table
 803 details taxa scores when *Elodea nuttallii* is fitted as the explanatory variable, variance
 804 explained by percentage cover of *Elodea nuttallii*, and the variance explained by the full
 805 model.

806

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

* within the class Gastropoda, superfamily is given instead of Order as Orders are not defined for these taxa

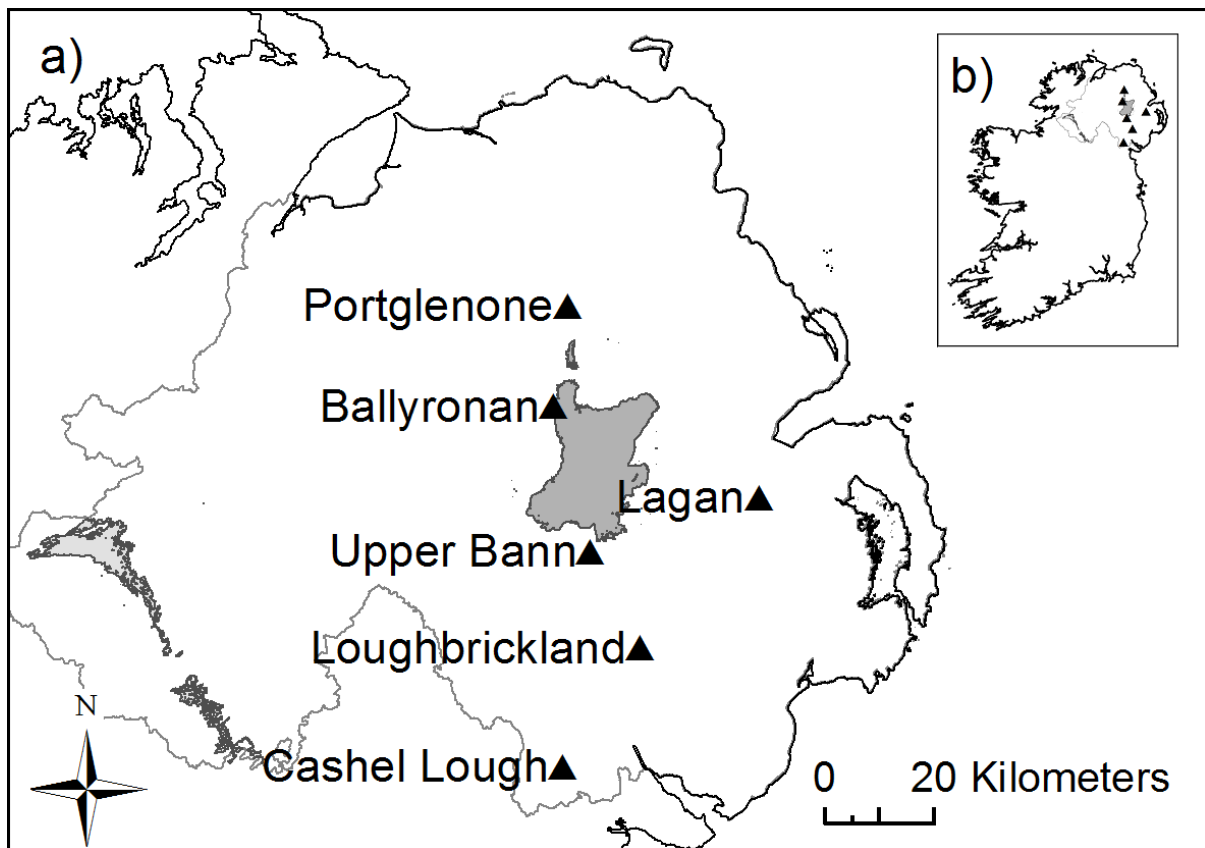
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809 **Table 4.** Results of partial Canonical Correspondence Analysis (pCCA) of invertebrate taxa
 810 living on macrophytes in rivers. Taxonomic groups which were present in more than one
 811 sample and for which > 0.5% of variation is explained by *Elodea nuttallii* are shown. Table
 812 details taxa scores when *Elodea nuttallii* is fitted as the explanatory variable, variance
 813 explained by percentage cover of *Elodea nuttallii*, and the variance explained by the full
 814 model.
 815

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

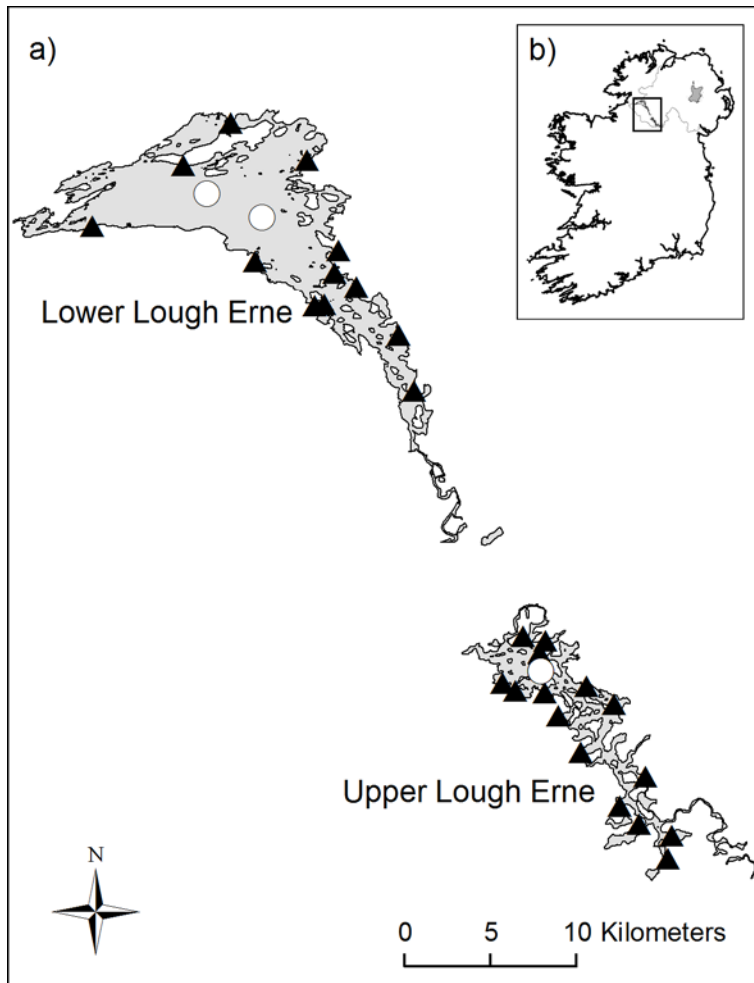
* within the class Gastropoda, superfamily is given instead of Order as Order is not defined for these taxa



818

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

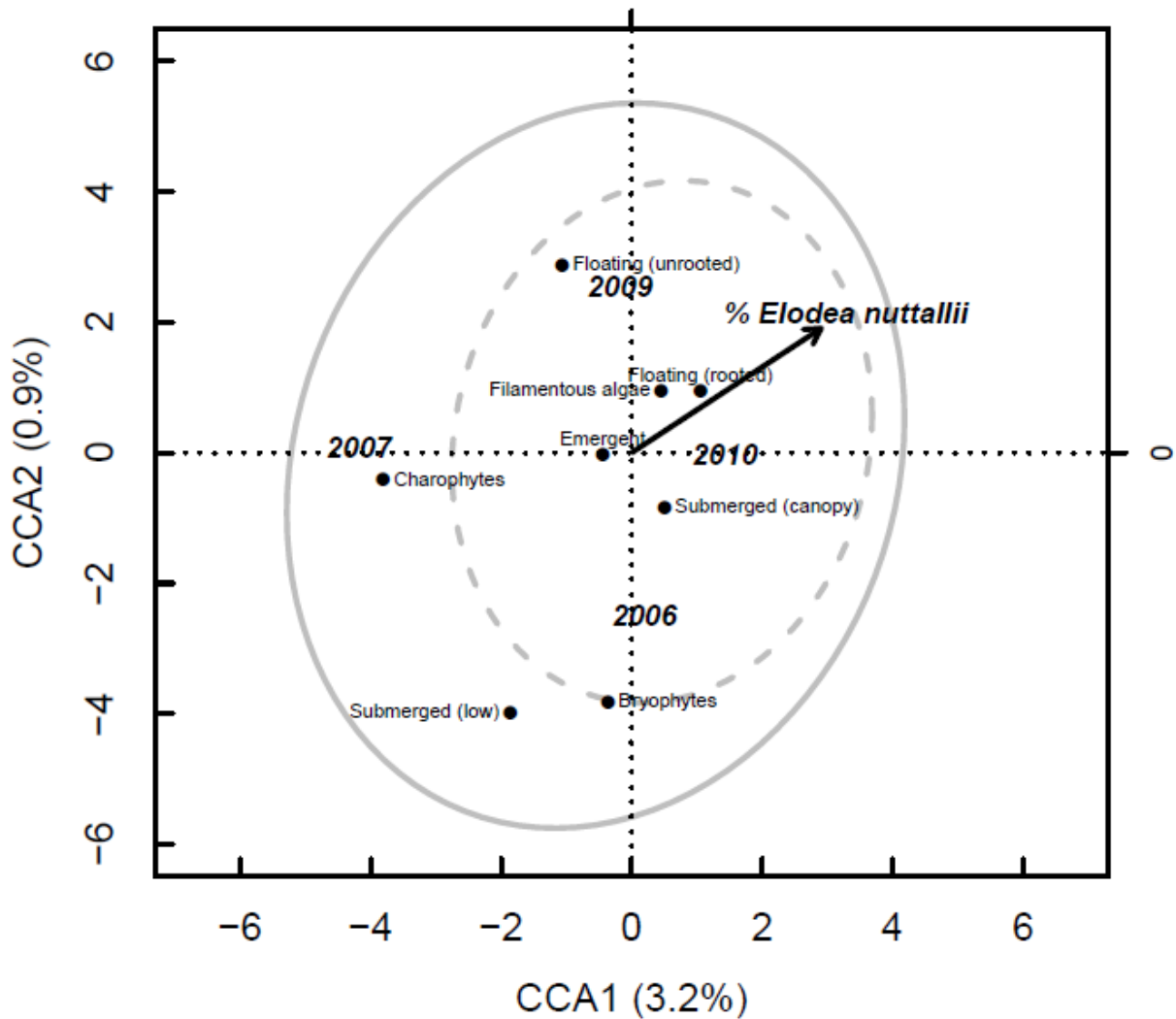
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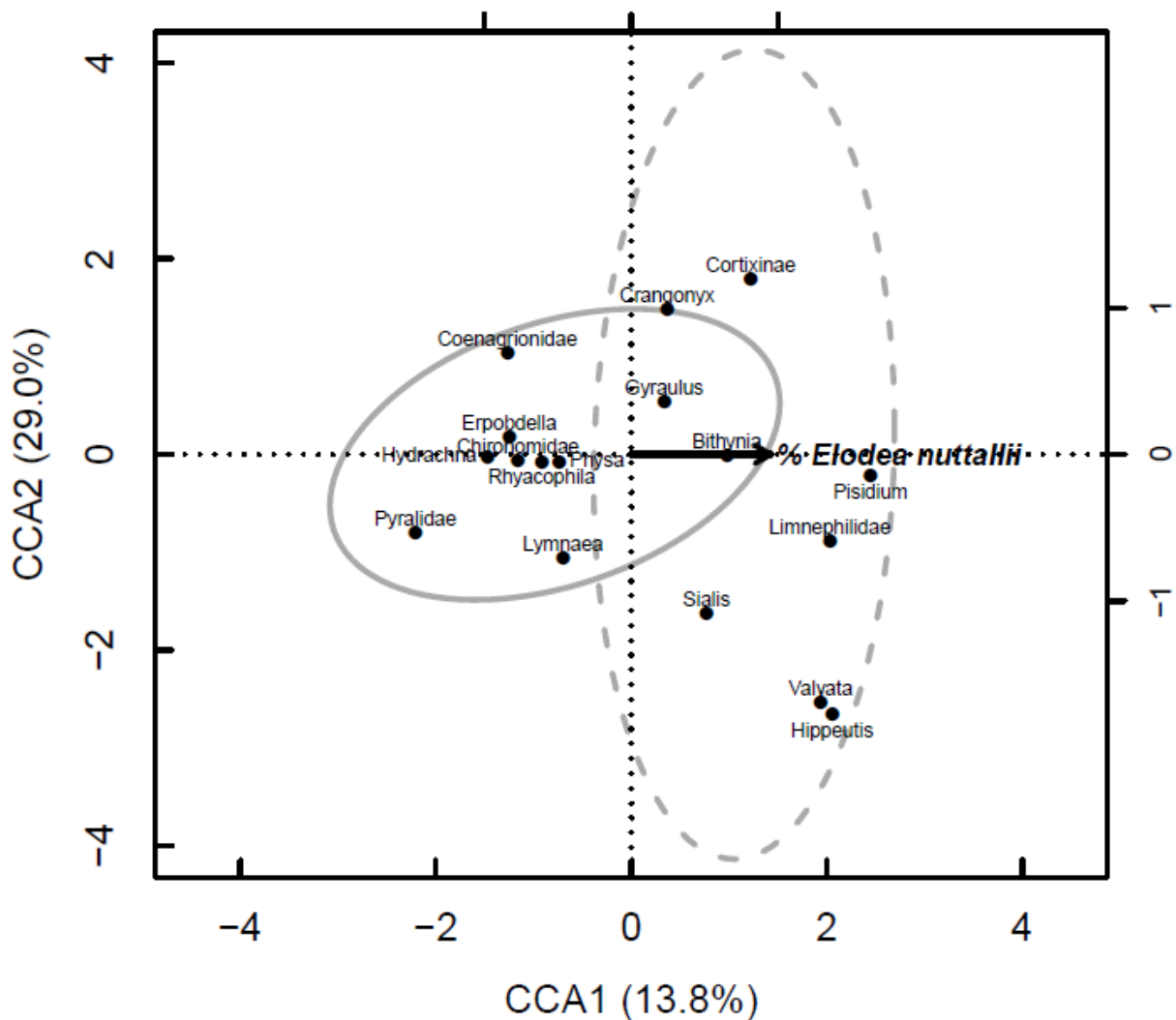
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826 **Fig. 2** a) Study sites for macrophytes in Lough Erne. Black triangles show the locations of
827 survey transects. White circles show locations where water chemistry parameters were
828 measured, b) inset map of Ireland showing location of Lough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



829

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



836

837 **Fig. 4** Plot of partial Canonical Correspondence Analysis showing relationships between

838 *Elodea nuttallii* and invertebrate taxa in lakes, when site is accounted for as a random factor.

839 Species scores are unscaled. Taxonomic groups which were present in more than one sample

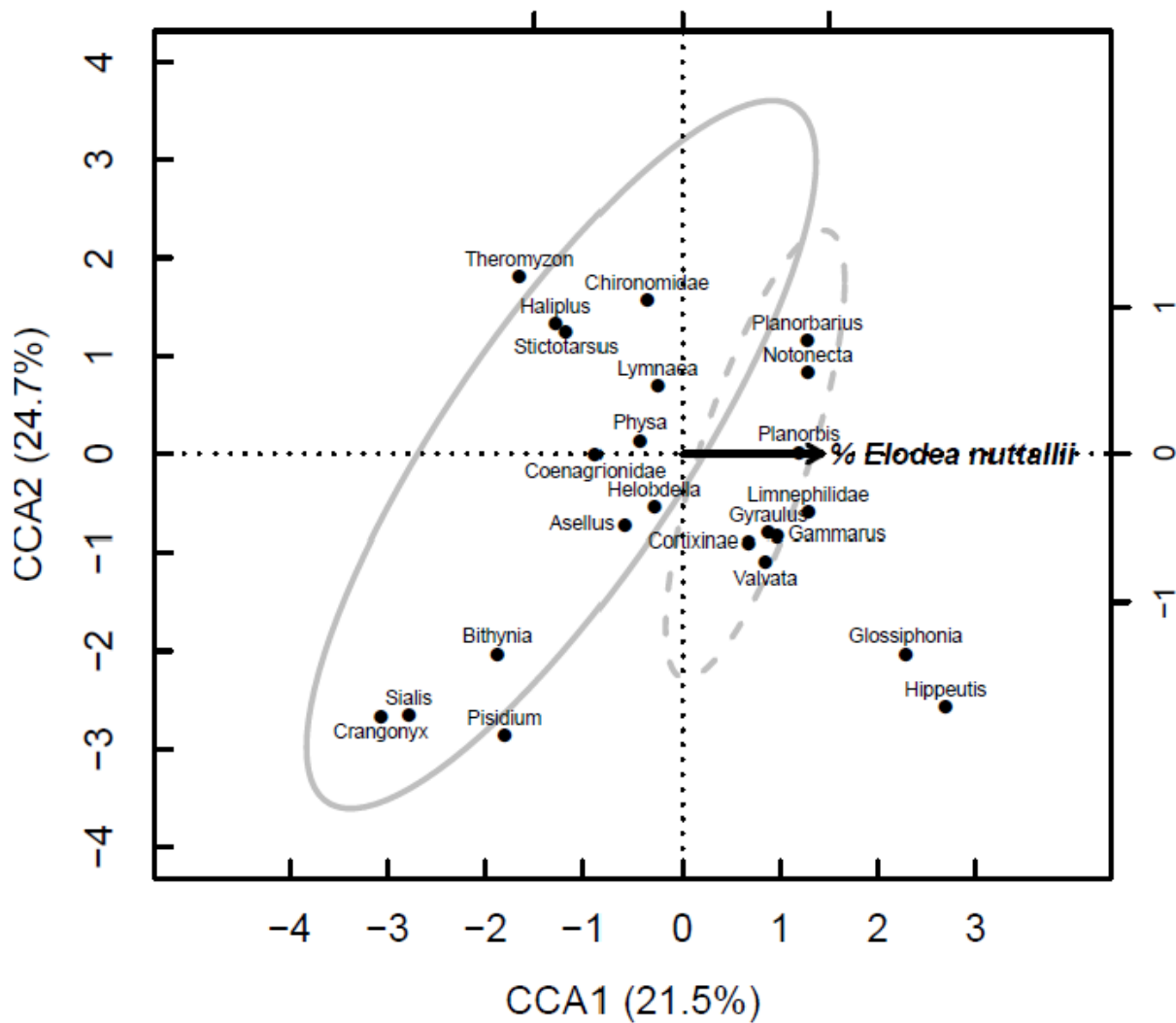
840 and for which > 0.5% of variation is explained by *Elodea nuttallii* are shown. Axis labels

841 show % of total variation in macrophyte communities explained by each CCA axis. Grey

842 ellipse shows 95% confidence interval around sites where *Elodea nuttallii* is present, dashed

843 grey ellipse shows 95% confidence interval around sites where *Elodea nuttallii* is not present.

844



845
 846 **Fig. 5** Plot of partial Canonical Correspondence Analysis showing relationships between
 847 *Elodea nuttallii* and invertebrate taxa in rivers, when site is accounted for as a random factor.
 848 Species scores are unscaled. Taxonomic groups which were present in more than one sample
 849 and for which > 0.5% of variation is explained by *Elodea nuttallii* are shown. Axis labels
 850 show % of total variation in macrophyte communities explained by each CCA axis. Grey
 851 ellipse shows 95% confidence interval around sites where *Elodea nuttallii* is present, dashed
 852 grey ellipse shows 95% confidence interval around sites where *Elodea nuttallii* is not present.
 853

854 **Supplementary material**

855

856 **Table S1** Algal functional groups used

857 **Table S2** Invertebrate biomass regression models

858 **Table S3** Invertebrate feeding guilds

859 **Table S4** Macrophyte structural groups

860 **Table S5** Model details of macrophyte GLMMs

861 **Table S6** Model details of macrophyte pCCAs

862 **Table S7** Model details of GLMMs of dissolved oxygen, chlorophyll *a*, pH and plant
863 biomass.

864 **Table S8** Model details of algae GLMMs

865 **Table S9** Model details of algae pCCAs

866 **Table S10** Model details of invertebrate GLMMs

867 **Table S11** Model details of invertebrate pCCAs

868 **Table S12** Model details for multivariate analyses of homogeneity.

869

Supplementary material

Table 1 Algal functional groups. Table shows which taxonomic groups were placed in each functional group for analysis.

Group	Key morphological features	Taxonomic group
1	Small organisms with high surface/volume ratio	<i>Lyngbya</i> , <i>Oscillatoria</i> , picoplankton, <i>Stichococcus</i>
2	Small, flagellated, with siliceous exoskeletal features	<i>Chromulina</i> , <i>Chrysophyta</i> , <i>Synura</i>
3	Large filaments with aerotopes	<i>Anabaena spiroides</i> , <i>Chroococcales</i> , <i>Hapalosiphon</i> , <i>Nostoc</i>
4	Medium size organisms, lacking specialised traits	<i>Ankyra</i> , <i>Aphanochaete magna</i> , <i>Bumilleriopsis</i> , <i>Characiochloris</i> , <i>Characiopsis</i> , <i>Characium</i> , <i>Closteriopsis acicularis</i> , <i>Closterium</i> , <i>Cosmarium</i> , <i>Microthamnion kuetzingianum</i> , <i>Monoraphidium</i> , <i>Mougeotia</i> , <i>Netrium</i> , <i>Oedogonium</i> , <i>Ophiocytium</i> , <i>Pediastrum duplex</i> , <i>Pediastrum tetras</i> , <i>Scenedesmus</i> , <i>Tetraedron</i> , <i>Tetrastrum staurogeniaeforme</i> , <i>Treubaria</i>
5	Medium to large flagellates	<i>Chlamydomonas</i> , <i>Chroomonas</i> , <i>Cryptomonas</i> , <i>Dinophyceae</i> , <i>Euglena</i> , <i>Gymnodinium</i> , <i>Haematococcus</i> , <i>Katodinium</i> , <i>Pandorina morum</i> , <i>Phacus</i> , <i>Trachelomonas</i>
6	Non-flagellates with siliceous exoskeletons	<i>Achnanthes</i> , <i>Achnantheidium</i> , <i>Amphora</i> , <i>Aulacoseira</i> , <i>Cocconeis</i> , <i>Cyclotella</i> , <i>Cymbella</i> , <i>Denticula</i> , <i>Diadesmis</i> , <i>Encyonema</i> , <i>Epithemia</i> , <i>Eunotia</i> , <i>Fragilaria</i> , <i>Frustulia</i> , <i>Gomphonema</i> , <i>Gyrosigma</i> , <i>Melosira varians</i> , <i>Meridion</i> , <i>Navicula</i> , <i>Nitzschia</i> , <i>Pinnularia</i> , <i>Pseudostaurosira</i> , <i>Rhoicosphenia curvata</i> , <i>Staurosirella</i> , <i>Stephanodiscus</i> , <i>Surirella</i>
7	Large mucilaginous colonies	<i>Chamaesiphon</i> , <i>Chlorococcales</i> , <i>Gomphosphaeria</i> , <i>Hydrococcus</i> , <i>Kirchneriella obesa</i> , <i>Lagerheimia genevensis</i> , <i>Merismopedia</i> , <i>Microcystis</i> , <i>Oscillatoria</i> , <i>Phormidium</i> , <i>Protoderma</i> , <i>Quadrigula</i> , <i>Radiococcus</i> , <i>Rhabdoderma</i>
8	Uncategorised genera	Unidentifiable genera

Table S2 Best fitting invertebrate biomass regression models and formulae. Optimal regressions based on width/length (mm) and biomass (mg) of invertebrate taxa.

Invertebrate Taxa	<i>n</i>	<i>p</i>	Adj R²	Intercept (SE)	Slope (SE)	X variable + transformation
Asellidae	162	<0.001	0.70	-5.07 (0.25)	2.67 (0.14)	Length (Ln)
Bithyniidae	57	<0.001	0.80	-2.59 (0.29)	2.01 (0.13)	Length (Ln)
Chironomus	29	<0.001	0.62	-4.18 (0.68)	1.67 (0.24)	Length (Ln)
Erpobdellidae	15	<0.001	0.92	-9.17 (0.72)	3.22 (0.25)	Length (Ln)
Glossiphonidae	24	0.0402	0.13	-1.82 (0.64)	0.63 (0.29)	Length (Ln)
Hydrobiidae	156	<0.001	0.40	-3.36 (0.22)	1.75 (0.17)	Length (Ln)
Lymnaeidae	81	<0.001	0.72	-3.76 (0.35)	2.59 (0.18)	Length (Ln)
Physidae	6	<0.001	0.85	-2.77 (0.64)	2.00 (0.37)	Length (Ln)
Planorbidae	24	<0.001	0.72	-1.23 (0.18)	2.06 (0.27)	Width (Log ₁₀)
Sphaeriidae	18	<0.001	0.74	-4.55 (0.56)	2.54 (0.35)	Width (Ln)
Valvatidae	52	<0.001	0.69	-3.41 (0.27)	2.75 (0.25)	Width (Ln)

Table S3 Invertebrate feeding guilds. Table shows which taxonomic groups were placed in each feeding guild for analysis.

Collector Filterer	Collector Gatherer	Herbivore Piercer	Predator	Scraper Grazer	Shredder
Chydoridae	<i>Baetidae</i>	Corixinae	<i>Argyroneta</i>	<i>Asellus</i>	Chrysomelidae
Culicidae	<i>Beraea</i>	Curculionidae	<i>Batracobdella</i>	<i>Bithynia</i>	Elminthidae
Cyclopoida	<i>Caenis</i>	<i>Donacia</i>	Chaoboridae	<i>Brychius</i>	<i>Gammarus</i>
Daphniidae	<i>Dicrotendipes</i>	<i>Macroplea</i>	Coenagrionidae	<i>Crangonyx</i>	<i>Helophorus</i>
<i>Pisidium</i>	<i>Endochironomus</i>		Dytiscidae	<i>Gyraulus</i>	Pyralidae
Polycentropodidae	Chironomidae		<i>Erpobdella</i>	Haliplidae	<i>Glyptotendipes</i>
<i>Microtendipes</i>	<i>Chironomus</i>		<i>Gerris</i>	<i>Halipilus</i>	<i>Polypedilum</i>
	Limnephilidae		<i>Glossiphonia</i>	<i>Hippeutis</i>	
	Oligochaeta		<i>Helobdella</i>	<i>Lymnaea</i>	
			<i>Hydrachna</i>	<i>Physa</i>	
			<i>Limnesia</i>	<i>Planorbarius</i>	
			<i>Nepidae</i>	<i>Planorbis</i>	
			<i>Notonecta</i>	<i>Potamopyrgus</i>	
			<i>Rhyacophila</i>	<i>Valvata</i>	
			<i>Sialis</i>		
			<i>Stictotarsus</i>		
			<i>Theromyzon</i>		
			<i>Velia</i>		

Table S4 Macrophyte structural groups. Table shows which taxonomic groups were placed in each structural group for analysis.

Structural group	Taxonomic group
Emergent	<i>Alisma lanceolatum</i> , <i>Alisma plantago-aquatica</i> , <i>Apium inundatum</i> , <i>Baldellia ranunculoides</i> , <i>Butomus umbellatus</i> , <i>Caltha palustris</i> , <i>Carex rostrata</i> , <i>Carex vesicaria</i> , <i>Cicuta virosa</i> , <i>Eleocharis palustre</i> , <i>Epilobium hirsutum</i> , <i>Equisetum fluviatile</i> , <i>Equisetum palustre</i> , <i>Filipendula ulmaria</i> , <i>Glyceria fluitans</i> , <i>Iris pseudacorus</i> , <i>Juncus bulbosus</i> , <i>Lythrum</i> spp., <i>Mentha aquatica</i> , <i>Menyanthes trifoliata</i> , <i>Myosotis scorpioides</i> , <i>Phalaris arundinacea</i> , <i>Phragmites australis</i> , <i>Persicaria amphibia</i> , <i>Potentilla palustris</i> , <i>Ranunculus flammula</i> , <i>Schoenoplectus</i> spp., <i>Solanum dulcamara</i> , <i>Sparganium erectum</i> , <i>Stachys palustris</i> , <i>Typha latifolia</i>
Free-floating	<i>Hydrocharis morsus-ranae</i> , <i>Lemna gibba</i> , <i>Lemna minor</i> , <i>Lemna minuta</i> , <i>Lemna polyrhiza</i> , <i>Lemna trisulca</i> , <i>Stratiotes aloides</i>
Floating rooted	<i>Nuphar lutea</i> , <i>Nymphaea alba</i> , <i>Potamogeton natans</i> , <i>Sagittaria sagittifolia</i>
Submersed, canopy forming	<i>Callitriche</i> spp., <i>Callitriche hamulata</i> , <i>Ceratophyllum demersum</i> , <i>Elodea canadensis</i> , <i>Elodea nuttallii</i> , <i>Myriophyllum alternifolium</i> , <i>Myriophyllum spicatum</i> , <i>Potamogeton alpina</i> , <i>Potamogeton crispus</i> , <i>Potamogeton filiformis</i> , <i>Potamogeton friesii</i> , <i>Potamogeton gramineus</i> , <i>Potamogeton lucens</i> , <i>Potamogeton obtusifolius</i> , <i>Potamogeton pectinatus</i> , <i>Potamogeton perfoliatus</i> , <i>Potamogeton praelongus</i> , <i>Potamogeton pusillus</i> , <i>Potamogeton trichoides</i> , <i>Potamogeton gramineus x lucens</i> , <i>Ranunculus penicillatus</i> , <i>Ranunculus circinatus</i> , <i>Sparganium emersum</i> , <i>Zannichella palustre</i>
Submersed, low growing	<i>Eleocharis acicularis</i> , <i>Isoetes</i> spp., <i>Littorella uniflora</i>
Bryophytes	<i>Fontinalis antipyretica</i> , <i>Fontinalis squamosa</i> , <i>Scapania</i> spp.
Filamentous algae	Chlorophyta
Charophytes	Charophyceae

Table S5. Univariate models of macrophyte cover and species richness, where quadrat nested within lake was fitted as a random factor. “na” indicates variables not included in the final model.

Model/explanatory variables	$\beta \pm \text{s.e.}$	Wald χ^2	<i>p</i>
a) % macrophytes cover ($\chi^2_{\text{df}=717} = 180.88, p < 0.001$)			
% <i>Elodea nuttallii</i>	0.013 ± 0.003	20.24	<0.001
% <i>Elodea canadensis</i>	0.029 ± 0.012	5.53	0.019
Depth	-0.470 ± 0.083	31.90	<0.001
Year	Factorial	8.47	0.037
Nutrient concentration	-3.690 ± 2.109	3.06	0.080
% <i>E. nuttallii</i> * % <i>E. canadensis</i>	na		
b) % native macrophytes cover ($\chi^2_{\text{df}=719} = 101.74, p < 0.001$)			
% <i>Elodea nuttallii</i>	na	na	na
% <i>Elodea canadensis</i>	na	na	na
Depth	-0.494 ± 0.087	32.42	<0.001
Year	Factorial	9.51	<0.001
Nutrient concentration	-4.082 ± 2.214	3.40	0.065
% <i>E. nuttallii</i> * % <i>E. canadensis</i>	na		
c) % native macrophyte richness ($\chi^2_{\text{df}=717} =, p < 0.001$)			
% <i>Elodea nuttallii</i>	0.002 ± 0.001	3.85	0.050
% <i>Elodea canadensis</i>	0.013 ± 0.004	11.58	
Depth	-0.397 ± 0.043	88.77	
Year	Factorial	26.86	
Nutrient concentration	3.407 ± 1.176	8.39	0.004
% <i>E. nuttallii</i> * % <i>E. canadensis</i>	na		

Table S6. Results of pCCA models of cover of macrophyte genera and cover of macrophyte structural groups, where quadrat is accounted for as a conditional factor. “na” indicates variables which were not included in the final model.

Model/explanatory variables	Variance explained (%)	<i>p</i>
a) % cover of macrophyte genera (df = 697, Conditional variance (Site) = 53.9, Constrained variance = 3.9, <i>p</i> = 0.010)		
% <i>Elodea nuttallii</i>	0.5	0.005
% <i>Elodea canadensis</i>	na	na
Depth	0.5	0.005
Year	2.0	0.005
Nutrient concentration	na	na
% <i>E. nuttallii</i> * % <i>E. canadensis</i>	na	na
b) % cover of structural groups (df = 361, Conditional variance (Site) = 69.0, Constrained variance = 4.6, <i>p</i> = 0.005)		
% <i>Elodea nuttallii</i>	0.6	0.005
% <i>Elodea canadensis</i>	na	na
Depth	na	na
Year	2.7	0.005
Nutrient concentration	na	na
% <i>E. nuttallii</i> * % <i>E. canadensis</i>	na	na

Table S7. Results of univariate models of dissolved oxygen, chlorophyll *a*, pH, and plant biomass where site is fitted as a random factor. “na” indicates variables not included in the final model.

Model/explanatory variables	$\beta \pm \text{s.e.}$	Wald χ^2	<i>p</i>
a) dissolved oxygen saturation ($\chi^2_{\text{df}=31} = 6.25, p=0.043$)			
<i>Elodea nuttallii</i>	Factorial	3.21	0.073
Month	na	na	na
Nutrient concentration	na	na	na
Nutrient concentration * <i>E. nuttallii</i>	na	na	na
River/Lake	Factorial	4.23	0.040
River/Lake * <i>E. nuttallii</i>	na	na	na
b) chlorophyll <i>a</i> ($\chi^2_{\text{df}=34} = 1.61, p=0.204$)			
<i>Elodea nuttallii</i>	na	na	na
Month	na	na	na
Nutrient concentration	na	na	na
Nutrient concentration * <i>E. nuttallii</i>	na	na	na
River/Lake	na	na	na
River/Lake * <i>E. nuttallii</i>	na	na	na
c) pH ($\chi^2_{\text{df}=33} = 40.45, p < 0.001$)			
<i>Elodea nuttallii</i>	na	na	na
Month	Factorial	125.69	<0.001
Nutrient concentration	na	na	na
Nutrient concentration * <i>E. nuttallii</i>	na	na	na
River/Lake	na	na	na
River/Lake * <i>E. nuttallii</i>	na	na	Na
d) plant biomass ($\chi^2_{\text{df}=23} = 1.99, p = 0.158$)			
<i>Elodea nuttallii</i>	na	na	na
Month	na	na	na
Nutrient concentration	na	na	na
Nutrient concentration * <i>E. nuttallii</i>	na	na	na
River/Lake	na	na	na
River/Lake * <i>E. nuttallii</i>	na	na	na

Table S8. Results of univariate models of algal biovolume and richness of algal taxa, where site is fitted as a random factor. “na” indicates variables which were not included in the final model.

Model/explanatory variables	$\beta \pm \text{s.e.}$	Wald χ^2	<i>p</i>
a) algal biovolume ($\chi^2_{\text{df}=29} = 7.32, p=0.026$)			
<i>Elodea nuttallii</i>	na	na	na
Month	Factorial	8.40	0.015
Nutrient concentration	na	na	na
Nutrient concentration * <i>E. nuttallii</i>	na	na	na
River/Lake	na	na	na
River/Lake * <i>E. nuttallii</i>	na	na	na
b) richness of algal taxa ($\chi^2_{\text{df}=27} = 177.68, p<0.001$)			
<i>Elodea nuttallii</i>	na	3.67	0.055
Month	na	20.19	<0.001
Nutrient concentration	na	na	na
Nutrient concentration * <i>E. nuttallii</i>	na	na	na
River/Lake	na	na	na
River/Lake * <i>E. nuttallii</i>	na	na	na

Table S9. Results of pCCA models of algal taxa and algal functional groups, where site is accounted for as a conditional factor. “na” indicates variables which were not included in the final model.

Model/explanatory variables	Variance explained (%)	<i>p</i>
a) biovolume of algal taxa		
(df = 23, Conditional variance(Site) = 34.5, Constrained variance = 15.5, <i>p</i> = 0.015)		
<i>Elodea nuttallii</i>	na	na
Month	7.1	0.041
Nutrient concentration	5.3	0.030
Nutrient concentration* <i>E.nuttallii</i>	na	na
River/Lake	na	na
River/Lake * <i>E. nuttallii</i>	na	na
b) biovolume of functional groups		
(df = 25, Conditional variance(Site) = 19.1, Constrained variance = 0, <i>p</i> = 0.340)		
<i>Elodea nuttallii</i>	na	na
Month	na	na
Nutrient concentration	na	na
Nutrient concentration* <i>E.nuttallii</i>	na	na
River/Lake	na	na
River/Lake * <i>E. nuttallii</i>	na	na

Table S10. Results of univariate models of invertebrate biomass and richness, where site is fitted as a random factor. “na” indicates variables which were not included in the final model.

Model/explanatory variables	$\beta \pm \text{s.e.}$	Wald χ^2	<i>p</i>
a) biomass of invertebrates on macrophytes ($\chi^2_{\text{df}=18} = 20.87, p < 0.001$)			
<i>Elodea nuttallii</i>	na	na	na
Month	Factorial	12.05	<0.001
Nutrient concentration	0.561 ± 0.200	7.85	<0.001
Nutrient concentration * <i>E. nuttallii</i>	na	na	na
Plant density	0.495 ± 0.120	17.01	< 0.001
River/Lake	na	na	na
River/Lake * <i>E. nuttallii</i>	na	na	na
b) richness of invertebrates on macrophytes ($\chi^2_{\text{df}=21} = 13.33, p = 0.002$)			
<i>Elodea nuttallii</i>	na	na	na
Month	Factorial	6.30	0.012
Nutrient concentration	na	na	Na
Nutrient concentration * <i>E. nuttallii</i>	na	na	Na
Plant density	0.125 ± 0.075	2.76	0.096
River/Lake	na	na	na
River/Lake * <i>E. nuttallii</i>	na	na	na
c) biomass of invertebrates in sediment ($\chi^2_{\text{df}=20} = 8.93, p < 0.001$)			
<i>Elodea nuttallii</i>	na	na	na
Month	na	na	na
Nutrient concentration	0.792 ± 0.341	9.54	0.002
Nutrient concentration * <i>E. nuttallii</i>	na	na	na
Plant density	na	na	na
River/Lake	na	na	na
River/Lake * <i>E. nuttallii</i>	na	na	na
d) richness of invertebrates in sediment ($\chi^2_{\text{df}=20} = 1.99, p = 0.158$)			
<i>Elodea nuttallii</i>	na	na	na
Month	na	na	na
Nutrient concentration	na	na	na
Nutrient concentration * <i>E. nuttallii</i>	na	na	na
Plant density	na	na	na
River/Lake	na	na	na
River/Lake * <i>E. nuttallii</i>	na	na	na

Table S11. Results of pCCA models of invertebrate taxa and feeding guilds, where site is accounted for as a conditional factor. “na” indicates variables which were not included in the final model.

Model/explanatory variables	Variance explained (%)	<i>p</i>
a) biomass of invertebrate taxa on macrophytes		
(df = 15, Conditional variance(Site) = 39.9, Constrained variance = 0, <i>p</i> =0.017)		
<i>Elodea nuttallii</i>	na	na
Month	na	na
Nutrient concentration	na	na
Nutrient concentration* <i>E.nuttallii</i>	na	na
Plant density	na	na
River/Lake	na	na
River/Lake * <i>E. nuttallii</i>	na	na
b) biomass of invertebrate feeding guilds on macrophytes		
(df = 17, Conditional variance(Site) = 45.2, Constrained variance = 10.5, <i>p</i> =0.005)		
<i>Elodea nuttallii</i>	na	na
Month	na	na
Nutrient concentration	na	na
Nutrient concentration* <i>E.nuttallii</i>	na	na
Plant density	na	na
River/Lake	na	na
River/Lake * <i>E. nuttallii</i>	10.45	0.044
c) biomass of invertebrate taxa in sediment		
(df = 17, Conditional variance(Site) = 42.4, Constrained variance = 0, <i>p</i> =0.005)		
<i>Elodea nuttallii</i>	na	na
Month	na	na
Nutrient concentration	na	na
Nutrient concentration* <i>E.nuttallii</i>	na	na
Plant density	na	na
River/Lake	na	na
River/Lake * <i>E. nuttallii</i>	na	na
c) biomass of invertebrate taxa in sediment		
(df = 17, Conditional variance(Site) = 42.4, Constrained variance = 0, <i>p</i> =0.005)		
<i>Elodea nuttallii</i>	na	na
Month	na	na
Nutrient concentration	na	na
Nutrient concentration* <i>E.nuttallii</i>	na	na
Plant density	na	na
River/Lake	na	na
River/Lake * <i>E. nuttallii</i>	na	na

Table S12. Results of analyses of multivariate homogeneity of group dispersion for macrophyte, algae and invertebrate taxa. Estimates show mean Jaccard dissimilarity between sites with *E. nuttallii* present and mean Jaccard dissimilarity between sites without *E. nuttallii*, based on presence and absence of taxa.

Model/explanatory variables	mean \pm se
a) macrophyte taxa ($F_{df=726} = 24.34, p < 0.001$)	
<i>Elodea nuttallii</i> present	0.43 \pm < 0.01
<i>Elodea nuttallii</i> absent	0.49 \pm < 0.01
b) algal taxa ($F_{df=24} = 0.42, p = 0.521$)	
<i>Elodea nuttallii</i> present	0.49 \pm < 0.01
<i>Elodea nuttallii</i> absent	0.48 \pm 0.02
c) invertebrate taxa on macrophytes ($F_{df=22} = 0.92, p = 0.179$)	
<i>Elodea nuttallii</i> present	0.55 \pm 0.03
<i>Elodea nuttallii</i> absent	0.60 \pm 0.03
d) invertebrate taxa in sediment ($F_{df=22} = 0.92, p = 0.179$)	
<i>Elodea nuttallii</i> present	0.51 \pm 0.02
<i>Elodea nuttallii</i> absent	0.53 \pm 0.03

