

# Declines in littoral species richness across both spatial and temporal nutrient gradients: a palaeolimnological study of two taxonomic groups

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## SUMMARY

1. Using a palaeolimnological approach in shallow lakes, we quantified the species richness responses of diatoms and Cladocera to phosphorus enrichment. We also examined differences in species richness responses between littoral and pelagic assemblages of our focal communities. To address both spatial and temporal relationships, our study includes an analysis of both surface sediments from 40 lakes and of a lake sediment record spanning *c.* 120 years. The objective of our study was to determine whether similar species richness patterns occurred across trophic levels, as well as along spatial and temporal gradients.

2. We found that both diatom and Cladocera species richness estimates significantly declined with increasing phosphorus across space and through time. When the assemblages were subdivided according to known habitat preferences, littoral biodiversity maintained a negative trend, whereas pelagic species richness tended to show no relationship with phosphorus.

3. Negative productivity–diversity patterns have been observed across almost all palaeolimnological studies that span large productivity gradients. This congruence in patterns is most likely due to the similarity in data collection methods and in focal communities studied. The contrasting responses between littoral and pelagic assemblages may be explained by the differences in physical habitat and the pool of taxa in each of these environments. Consistent with the literature, we found statistical support for the idea that littoral diversity declines could be explained by an interaction between macrophytes and nutrients along strong trophic gradients. The general lack of a diversity response in our pelagic assemblages could be attributable to the limited pool of subfossil taxa. The response of the pelagic diatom could also be related to their broad range of nutrient tolerances.

4. The observed negative response of species richness to phosphorus enrichment, particularly in the littoral assemblages, has implications for ecosystems functioning because communities with reduced biodiversity often are less resilient to anthropogenic change.

*Keywords:* biodiversity, Cladocera, diatoms, eutrophication, species richness

## Introduction

Understanding the drivers of biodiversity has been a central tenet in ecology for the past century. Interest has recently increased owing to widespread declines in species richness across the globe (Sala *et al.*, 2000; Millen-

nium Ecosystem Assessment, 2005). Developing generalities about diversity in freshwater ecosystems is of particular interest because these sites are home to a disproportionate number of species per unit area as well as a relatively high number of vulnerable taxa compared with marine and terrestrial environments (Strayer &

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Dudgeon, 2010). Despite years of study, many biodiversity patterns and processes, such as the productivity–diversity relationship, remain ambiguous.

Large syntheses of diversity–productivity relationships have concluded that a multitude of patterns exist within aquatic ecosystems (Waide *et al.*, 1999; Mittelbach *et al.*, 2001; Field *et al.*, 2009). For example, patterns observed with zooplankton include quadratic (e.g. Dodson, Arnott & Cottingham, 2000; Jeppesen *et al.*, 2000; Barnett & Beisner, 2007), positive (e.g. Hessen *et al.*, 2006; Thackeray, 2007; Dodson, 2008; Korhonen, Wang & Soininen, 2011), negative (e.g. Dodson *et al.*, 2000; Declerck *et al.*, 2005; Dodson, 2008), asymptotic (Golubkov *et al.*, 2007) and non-significant (e.g. Dodson *et al.*, 2000; Declerck *et al.*, 2005; Dodson, 2008). Several hypotheses have been proposed as to why these different patterns arise among studies such as (i) differences in the way productivity is measured, (ii) differences in the way samples are collected and (iii) differences in study scale. For example, comparing studies that have used surrogate measurements of productivity (such as biomass or nutrients, e.g. Jeppesen *et al.*, 2000; Barnett & Beisner, 2007; Declerck *et al.*, 2007; Thackeray, 2007) with those who have used *in situ* measures of productivity (e.g. Dodson *et al.*, 2000; Chase & Leibold, 2002) may bring about conflicting results because of confounding factors. Whereas biomass and nutrient concentrations are often correlated with productivity (Kalff, 2002), they can be influenced by multiple environmental factors such as light limitation or grazing (Polis, 1999), which could give rise to different productivity–diversity patterns (Waide *et al.*, 1999). Furthermore, differences in species richness measurement can arise when diverse sampling methods are adopted. For example, biodiversity estimates can vary greatly depending on the choice of sampling apparatus (Cheal *et al.*, 1993; Meyer, Peterson & Whiles, 2011) and on which lake habitat is considered (Walseng *et al.*, 2006; Stendera, 2008). Finally, different patterns of biodiversity are also known to emerge based on the grain (size of plot) and extent (distance between plots) at which productivity–biodiversity relationships are studied. For example, Chase & Leibold (2002) found that the relationship between taxonomic richness and productivity at the local scale (among ponds) was unimodal but became positive at the regional scale (across catchments).

Another consideration of scale is the potential for contrasting patterns and processes to arise through time at a single site as opposed to those that occur across the landscape because of their different histories of community assemblage (Fukami & Morin, 2003). Contemporary productivity–species richness relationships across broad temporal scales (e.g. >5 years) have been investigated in

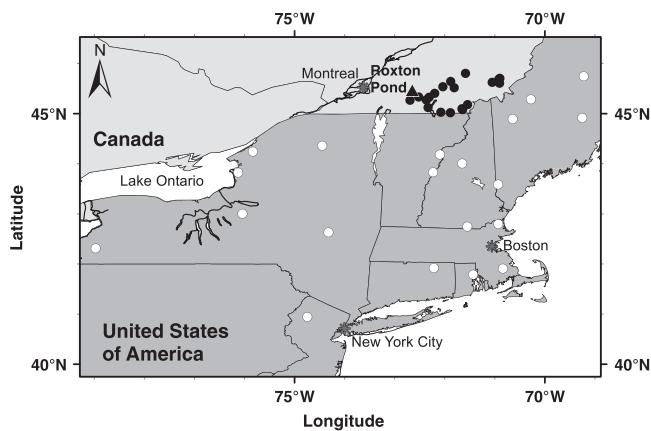
several aquatic ecosystems (Thackeray, 2007; Crossetti *et al.*, 2008), but almost none have compared patterns across space with those through time or across several taxonomic groups (notable exception, Dodson *et al.*, 2000). With this gap in knowledge, it is not entirely clear whether the numerous statistical models that have been developed from surveys of aquatic systems across landscapes will be able to predict with a reasonable degree of accuracy the changes in diversity that might occur at any one site over time. Palaeolimnological research provides an opportunity to examine the patterns and processes of biodiversity over broad spatial and temporal gradients (Gregory-Eaves & Beisner, 2011). To date, a few palaeolimnological studies have quantified productivity–diversity relationships (e.g. Rusak *et al.*, 2004; Das, Nordin & Mazumder, 2008; Richard Albert *et al.*, 2010), but all of these have focused on a single organismal group, and only one (Richard Albert *et al.*, 2010) has examined both spatial and temporal patterns.

Here, we have designed a study to examine whether similar productivity–diversity patterns exist across trophic levels as well as between spatial and temporal scales. Specifically, we quantified the relationship between phosphorus and species richness of diatoms (Bacillariophyceae) and Cladocera zooplankton using palaeolimnological approaches. We also evaluated whether there is a congruent response model across broad spatial (maximum distance between lakes is *c.* 850 km) and temporal (*c.* 120 years) extents. We selected shallow lakes spanning a broad range in nutrient loading over space and time, while minimising variations in lake morphometry.

## Methods

### Study sites

*Spatial study – northeastern United States and southern Quebec* For our spatial study, a total of 40 lakes were sampled during two different sampling campaigns. First, during the 1990s, the United States Environmental Protection Agency (EPA) surveyed 257 lakes in the northeastern United States and compiled a biological, chemical and physical database as part of the Environmental Monitoring and Assessment Program (EMAP, available from <http://www.epa.gov/emap/>). From this database, we selected a subset of 20 shallow lakes for our analysis from which sediments were available (Fig. 1). These lakes were selected to span a large phosphorus gradient, have a circumneutral pH and be of similar size (Table 1; full details regarding our lake selection protocol are provided in Richard Albert *et al.*, 2010). Further details regarding



**Fig. 1** Map of the United States and Canada showing the location of the lakes from the EMAP data set (light circles) and southern Quebec region (dark circles) and Roxton Pond (dark triangle). The locations of the cities of New York and Boston (U.S.A.) and Montreal (Canada) are highlighted by grey stars, for reference.

these lakes and their catchments are also provided in Dixit *et al.* (1999).

In addition to the EMAP data set lakes, another 20 shallow lakes were sampled in southern Quebec, Canada (Fig. 1) between 2006 and 2010. This study region is located c. 150 km east of the city of Montreal and north of the states of Vermont, New Hampshire and Maine where some of the EMAP lakes are located. Similar to the EMAP data set, the southern Quebec lakes all span a large total phosphorus (TP) gradient, have a circumneutral pH and are similar in surface area (Table 1).

Our study lakes were chosen explicitly to maximise a strong productivity gradient (TP ranging from 1 to 154  $\mu\text{g L}^{-1}$ ). This range in TP provides a broad overlap with previous productivity–diversity studies in North American lakes that have detected unimodal response curves for both zooplankton (i.e. peaks in species richness

detected at 20–50  $\mu\text{g L}^{-1}$  TP; Leibold, 1999; Thackeray, 2007) and algae (c. 50  $\mu\text{g L}^{-1}$  TP; Leibold, 1999). Our set of lakes is also representative of the range in trophic conditions found in lakes across North America (where c. 85% of lakes have <150  $\mu\text{g L}^{-1}$  TP, US Environmental Protection Agency 2010, data available at [http://water.epa.gov/type/lakes/NLA\\_data.cfm](http://water.epa.gov/type/lakes/NLA_data.cfm)).

**Temporal study – Roxton Pond** Roxton Pond is located in southern Quebec, Canada (+45.468, –72.653; Fig. 1). Roxton Pond is a small (surface area = 1.93 km<sup>2</sup>), shallow lake ( $z_{\text{mean}} = 3.1$  m) that is currently eutrophic (mean  $\pm 1$  standard deviation in TP concentrations from 2000 to 2011 =  $32 \pm 11 \mu\text{g L}^{-1}$ ). Given that the water chemistry and lake morphometry of Roxton Pond was close to the average conditions in both regional lake surveys (Table 1) and because the fossil pigment analyses of the Roxton sediment core showed a distinct trophic change over the past c. 150 years (Vermaire, 2011), this site was an ideal candidate for our temporal study.

#### Palaeolimnological analyses

Sediment cores were collected from an offshore depositional zone of each lake using a Glew gravity corer (Glew, 1989). The cores were sectioned at 1-cm interval resolution using a vertical extruding device (Glew, 1988) and kept cool and dark until further processing. The top 1 cm of each core represents the past few years of sediment deposition (Brothers, Vermaire & Gregory-Eaves, 2008) and was used to represent the modern species assemblage of each lake in our spatial survey. The downcore sediment samples from Roxton Pond were collected in a similar manner, and the full core was extruded at 1 cm. A single sediment core was extracted

**Table 1** Summary of environmental variables from our two study regions including mean, minimum, maximum and standard deviations (SD) and environmental data from this day Roxton Pond. None of these variables were significantly different between study regions (based on *t*-test, data log-transformed or square-root-transformed prior to testing). Roxton Pond environmental data falls around the average of both regions

	Region 1: Northeastern United States (EMAP data set)				Region 2: Southern Quebec				Roxton Pond
	Mean	Minimum	Maximum	SD	Mean	Minimum	Maximum	SD	
Total phosphorus ( $\mu\text{g L}^{-1}$ )	28	1	155	34	21	3	117	26	32
Total nitrogen ( $\mu\text{g L}^{-1}$ )	573	179	1814	387	499	300	1063	208	650
TN : TP	51	6	333	82	37	7	144	29	20
Chlorophyll- <i>a</i> ( $\mu\text{g L}^{-1}$ )	9	1	35	10	21	3	165	36	21
Secchi depth (m)	3.2	0.8	13.3	3.0	2.0	0.3	6.3	1.6	1.4
Conductivity ( $\mu\text{S m}^{-1}$ )	160	16	1073	230	92	32	273	54	122
pH	7.9	6.7	8.5	0.5	8.0	6.8	10.0	0.8	8.1
Mean lake depth (m)	3.1	0.6	10.9	2.8	2.2	0.6	4.3	1.1	3.1

EMAP, Environmental Monitoring and Assessment Program.

from this lake in 2008 and used for both diatom and Cladocera enumeration.

**Radioisotope dating** A chronology for the Roxton Pond sediment core was obtained based on the isotopic activities of  $^{210}\text{Pb}$ ,  $^{214}\text{Pb}$  and  $^{214}\text{Bi}$  of freeze-dried samples of known mass (0.4–1.0 g) and volume, measured using a Canberra well-detector gamma-ray spectrometer (Canberra, Meriden, CT, U.S.A.) and the constant rate supply model (Appleby, 2001). Full details regarding the chronology of the core from Roxton Pond are provided in Appendix S1.

**Diatoms** Diatom slides were prepared according to a standard procedure outlined by Battarbee *et al.* (2001). Briefly, c. 0.5 g of wet homogenised sediment was weighed in a 20-mL glass scintillation vial. Seventeen millilitres of 10% hydrochloric acid was added to bring carbonates, oxides and metal salts into solution. After 24 h, the supernatant was aspirated, and de-ionised water was added. The latter procedure was repeated four more times, allowing the sediments to settle in the bottom of the vials after each wash. After the fifth aspiration, 10 mL of 30% hydrogen peroxide ( $\text{H}_2\text{O}_2$ ) was added to oxidise the remaining organic material. Once the reaction was complete, the supernatant was aspirated, and de-ionised water was added. The previous procedure was repeated every 24 h for eight days. Finally, the slurry was plated onto coverslips that were mounted onto slides using Zrax<sup>®</sup> mounting medium.

For each sample, a minimum of 400 diatom valves were identified along parallel transects with a Leica DM 2500 compound microscope, (Leica Microsystems, Wetzlar, Germany) at 1000 $\times$  magnification. Diatoms were identified to the species level according to taxonomy defined in books by Krammer & Lange-Berthlot (1986–1991) and Cumming *et al.* (1995). Diatom counts from the EMAP have been previously published by Dixit *et al.* (1999). The subdivision of diatom taxa according to their habitat preference, either littoral/benthic (for simplification, henceforth referred to only as littoral) or pelagic, was made based on Round, Crawford & Mann (1990).

**Cladocera** Cladocera are one of the few groups of zooplankton whose skeletal remains are adequately preserved in the sedimentary record (Korhola & Rautio, 2001). When using skeletal microfossils, most of the Cladocera diversity in shallow lakes is represented by the chydorid (*Chydoridae*) family. Cladocera slides were prepared according to a standard procedure outlined by Korhola & Rautio (2001). Approximately 0.2 g of homogenised dry sediment was added to 50 mL of 10%

potassium hydroxide (KOH) and heated to 70 °C for 30 min to deflocculate the sediments. Five millilitres of 10% HCl was then added to neutralise the sample. The suspension was filtered on a 36- $\mu\text{m}$  sieve, rinsed with water and finally transferred to a 15-mL polypropylene centrifuge tube. The Cladocera remains were then plated on slides using safranin–glycerine jelly.

For each sample, a minimum of 60 chydorid remains were identified using a Leica DM 2500 compound microscope at 200–400 $\times$  magnification. We adjusted the counts of remains to be representative of the Cladocera as individuals such that one individual is comprised of one head shield, two carapace halves and one post-abdomen (Korhola & Rautio, 2001). The most abundant remain was used to represent the count of each species. Following this approach, the average total number of individual Cladocera counted (including both pelagic and littoral taxa) was  $278 \pm 182$  (mean  $\pm 1$  standard deviation); this value is much greater than the minimum count sizes recommended by Kurek *et al.* (2010). Chydorids were identified to the lowest possible taxonomic resolution using references by Frey (1959, 1960, 1961, 1962, 1965, 1969, 1980), Goulden & Frey (1963), Chengalath & Hann (1981), Bos (2000), Sweetman & Smol (2006) and Szeroczyńska & Sarmaja-Korjonen (2007). All *Chydoridae* were identified to the species level with the exception of *Chydorus sphaericus* spp., a species group that encompasses morphologically similar species (*C. sphaericus*, *C. brevilabris*, *C. biovatus* and *C. bicornutus*); these taxa are very difficult to distinguish using only the disarticulated sedimentary remains (Szeroczyńska & Sarmaja-Korjonen, 2007). *Daphnidae* were identified as *Daphnia pulex* and *D. longispina*, whereas the *Bosminidae* were identified as *Bosmina longirostris*, *Eubosmina longispina* and *Eubosmina coregoni* (identifications were made using a combination of post-abdominal claws, carapaces and headshields, using the references cited above).

#### *Productivity surrogates*

In our study, we used phosphorus measurements as our surrogate for productivity. For our spatial survey, lake-water TP was calculated using standard techniques (Wetzel & Likens, 2000) using epilimnetic water collected during the summer. To estimate phosphorus loads entering Roxton through time, we used a historical mass balance approach based on agricultural and population census data from the Government of Canada from 1871 to 2001. Specifically, these census data allowed us to quantify the amount of phosphorus applied as fertiliser and livestock manure, as well as the amount of phosphorus removed from the catchment as crops (Macdonald & Bennett, 2009).



The phosphorus load index (P load index) was calculated as yearly phosphorus inputs (fertiliser + manure) minus phosphorus exports (crops) to the catchment (per unit area) divided by lake volume. Because fertilisers applied to catchments runs off into lakes and streams (Howarth *et al.*, 1996; Bouwman *et al.*, 1997), the P load index will be used as our temporal estimate of lake trophic status. We chose to use this catchment metric over reconstructing past lake-water TP using the diatom assemblage because such nutrient reconstructions are problematic in shallow lakes (Bennion *et al.*, 2010). Furthermore, this phosphorus balance metric provides an estimate of nutrient loading that is completely independent from our diatom results.

### Statistical analyses

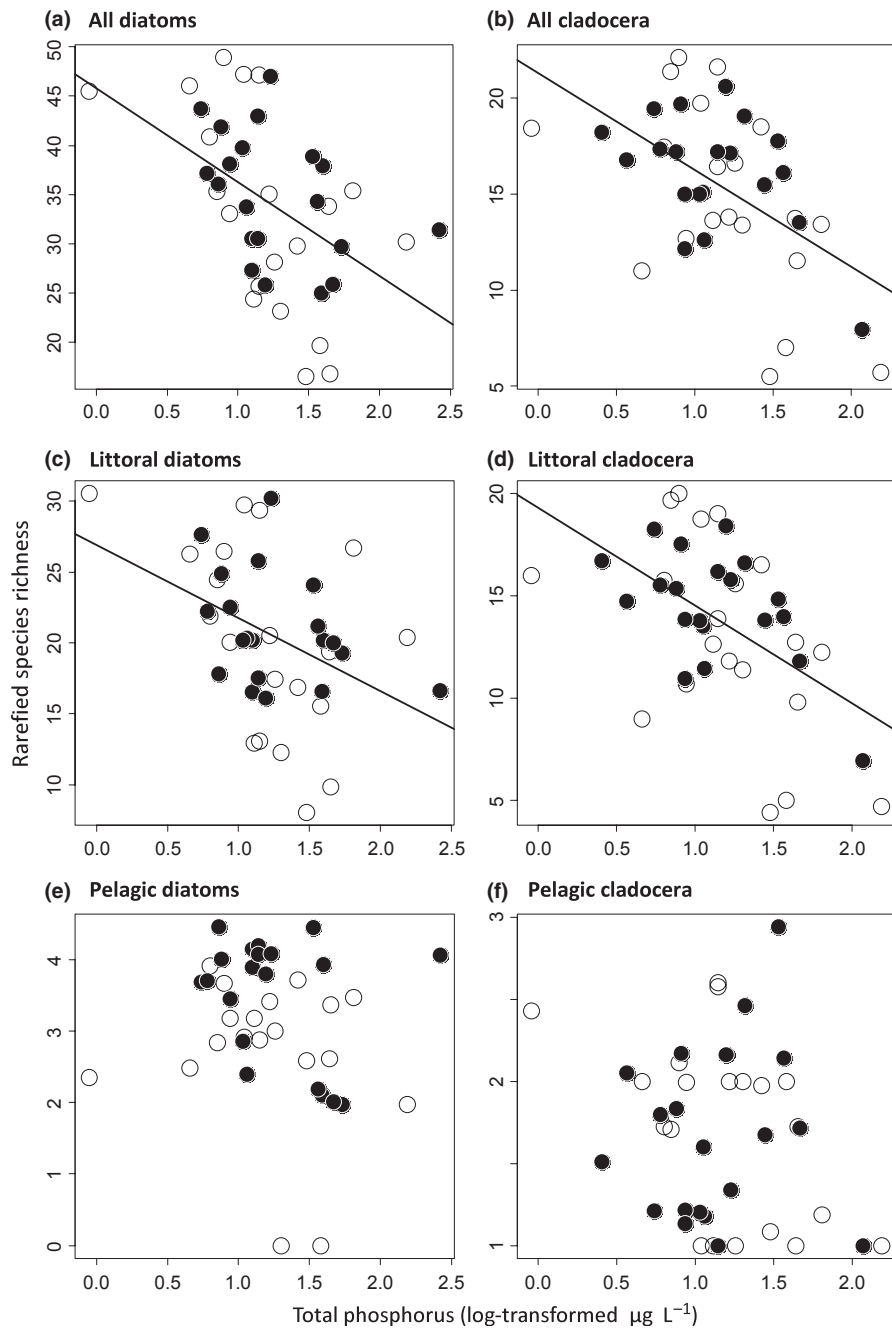
To quantify subfossil diatom and Cladocera diversity, we used rarefied species richness estimates (Magurran, 2004). For diatom and Cladocera data, the rarefied species richness estimates were standardised to the minimum count sizes for each of the taxonomic groups using the vegan package (Oksanen *et al.*, 2011) in R Statistical Software (R Development Core Team, 2012). Given that a previous study by Smol (1981) highlighted that performing species richness analyses on sedimentary assemblages can be problematic because of differential sedimentation across lakes and through time, we conducted two different analyses to evaluate the importance of this factor. To explore whether differences in sedimentation rates across lakes was a large part of the species richness signal, we conducted an analysis on a subset of 14 lakes where we had collected a second set of surface sediments within 4 years of the first sampling. Specifically, we compared the diatom species richness estimates from the original surface sediment sample to estimates generated from the pooling and rarefaction of data from two surface samples collected in different years, such that these pooled samples would be integrating over longer periods of time. We then computed an intraclass correlation coefficient (ICC, Gamer *et al.*, 2010) to determine whether the species richness estimates measured on the most recent sampling date were more similar to species richness estimates based on a pooling and rarefaction of two sampling dates, relative to the among-lake species richness variation. The ICC permits the calculation of an index of similarity between samples that are *a priori* believed to be correlated (Shrout & Fleiss, 1979). For our surface sediment analyses, we only had diatom data from two sampling events, but for our temporal study of Roxton Pond, we were able to evaluate the effect of changes in sedimentation rate on both diatom and Cladocera assemblages. To examine how changes in sedimentation

rates within the core from Roxton Pond might influence species richness patterns, we followed an approach outlined in Richard Albert *et al.* (2010). Specifically, we lumped assemblage data at 15-year time steps ( $\pm 2$  years) throughout the core and then rarefied these pooled data. We then presented species richness estimates based on the raw data as well as an aggregated data.

Regression analyses ( $r^2_{\text{adjusted}}$ ) were run to quantify the relationship between rarefied species richness estimates and log-transformed TP (spatial data) or P load index (temporal data). Log transformation was applied to TP to normalise the data. Linear and quadratic models were compared using Akaike's Information Criterion (Akaike, 1987) but linear models consistently had lower AICs, so only these results are shown. An analysis of covariance (ANCOVA) was performed to determine whether slopes of the relationships differed between regions. To determine whether there were any physical or chemical differences between the two regions, *t*-tests were performed on normalised (square-root- or log-transformed) environmental data. All regression and correlation analyses, associated *post hoc* tests and *t*-tests were performed in R Statistical Software (R Development Core Team, 2012).

### Results

With our lake survey analysis, we found that rarefied species richness for both diatom and Cladocera was significantly negatively correlated to phosphorus in both regions, and so the regional data were pooled for all subsequent analyses. On the basis of our ICC analysis, we found that there was significant within-lake consistency in species richness estimates (ICC = 0.74,  $P < 0.001$ ,  $n = 14$ , Appendix S2), which shows that differences in sedimentation rates did not significantly affect our species richness estimates among lakes. Therefore, we proceeded to only use the data based on a single sampling of lake surface sediments. With these result, we found TP explained c. 25% of the variation in diatom and Cladocera rarefied species richness (Fig. 2a,b; Table 2). When assemblages were subdivided according to habitat, only the littoral rarefied species richness estimates were negatively related to TP (Fig. 2c,d; Table 2). No significant relationships were observed with the pelagic richness estimates (Fig 2e,f; Table 2). Across all lakes, we found that TP was correlated with other metrics of lake productivity such as total nitrogen, chlorophyll-*a*, secchi disc depth (total nitrogen,  $r = 0.70$ ,  $P < 0.001$ ; chlorophyll-*a*,  $r = 0.66$ ,  $P < 0.001$ ; secchi disc depth,  $r = -0.66$ ,  $P < 0.001$ ) and more modestly related to surface water pH and conductivity (pH,  $r = 0.40$ ,  $P = 0.010$ ; conductivity,  $r = 0.32$ ,  $P = 0.042$ ).



**Fig. 2** Scatterplot showing the relationship between rarefied species richness estimates and total phosphorus in the northeastern United States (light circles) and southern Quebec (dark circles). Diatom and Cladocera species richness estimates and phosphorus relationships were calculated for the whole assemblage (a and b, respectively) and then for littoral (c and d) and pelagic assemblages (e and f). All  $r^2_{\text{adj}}$  and  $P$ -values can be found in Table 2.

We observed similar species richness–productivity relationships in Roxton Pond over time as in our spatial survey. When samples were integrated to form equal time steps, both diatom and Cladocera rarefied species richness were negatively related to the P load index (Fig. 3a,b; Table 2). Likewise, negative relationships were apparent when only the littoral portion of the assemblage was retained (Fig. 3c,d; Table 2). We failed to detect significant relation-

ships with most of the analyses associated with pelagic assemblages from Roxton Pond (Fig. 3e,f; Table 2). However, we identified a linear trend with the unpooled pelagic Cladocera species richness estimates, which is associated with the appearance of the invasive *Eubosmina coregoni*.

Substantially, more variation (c. 30%) was explained in our temporal analyses relative to the spatial survey. To evaluate whether the difference in the proportion of

**Table 2** Summary of regression analyses of rarefied species richness estimates and phosphorus. Statistically reduced sample sets refer to the random subsampling of the larger spatial survey to represent an equivalent sample size as in the temporal study

	Diatoms		Cladocera		<i>n</i>
	$r_{adj}^2$	<i>P</i> -value	$r_{adj}^2$	<i>P</i> -value	
<b>All</b>					
Spatial survey	0.22	0.001	0.26	<0.001	40
Statistically reduced spatial survey	0.19	0.224	0.21	0.264	8
Temporal study	0.04	0.233	0.52	0.002	14
Integrated 15 year temporal study	0.44	0.042	0.63	0.011	8
<b>Littoral</b>					
Spatial survey	0.15	0.008	0.26	<0.001	40
Statistically reduced spatial survey	0.11	0.322	0.21	0.232	8
Temporal study	0.25	0.040	0.56	0.001	14
Integrated 15 year temporal study	0.45	0.041	0.55	0.022	8
<b>Pelagic</b>					
Spatial survey	0.01	0.287	0.03	0.162	40
Statistically reduced spatial survey	0.04	0.465	0.01	0.455	8
Temporal study	0.19	0.067	0.30	0.024	14
Integrated 15 year temporal study	0.04	0.301	0.01	0.337	8

$r_{adj}^2$  values highlighted in grey indicate significance ( $P < 0.05$ ).

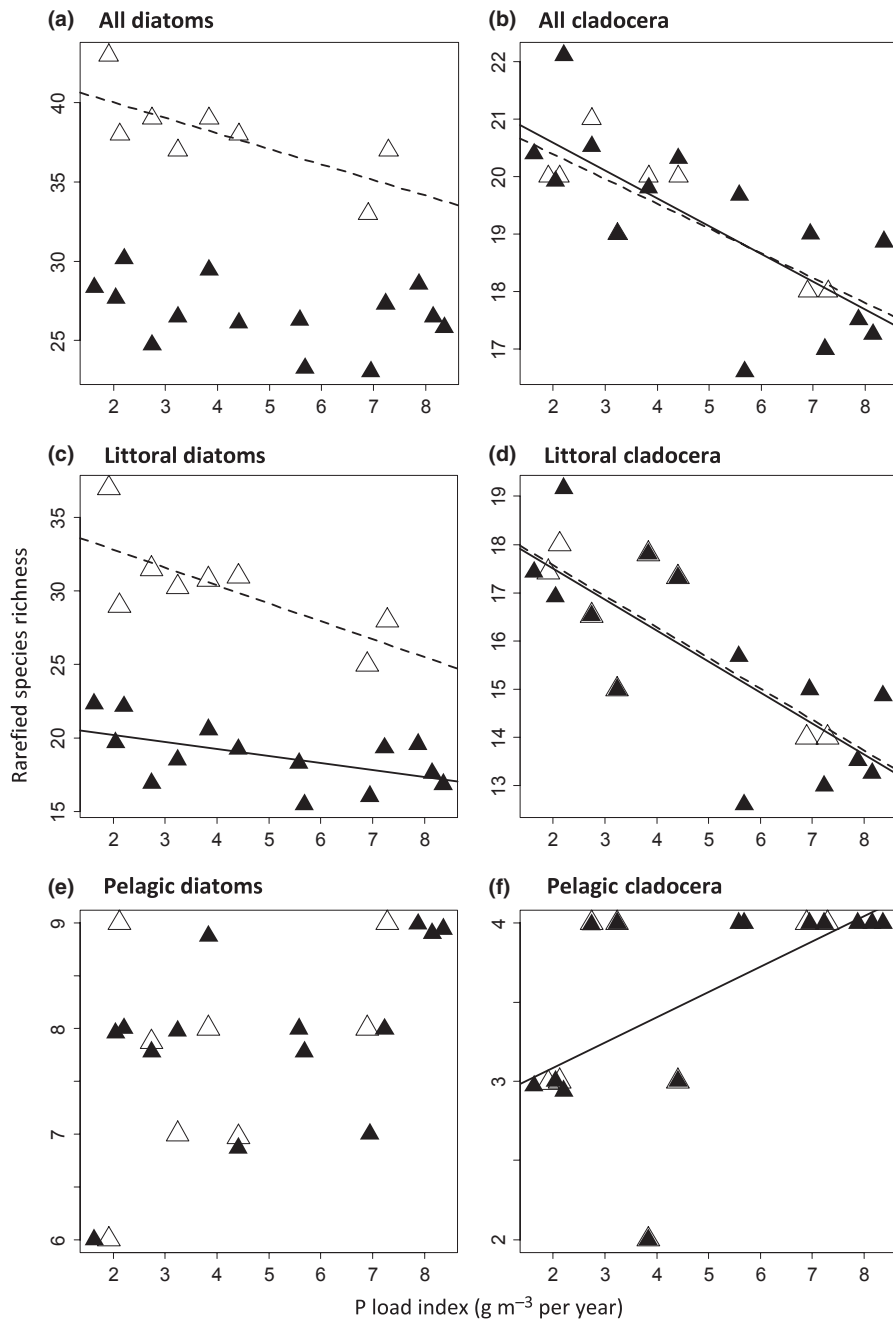
variance explained across these two different scales was attributable to sample size, we performed a resampling exercise by randomly selecting eight data points from the spatial survey (same number of data points as the temporal study when data were integrated at *c.* 15-year time steps) and performing a regression analysis. This exercise was repeated 999 times, and a mean  $r_{adj}^2$  and *P*-value were calculated (Table 2). We found that still the integrated temporal analyses consistently had a higher proportion of variance explained ( $r_{adj}^2 = 0.44$ – $0.63$ ) than the spatial analyses ( $r_{adj}^2 = 0.1$ – $0.21$ ; Table 2).

## Discussion

On the basis of the complete subfossil assemblages, we found that both diatom and Cladocera species richness estimates were negatively related to phosphorus across lakes and through time. Patterns across lakes were weaker than those through time, most likely because of the greater variability in morphometry across lakes, despite our efforts to minimise this effect. Furthermore, habitat was identified as a key variable because negative productivity–diversity patterns were only observed with the littoral assemblages.

Most palaeolimnological studies that have quantitatively assessed the relationship between diversity and productivity across a broad trophic gradient have found negative species richness responses similar to our own. Indeed, our results are consistent with those of the previous studies of subfossil diatoms (Rusak *et al.*, 2004; Weckström, Korhola & Weckström, 2007) and Cladocera (Whiteside & Harmsworth, 1967; Amsinck, Jeppesen & Landkildehus, 2005; Richard Albert *et al.*, 2010). These palaeolimnological studies have used the same focal communities and almost identical data collection techniques, which, when taken together, probably explain the congruence of results across studies. Few of these studies, however, have considered how changes in sedimentation rate might affect species richness patterns. Both our spatial and temporal analyses show that this effect was not important in our lakes. This conclusion echoes the findings of Richard Albert *et al.* (2010) and Pla-Rabes *et al.* (2011), but future palaeodiversity studies should take into account the relative importance of sedimentation rates in their region.

By subdividing taxa according to their habitat preferences, we found that only the littoral diatom and Cladocera species richness estimates exhibited a negative response to phosphorus. Previous studies have attributed such patterns of decreased littoral diversity to the indirect effect of nutrients on littoral habitats, rather than its direct effect on organisms (Whiteside & Harmsworth, 1967; Hofmann, 1987; Declerck *et al.*, 2011). At low levels of phosphorus in the water column, most of the nutrients are sequestered in the sediments, favouring the growth of macrophytes and periphyton (Carignan & Kalff, 1980; Vadeboncoeur *et al.*, 2003). Large macrophyte biomass in oligotrophic waters prevents algal blooms via direct competition for light (Scheffer *et al.*, 1993). As the water column becomes more nutrient rich, algae tap into the pelagic pool of resources, become dominant and outcompete macrophytes for light. The high degree of structural complexity produced by macrophytes has been previously associated with higher taxonomic richness in both zooplankton (Duggan, 2001; Kuczynska-Kippen & Nagen-gast, 2003; Declerck *et al.*, 2007, 2011; Lucena-Moya & Duggan, 2011) and algae (Cattaneo *et al.*, 1998; Declerck *et al.*, 2007; Muylaert *et al.*, 2010). Consistent with this literature, we found that littoral Cladocera richness was significantly greater ( $t$ -value = 3.99,  $P = 0.002$ ) in zones of the Roxton sediment record that were inferred to reflect low nutrient (<35  $\mu\text{g L}^{-1}$  TP) and macrophyte conditions versus high nutrient conditions (>35  $\mu\text{g L}^{-1}$  TP) as based on the diatom assemblage (Vermaire, 2011; Vermaire, Prairie & Gregory-Eaves, 2011). Likewise, for the 20



**Fig. 3** Scatterplot showing the relationship between rarefied species richness estimates and the P load index through time in Roxton Pond. Diatom and Cladocera species richness estimates and phosphorus relationships were calculated for the whole assemblage (a and b, respectively) and then for littoral (c and d) and pelagic assemblages (e and f). Data from individual time steps (dark solid triangle, full line when significant) and integrated equal time steps (c. 15 years, light open triangle, dashed line when significant) are shown. All  $r^2_{\text{adj}}$  and  $P$ -values can be found in Table 2.

southern Quebec lakes for which we had data on macrophyte abundances (Vermaire *et al.*, 2011), we found that TP and the percentage cover of macrophytes were both significant predictors of littoral cladoceran species richness ( $r^2_{\text{adj}} = 0.47$ ,  $P < 0.01$ ).

In contrast to the littoral assemblages, most of the pelagic communities showed no diversity response to

phosphorus. This observation may be due to our focus on shallow lakes, where the pelagic environment represents a smaller proportion of the available habitat relative to deep lakes. This, in turn, could limit the pool of pelagic taxa and thus our ability to detect a response. Certainly, palaeolimnological studies focusing on deep lakes from nearby regions have reported higher species richness of



pelagic taxa (Kurek, Weeber & Smol, 2011; Shaw Chraïbi, Bennett & Gregory-Eaves, 2011). The lack of species richness responses in the pelagic diatom communities to nutrient enrichment could also be attributable to compensatory dynamics. Such an explanation was proposed by Passy (2008), who examined a large contemporary stream diatom data set. According to her analyses, benthic diatom species richness was negatively related to nutrient concentrations, but no trend was apparent with pelagic diatom diversity. Passy (2008) postulated that this lack of biodiversity response from the pelagic diatom community was because many pelagic species tolerate broad ranges in nutrient concentrations and adapt by changing their relative abundances. Future palaeolimnological studies focusing on diversity responses of pelagic and littoral assemblages from deep lakes are needed to sort out whether the diatom patterns we have reported for shallow lakes are applicable to a wider range of lake morphometries.

With respect to the pelagic Cladocerans, the almost complete lack of diversity–nutrient relationship could also be attributable to our palaeolimnological approach. Indeed, the skeletal remains of only few pelagic Cladocera (e.g. Bosminidae) have been found to be reflective of the abundances of living populations or can be identified beyond species groups (Korhola & Rautio, 2001; Davidson *et al.*, 2007). In most cases, more pelagic Cladocera species are present in the contemporary community, but cannot be measured in lake sediments using skeletal remains alone. However, with the application of emerging molecular techniques, we may be able to identify a greater range of subfossil zooplankton diversity (e.g. Montero-Pau, Gómez & Muñoz, 2008; Briski *et al.*, 2011). A notable exception to the general patterns apparent with the pelagic Cladocerans was the positive relationship between species richness and nutrient loading in Roxton Pond. This trend is driven by the addition of a single taxon, which is an invasive the invasive *Eubosmina coregoni*, and coincides with the eutrophication of this lake as it has in others (e.g. Suchy, Salki & Hann, 2010).

Our study has demonstrated that organisms of different trophic levels have similar negative biodiversity responses to nutrient enrichment both across space and through time. Aquatic ecosystems that are species poor tend to be more susceptible to stressors such as warming, acidification and eutrophication (Vinebrooke *et al.*, 2004; Cardinale, 2011). With current trends of increased global warming (Walther *et al.*, 2002) and intensive agriculture (Tilman *et al.*, 2001), freshwater ecosystems will be increasingly subjected to multiple stressors and will be susceptible to reduced resilience in the face of environ-

mental change (Scheffer *et al.*, 2001). Evidence from our study suggests that preserving littoral habitat heterogeneity via reductions in nutrient loading promotes a higher biodiversity of algal and zooplankton assemblages, potentially increasing the resilience of lake ecosystems to cumulative environmental impacts.

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### Supporting Information

Additional Supporting Information may be found in the online version of this article:

**Appendix S1.** Roxton Pond chronology.

**Appendix S2.** Sedimentation rates across lakes and species richness estimates.

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