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LETTER

Evenness effects mask richness effects on ecosystem functioning at macro-scales in lakes

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Abstract

Biodiversity–ecosystem functioning (BEF) theory has largely focused on species richness, although studies have demonstrated that evenness may have stronger effects. While theory and numerous small-scale studies support positive BEF relationships, regional studies have documented negative effects of evenness on ecosystem functioning. We analysed a lake dataset spanning the continental US to evaluate whether strong evenness effects are common at broad spatial scales and if BEF relationships are similar across diverse regions and trophic levels. At the continental scale, phytoplankton evenness explained more variance in phytoplankton and zooplankton resource use efficiency (RUE; ratio of biomass to resources) than richness. For individual regions, slopes of phytoplankton evenness–RUE relationships were consistently negative and positive for phytoplankton and zooplankton RUE, respectively, and most slopes did not significantly differ among regions. Findings suggest that negative evenness effects may be more common than previously documented and are not exceptions restricted to highly disturbed systems.

Keywords

Biodiversity, ecosystem functioning, evenness, lakes, macrosystems, National Lakes Assessment, phytoplankton, richness, zooplankton.

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INTRODUCTION

Concern over the effects of global biodiversity loss on ecosystem functioning and the provisioning of ecosystem services has contributed to a rich literature base of biodiversity–ecosystem functioning (BEF) experimental and theoretical studies over the past three decades (e.g. Tilman *et al.* 1996; Loreau 1998; Eisenhauer *et al.* 2016). Meta-analyses have demonstrated positive relationships between biodiversity and ecosystem functioning across ecosystem types (Cardinale *et al.* 2012), which are thought to result from either more complete use of resources in more diverse communities (complementarity) or increased probability of selecting taxa with certain functional traits in these communities (selection effects), although specific mechanisms depend on both environmental and trait variability (Huston 1997; Tilman *et al.* 1997; Cardinale *et al.* 2011; Hodapp *et al.* 2016). Because BEF theory is largely advanced from studies on terrestrial ecosystems, these same relationships may not translate to aquatic ecosystems due to differences in ecosystem properties or organismal traits (Giller *et al.* 2004; Daam *et al.* 2019).

Recent debate surrounding interpretation of static or increasing temporal trends in local species richness and studies demonstrating that these trends may not be sensitive indicators of biodiversity change (Cardinale *et al.* 2018; Hillebrand *et al.* 2018; Larsen *et al.* 2018) justify the need for a more complete understanding of BEF relationships. The focus on species richness as the primary measure of biodiversity has resulted in a poor understanding of the effects of other biodiversity metrics on ecosystem functioning (Wilsey *et al.* 2005; Hillebrand *et al.* 2008; Hillebrand & Matthiessen 2009; Hooper *et al.* 2012). Evenness has been demonstrated to have stronger effects on ecosystem functioning than richness in regional observational and small-scale experimental studies, although the direction of these effects has differed (e.g. Wilsey & Potvin 2000; Filstrup *et al.* 2014a; Hodapp *et al.* 2015). While positive effects of evenness on ecosystem functioning align with theoretical expectations (more equitable distribution of different functional traits), negative effects were hypothesised to be driven by selection effects (functional traits of the dominant species) in highly disturbed ecosystems where the dominant taxa had the highest rates of functioning (Filstrup *et al.* 2014a). Similar negative effects may not hold in more heterogeneous landscapes with diverse resource pools, however, where a single dominant taxon is unlikely to use resources as completely as a more even community (Hodapp *et al.* 2016). Because these relationships have not been adequately tested, it is unknown whether negative effects of evenness on ecosystem functioning are rare and restricted to certain extreme ecosystem conditions or whether they are common across diverse environmental conditions.

Furthermore, most BEF studies have focused on biodiversity effects within individual trophic levels (i.e. horizontal biodiversity effects), whereas few studies have examined the magnitude and direction of biodiversity effects across multiple trophic levels (i.e. vertical biodiversity effects; Duffy *et al.* 2007). Previous studies that have considered biodiversity effects of primary producers across trophic levels have found that horizontal and vertical biodiversity effects can have differing effects on food web and ecosystem functioning (Srivastava & Bell 2009; Filstrup *et al.* 2014a). Because primary producers have functional traits that influence growth and competition (resource capture) vs. susceptibility to herbivory (predator defences), the allocation of energy to different combinations of life history strategies could lead to differing biodiversity effects within and across trophic levels (Tilman 1990; Duffy 2002). Furthermore, the causal direction of relationships between prey biodiversity and herbivory is complex. While a more equitable distribution of prey may lead to more complete consumption, grazing pressure may also help maintain prey coexistence by restricting competitive exclusion to both low (fast growing prey species) and high (herbivory resistant prey species) rates of grazing, although even these relationships can vary depending on functional traits of competing taxa (Sarnelle 2005). These functional traits may lead to heterogeneous responses of ecosystem functions to biodiversity changes that do not align with theoretical expectations, and therefore hinder our ability to predict ecosystem responses to global change.

Additionally, BEF theory has largely advanced from short-term, small-scale experimental plots, but it is unknown how these results extrapolate to broad spatial scales (i.e. regional to continental; Naeem & Wright 2003; Symstad *et al.* 2003; Cardinale *et al.* 2012). Because more species are needed to maintain ecosystem function when considering more years, places and functions (Isbell *et al.* 2011; Lefcheck *et al.* 2015), this knowledge gap remains a critical barrier to understanding broad-scale ecosystem responses to biodiversity changes under the context of global change, including those both within and across different geographical regions (e.g. with variable climate or land use). It was previously difficult to address these knowledge gaps because broad-scale ecological experiments were impractical and long-term observational data were rare (but see Harpole *et al.* 2016). Continental-scale environmental monitoring programmes offer novel opportunities to expand our knowledge of BEF relationships based on observations along wide ecological gradients. Thus far, freshwater studies at the continental scale have not looked at differences in the effects of species richness and evenness on ecosystem functioning or examined differences among trophic levels (e.g. Stomp *et al.* 2011; Zimmerman & Cardinale 2014; Zwart *et al.* 2015).

Here, we tested the effects of richness and evenness on ecosystem functioning in lakes to determine whether BEF relationships follow theoretical expectations at broad spatial scales and whether BEF relationships are consistent across diverse regions (both in direction and magnitude). We used phytoplankton genus richness and evenness as biodiversity metrics and the resource use efficiency (RUE; ratio of biomass to resource) of phytoplankton and zooplankton communities as measures of ecosystem functioning for 1130 lakes distributed across the continental US. We hypothesised that (1) evenness would have stronger effects than richness on ecosystem functioning, (2) phytoplankton evenness would consistently have negative effects on phytoplankton RUE (RUE_{pp}) but positive effects on zooplankton RUE (RUE_{zp}) and (3) model parameters describing BEF relationships would differ among regions. Briefly, we found that phytoplankton evenness had stronger effects than richness on RUE within most regions, that the direction of BEF relationships differed across trophic levels and that the slopes of relationships did not significantly differ among most regions.

MATERIALS AND METHODS

Dataset used

We used data from the US Environmental Protection Agency's (USEPA) 2012 National Lakes Assessment (NLA), which includes lakes spanning the continental US. Sample lakes were chosen using a random stratified sample design (by EPA ecoregion and lake area) from a population of freshwater lakes, ponds and reservoirs ≥ 1 ha in area, ≥ 1 m in depth, ≥ 0.1 ha of open water and ≥ 1-week retention time (USEPA 2016a). Additionally, a small number of lakes considered 'least disturbed' was targeted to serve as reference lakes based on federal, state and tribe recommendations that were screened for water quality or visual inspection of human disturbance (USEPA 2017). Field crews sampled each lake once during the months of May through September, and some locations were sampled twice for quality control and assurance; however, we only selected one sample per lake, which were labelled index sites by the EPA (first sample or sample with associated habitat data) (USEPA 2016a). We used both random and least disturbed sites, resulting in 1130 unique lakes for our study (Fig. 1).

Detailed sampling methods and identification of phytoplankton and zooplankton can be found in the USEPA field and lab manuals (USEPA 2011; USEPA 2012). Briefly, samples for total phosphorus (TP), chlorophyll-a (Chl-a) and phytoplankton were collected using an integrated collection tube from the top 2 m of the water column at the deepest part of a lake (USEPA 2011). Zooplankton samples were collected using a vertical tow through the water column using two net mesh sizes, with a cumulative tow length of 5 m (USEPA 2011). TP samples were digested with persulfate and analysed using the automated ascorbic acid colorimetric method (USEPA 2012). Chl-a samples were filtered in the field, extracted in 90% acetone and measured by fluorometry or visible spectrophotometry (USEPA 2012). Phytoplankton and zooplankton were identified to the lowest possible taxonomic level (i.e. species when possible; USEPA 2012). Phytoplankton were counted until a minimum of 400 natural taxonomic units from a minimum of eight fields of view or one complete transect were identified in each sample. In highly eutrophic lakes with high algal biomass contributed by few taxa, such as those experiencing algal blooms, the counting method may underestimate the number of rare taxa, which would subsequently bias biodiversity measures for these lakes. EPA laboratories quantified cell biovolume for phytoplankton taxa by multiplying the abundance (cell mL^{-1}) by the average biovolume of each cell (μm^3; USEPA 2012). Zooplankton biomass was estimated for individuals from published length–width relationships for each species, then the mean biomass was multiplied by the species abundance for each sample (USEPA 2012).

The USEPA datasets were acquired from NLA raw data files (USEPA 2016b) and we made several *a priori* data decisions. We considered diversity based on living organisms; therefore, we excluded cysts from our total phytoplankton biovolume calculations. Zooplankton biomass was calculated as total zooplankton biomass across all taxa for individuals > 50 μm (NLA designation: ZOFN). Because of concerns

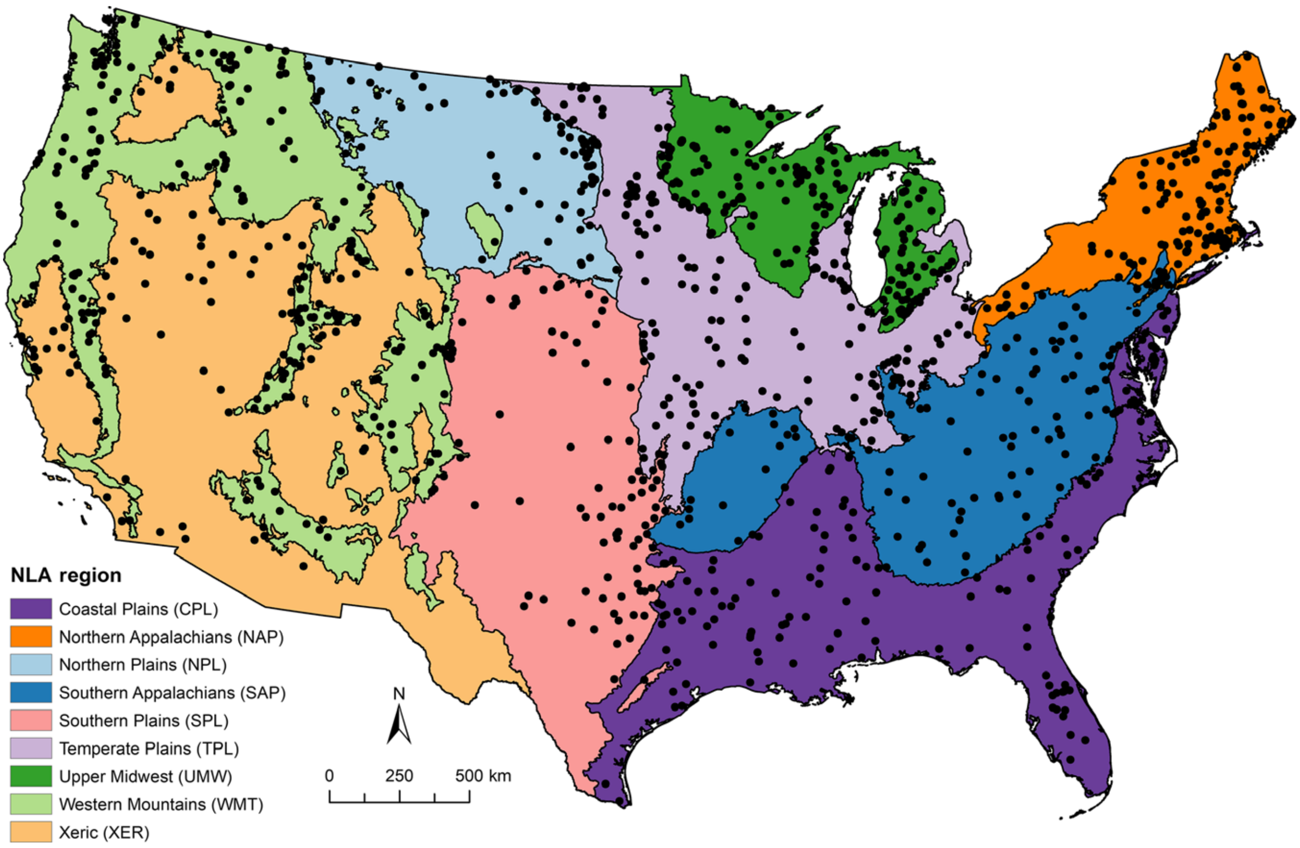

Figure 1 Regions and sampled lakes (n = 1130; points) in the 2012 National Lakes Assessment (NLA) database.

surrounding cross-laboratory identifications at species level, we aggregated taxonomy to genus level when calculating biodiversity metrics, consistent with the taxonomic resolution of previous studies (Ptacnik *et al*. 2008; Filstrup *et al*. 2014a). Generic taxonomic names were assigned as unique identifiers when organisms were only identified to higher taxonomic levels (i.e. genus names were missing). Although we realise that this may underestimate biodiversity, especially richness, if multiple genera are aggregated into higher taxonomic levels, we wanted to account for these organisms that were morphologically different from other identified taxa.

Derived variable calculation and statistical considerations

We used two biodiversity metrics to investigate BEF relationships in lakes across regions. Phytoplankton richness was quantified as the number of unique genera within a lake. Phytoplankton evenness was calculated as Pielou's evenness using biovolume proportions, where low numbers indicate less evenness in communities. Both metrics were quantified within the 'VEGAN' R package (Oksanen *et al.,* 2018).

As measures of lake ecosystem functioning, we evaluated RUE of phytoplankton (RUE$_{pp}$) and zooplankton (RUE$_{zp}$) communities, which quantifies the ratio of realised to potential productivity (Hodapp *et al*. 2019). Simply, RUE represents the amount of standing stock biomass per unit resource in lakes. RUE$_{pp}$ was calculated as the ratio of phytoplankton biovolume to TP concentrations, whereas RUE$_{zp}$ was calculated as the ratio of zooplankton biomass to phytoplankton biovolume (Ptacnik *et al*. 2008; Filstrup *et al*. 2014a).

We modelled relationships among RUE, phytoplankton diversity and phytoplankton biomass using parametric and nonparametric approaches and evaluated statistical differences among regional relationships using analysis of covariance (ANCOVA). To be consistent with previous studies, we used ordinary least squares regression to model bivariate relationships between RUE and phytoplankton genus richness or evenness. Because of potential biases introduced by phytoplankton counting methods for low evenness samples, we also sequentially modelled RUE – evenness relationships using trimmed datasets, in which the lower and upper 2.5% followed by 5.0% of evenness values were removed, to determine whether relationships derived from the full dataset held. Additionally, generalised additive models (GAMs) using cubic regression splines ('MGCV' R package; Wood 2011) were used to evaluate the joint and individual effects of phytoplankton richness, phytoplankton evenness and phytoplankton biomass (estimated as Chl-a) on RUE and to allow for nonlinearities in these effects. Chl-a was used as an overall measure of lake productivity because other measures that are commonly used to assess lake productivity (i.e. TP and phytoplankton biovolume) were used to calculate ecosystem functioning measures. ANCOVA was used to evaluate whether regional differences in richness or evenness affect variation in RUE. If the region × biodiversity interaction term was significant for a particular ANCOVA model, then we used *post hoc* pairwise comparisons to identify significant differences in slopes among regions using the 'EMMEANS' R package (Lenth 2018). $\mathrm{RUE}_{\mathrm{pp}}$ and $\mathrm{RUE}_{\mathrm{zp}}$ were natural log-transformed prior to analyses while Chl-a was natural log $(x + 0.1)$ transformed to meet assumptions of homoscedasticity and symmetrical distribution of residuals. Statistical analyses were performed using R version 3.5 (R Core Team 2018). Data and R scripts are available at Filstrup *et al.* (2019).

RESULTS

Biodiversity effects within and across trophic levels

Phytoplankton diversity metrics and ecosystem functioning measures varied widely across lakes in the NLA dataset. Lakes varied from oligotrophic to hyper-eutrophic conditions, in which Chl-a concentrations ranged from < 0.1 to 764.6 $\mu g\ L^{-1}$ (median = 8.0 $\mu g\ L^{-1}$). Genus richness ranged from 1 to 41, with a median of 16 genera. Pielou's evenness ranged from < 0.01 to 0.85 (median = 0.56), resulting in a distribution that was slightly negatively skewed. Although phytoplankton genus richness and evenness were significantly correlated, the correlation was weak ($r = 0.22$, $P < 0.001$; Fig. S1). Additionally, phytoplankton genus richness and evenness were only weakly related to Chl-a and variables used to calculate RUE (i.e. TP, phytoplankton biovolume, zooplankton biomass), with the strongest relationship occurring between phytoplankton genus evenness and phytoplankton biovolume ($r = -0.32$, $P < 0.001$; Fig. S1). Although several strong correlations existed among water quality variables that are commonly related in lakes (i.e. TP, Chl-a, phytoplankton biovolume; Fig. S1), the weak correlation structure among biodiversity measures and water quality variables allowed us to evaluate the joint and individual effects of these three predictors in subsequent multivariate models (see below). Distributions for $\mathrm{RUE}_{\mathrm{pp}}$ and $\mathrm{RUE}_{\mathrm{zp}}$ were both strongly positively skewed. $\mathrm{RUE}_{\mathrm{pp}}$ ranged across five orders of magnitude (range: < 0.01–2.65; median: 0.05), whereas $\mathrm{RUE}_{\mathrm{zp}}$ ranged across seven orders of magnitude (range: < 0.01–4928.68; median: 12.37).

Across all lakes at the continental scale, biodiversity measures explained little variance in $\mathrm{RUE}_{\mathrm{pp}}$ and $\mathrm{RUE}_{\mathrm{zp}}$, with phytoplankton evenness explaining slightly more variance than phytoplankton richness. $\mathrm{RUE}_{\mathrm{pp}}$ was significantly positively related to phytoplankton richness ($F_{1,1128} = 65.6$; $P < 0.001$; adj. $r^2 = 0.05$), but was significantly negatively related to phytoplankton evenness ($F_{1,1122} = 95.0$; $P < 0.001$; adj. $r^2 = 0.08$; Fig. 2a, b). $\mathrm{RUE}_{\mathrm{zp}}$ was not significantly related to phytoplankton richness ($P = 0.964$), but was significantly positively related to phytoplankton evenness ($F_{1,1122} = 119.5$; $P < 0.001$; adj. $r^2 = 0.10$; Fig. 2c, d). Nonlinearities in these bivariate relationships were evaluated using GAMs, but analyses did not lead to substantial increases in the amount of explained variance in $\mathrm{RUE}_{\mathrm{pp}}$ or $\mathrm{RUE}_{\mathrm{zp}}$ and the $\mathrm{RUE}_{\mathrm{zp}}$–richness relationship remained not significant ($P = 1.000$; not shown).

Linear relationships between phytoplankton evenness and RUE developed using the trimmed datasets were similar to models based on the full dataset, although the amount of explained variance decreased slightly with progressively restricted datasets. $\mathrm{RUE}_{\mathrm{pp}}$ was significantly negatively related to phytoplankton evenness for each dataset, with evenness in the 95.0 and 90.0% trimmed datasets explaining 6.7% ($F_{1,1064} = 77.6$; $P < 0.001$) and 5.1% ($F_{1,1008} = 55.1$; $P < 0.001$) of variance in $\mathrm{RUE}_{\mathrm{pp}}$, respectively. $\mathrm{RUE}_{\mathrm{zp}}$–phytoplankton evenness relationships had a significant positive slope for each dataset, in which explained variance decreased from 6.8% for the 95.0% trimmed dataset ($F_{1,1054} = 77.8$; $P < 0.001$) to 4.7% for the 90.0% trimmed dataset ($F_{1,998} = 49.7$; $P < 0.001$).

GAMs including phytoplankton richness, phytoplankton evenness and Chl-a (proxy for phytoplankton biomass) as predictors explained more variance in $\mathrm{RUE}_{\mathrm{pp}}$ and $\mathrm{RUE}_{\mathrm{zp}}$ than any of the predictors did individually. Models explained 29.4% of variance (deviance explained = 30.1%) in $\mathrm{RUE}_{\mathrm{pp}}$ with phytoplankton richness, phytoplankton evenness and Chl-a as significant predictors. When holding other predictors constant, $\mathrm{RUE}_{\mathrm{pp}}$ displayed positive saturating relationships with phytoplankton richness and Chl-a, but a negative nearly linear relationship with phytoplankton evenness (Fig. 3a–c). Models explained 25.7% of variance (deviance explained = 26.7%) in $\mathrm{RUE}_{\mathrm{zp}}$ with phytoplankton richness, phytoplankton evenness and Chl-a as significant predictors. When accounting for variation in other predictors, $\mathrm{RUE}_{\mathrm{zp}}$ displayed a positive nearly linear relationship with phytoplankton evenness and a non-linear decreasing relationship with Chl-a, but did not display a discernable monotonic relationship with phytoplankton richness (Fig. 3d–f).

Regional BEF relationships

Measures of ecosystem functioning for both phytoplankton and zooplankton overlapped considerably among regions. Pairwise comparisons revealed that both phytoplankton richness and evenness were lower in some western regions (Xeric, Western Mountains) and the Northern Plains and higher in some central and eastern regions (Fig. S2a, b). $\mathrm{RUE}_{\mathrm{pp}}$ in the Western Mountains, Xeric and Northern Plains regions was statistically similar ($P \geq 0.396$) but often significantly lower than in other regions ($P \leq 0.085$; Fig. S2c). For $\mathrm{RUE}_{\mathrm{zp}}$, the Temperate Plains and Xeric regions were both significantly lower than the Northern Appalachians (t-ratio = 4.284, $P < 0.050$ and t-ratio = 3.587, $P < 0.050$, respectively) and Western Mountains (t-ratio = −4.146, $P < 0.050$ and t-ratio = 3.351, $P < 0.050$, respectively), and the Temperate Plains were also significantly lower than the Northern Plains (t-ratio = 3.398, $P < 0.050$; Fig. S2d).

Within individual regions, $\mathrm{RUE}_{\mathrm{pp}}$ was consistently positively and negatively related to phytoplankton richness and evenness, respectively, although the strength of these relationships differed among regions (Fig. 4a, b). $\mathrm{RUE}_{\mathrm{pp}}$–richness relationships were significant in four of nine regions, with the amount of explained variance ranging from 3 to 12% (Table S1). In contrast, evenness had a significant negative effect on $\mathrm{RUE}_{\mathrm{pp}}$ in seven of nine regions, with the amount of explained variance ranging from 2 to 28%. While $\mathrm{RUE}_{\mathrm{zp}}$ was not significantly related to phytoplankton richness within individual regions, it was significantly and positively related to phytoplankton evenness in eight of nine regions (Fig. 4c, d). The Southern Appalachian region was the only one that did

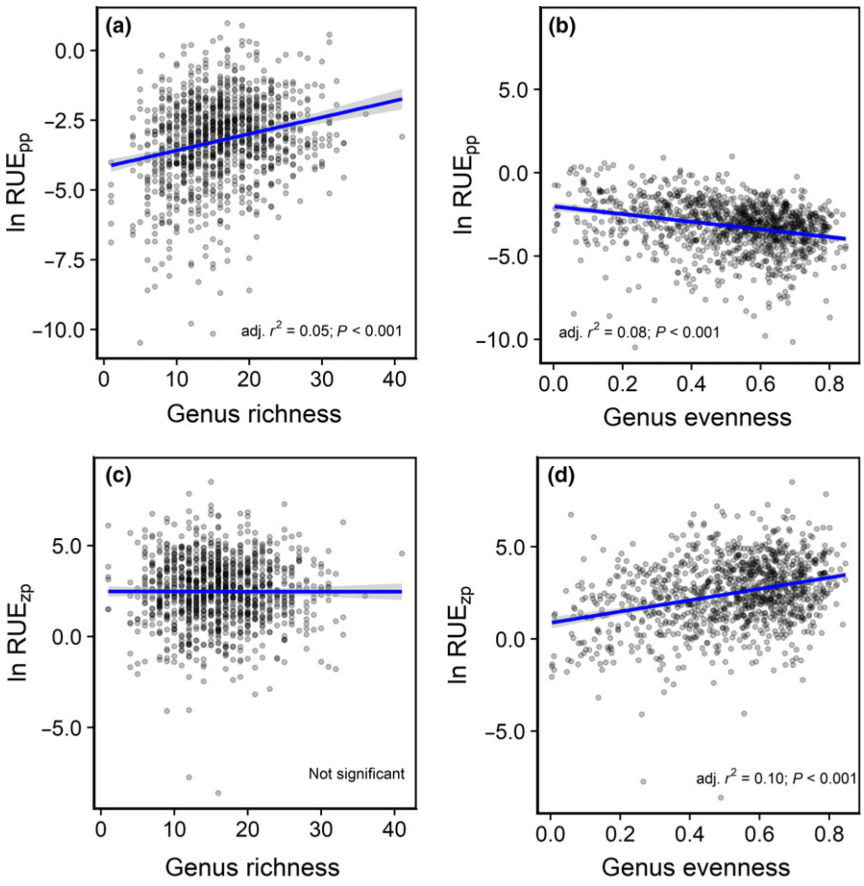

Figure 2 Biodiversity–ecosystem functioning relationships across all lakes. Response variables are resource use efficiency of phytoplankton (RUE_{pp}; top row) and zooplankton (RUE_{zp}; bottom row), with phytoplankton genus richness (left column) and phytoplankton genus evenness (right column) serving as predictor variables. Grey-shaded region represents 95% confidence intervals. Response variables were natural log-transformed prior to analyses.

not display a significant RUE_{zp}–evenness relationship. Phytoplankton evenness explained 6–18% of the variance in RUE_{zp} (Table S1).

Counter to expectations, slopes of BEF relationships did not significantly differ among regions, with very few exceptions (Table 1). Interaction terms between either richness or evenness and region were not significant for ANCOVA models of RUE_{pp} or RUE_{zp} vs. richness and RUE_{zp} vs. evenness. The ANCOVA model of RUE_{pp} vs. evenness had a significant interaction term, but the only significant differences in regional slopes were between the most negative slope (Xeric) and regional slopes that were not significant (i.e. flat relationships; Northern Plains and Temperate Plains). Specifically, the Xeric region had a more negative slope than either the Northern Plains (t-ratio = −3.346, $P < 0.050$) or Temperate Plains (t-ratio = −3.345, $P < 0.050$) regions (Table S2).

DISCUSSION

While most BEF studies have largely focused on richness effects at small spatial scales to unravel underlying mechanisms, our study of lakes across the continental US demonstrated that phytoplankton evenness had stronger effects on RUE_{pp} and RUE_{zp} than phytoplankton richness and that phytoplankton evenness had opposing effects on the functioning of primary producer communities (RUE_{pp}; horizontal effects) vs. that of herbivore communities (RUE_{zp}; vertical effects). These strong evenness effects were maintained when accounting for variation in phytoplankton richness and phytoplankton biomass (Chl-a) and were not artefacts of potential biases in phytoplankton counting methods. At regional scales, evenness consistently had negative effects on RUE_{pp} and positive effects on RUE_{zp}, whereas phytoplankton richness only had significant positive effects on RUE_{pp} for few regions and no significant effects on RUE_{zp}. Furthermore, biodiversity effects were consistent across regions despite large differences in landscape characteristics (e.g. topography, land use and land cover), climate and species composition, suggesting that they may be the rule rather than the exception in lake plankton communities.

Biodiversity effects within and across trophic levels

Although strong evenness effects on ecosystem functioning have been demonstrated in previous regional studies (e.g. Filstrup *et al.* 2014a; Hodapp *et al.* 2015), our study extends these relationships to continental scales (Figs 2 and 3), thereby echoing recent calls to consider measures of biodiversity beyond richness in BEF relationships (Hillebrand *et al.* 2018; Larsen *et al.* 2018). Evenness has been argued to be

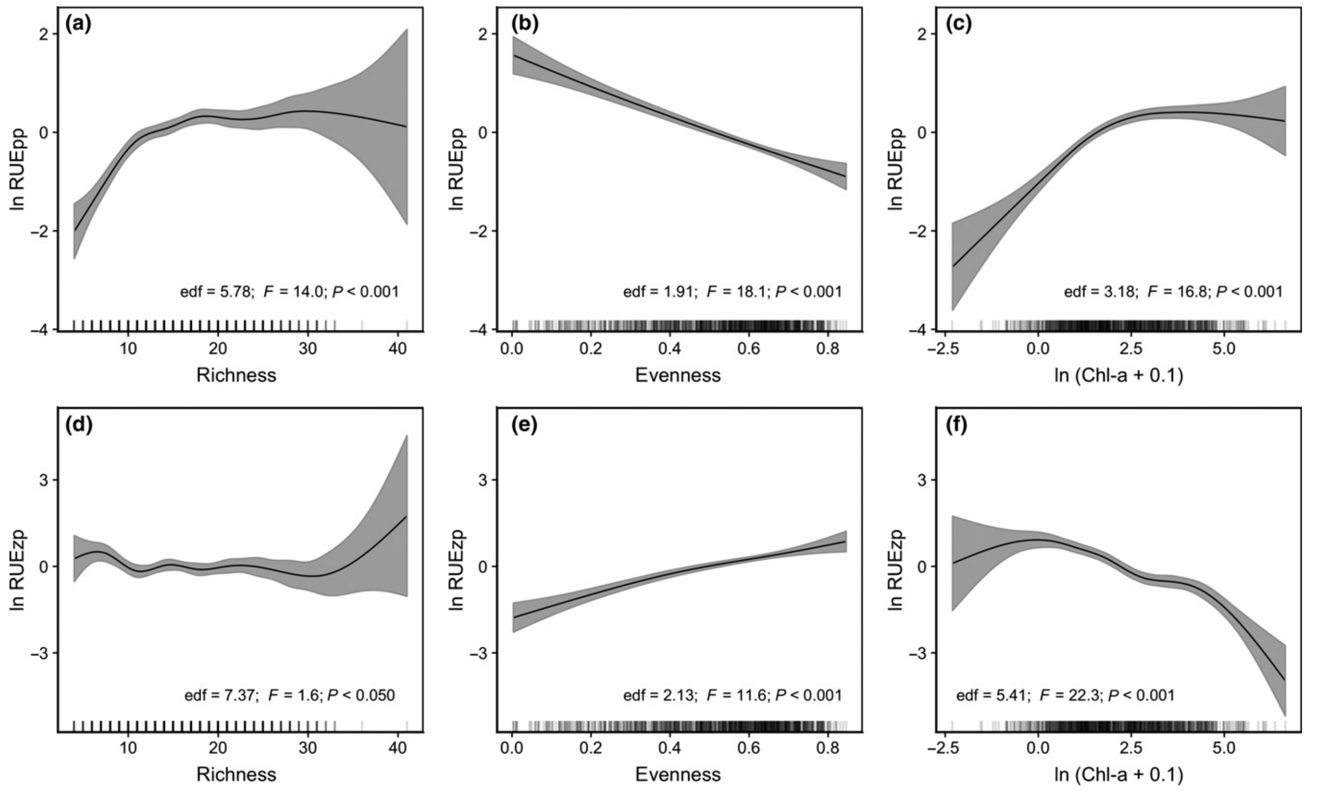

Figure 3 Generalised additive models of resource use efficiency of phytoplankton (RUE_{pp}; top row) and zooplankton (RUE_{zp}; bottom row) as functions of phytoplankton genus richness, phytoplankton genus evenness and chlorophyll *a* (Chl-a). Grey-shaded region represents 95% confidence intervals. Effective degrees of freedom (edf) represents the smoothness of the relationship, where an edf = 1 approximates a linear relationship and higher edf values represent increasingly complex curves. The 'rug' (lines above *x*-axis) represents the location of data points along the *x*-axis. Response variables were natural log-transformed prior to analyses while Chl-a was natural log (x + 0.1) transformed.

more sensitive to environmental change than richness because species tend to become rare in communities before becoming extinct (Hillebrand *et al.* 2008; Hillebrand & Matthiessen 2009). Findings from our study further suggest that ecosystem function may be more sensitive to changes in evenness than changes in richness. Therefore, it may be the equitable distribution of functional traits, rather than simply their number, that drive ecosystem function (Hillebrand *et al.* 2008). Evenness may better reflect contributions to an ecosystem function at any period of time by minimising the influence of rare species, although current rare species may be important contributors to overall ecosystem functioning at other places, at other times, or when considering other functions (Isbell *et al.* 2011; Lefcheck *et al.* 2015).

Additionally, our study has demonstrated that the same aspect of biodiversity can have different effects on functioning when evaluated within vs. across trophic levels, thereby supporting findings of a previous regional study (Fig. 2; Filstrup *et al.* 2014a). While positive evenness effects on RUE_{zp} align with theoretical expectations, negative effects of evenness on RUE_{pp} seem to counter them (e.g. Hillebrand *et al.* 2008; Cardinale *et al.* 2012). Because the direction of relationships for either RUE_{pp} or RUE_{zp} was consistent across regions, findings suggest that these relationships are not exceptions restricted to highly disturbed systems, as previously suggested (Fig. 3; Filstrup *et al.* 2014a). Based on the scales considered in this study, negative evenness effects on RUE_{pp} may even occur throughout heterogeneous landscapes with diverse resource bases (see Hodapp *et al.* 2016). Hodapp *et al.* (2019) did caution that biodiversity effects on RUE may be considerably variable, however, and may ultimately depend on functional traits related to resource uptake.

Previous studies have postulated that opposing effects of evenness within and across trophic levels were due to selection effects based on functional traits of the dominant taxa. In highly disturbed lakes, cyanobacteria were thought to have keystone effects on ecosystem functioning because of their large cell sizes, and therefore biovolumes, compared to eukaryotic algae (Filstrup *et al.* 2014a; Heathcote *et al.* 2016). Larger cell sizes would translate to higher RUE_{pp} when cyanobacteria dominate (low evenness), but this would also decrease RUE_{zp} by increasing the proportion of inedible algae. As biomass becomes more equitably distributed in the phytoplankton communities, the strength of these keystone effects would be reduced. Likewise, Hodapp *et al.* (2015) found similar negative effects of evenness on RUE_{pp} in marine phytoplankton communities, in which the dominant taxa were those that had the largest cell sizes.

In contrast to previous studies, low evenness lakes in our study included several different taxonomic groups as the dominant taxon, suggesting that biodiversity itself, rather than

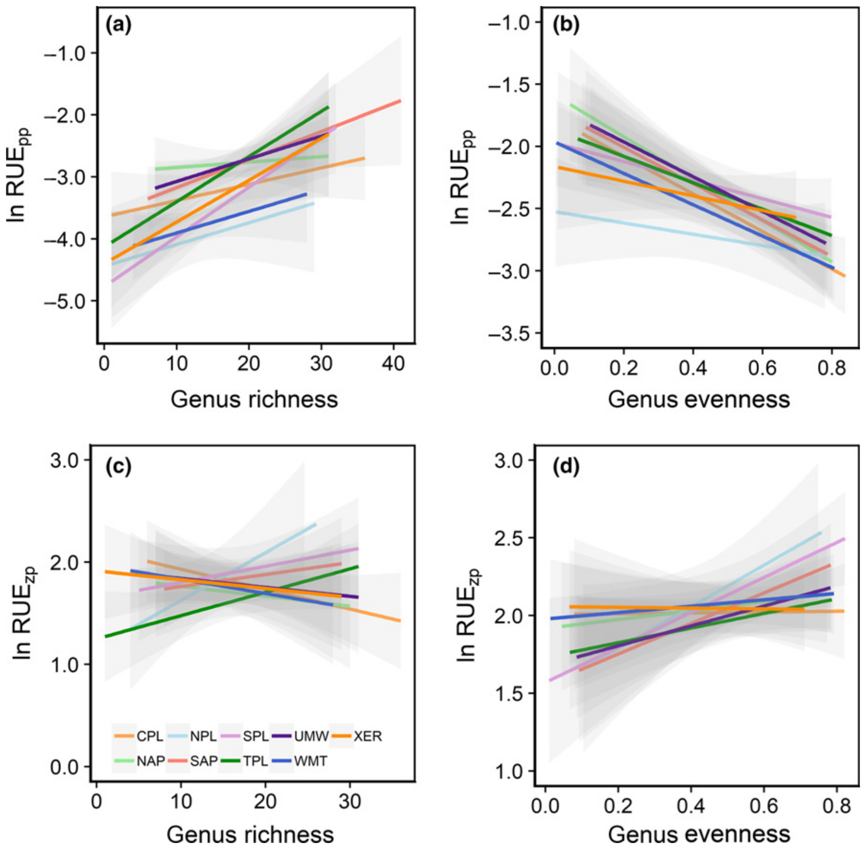

Figure 4 Biodiversity–ecosystem functioning relationships by region. Response variables are resource use efficiency of phytoplankton (RUE_{pp}; top row) and zooplankton (RUE_{zp}; bottom row), with genus richness (left column) and evenness (right column) serving as predictor variables. Lines are colour coded by region to match colours displayed in Fig. 1. Grey-shaded region represents 95% confidence intervals. Response variables were natural log-transformed prior to analyses.

functional traits of a specific taxon, was influencing observed BEF relationships. Of the 32 samples with phytoplankton taxonomic evenness < 0.10, dominant taxa included cyanobacteria (15 lakes), dinoflagellates (eight lakes), green algae (three lakes), golden algae (two lakes) and diatoms (one lake), which have diverse life history strategies, competitive abilities and resistance to grazing. Although cyanobacteria were the predominate taxon in almost half of these samples, their contribution remains much lower than that of a previous regional study, where cyanobacteria dominated in almost all of the low evenness lakes (Filstrup *et al.* 2014a). We did not assess functional traits of these dominate taxa, however, so it is possible that they share common characteristics, such as larger individual or colonial sizes, that may be influencing relationships. If driven by biodiversity, then the negative relationship between evenness and RUE_{pp} at the primary producer level may stem from a decrease in the relative abundance of the best-performing taxon, which tends to dominate in aquatic ecosystems (i.e. similar to selection effects when considering richness). Here, best performing refers to the ability to produce the most biomass per unit limiting resource, although it is not clear whether dominance of these taxa results from competition for limiting nutrients under low grazing pressure (i.e. competitive exclusion), resistance to herbivory under high grazing pressure or both (McCauley & Briand 1979; Worm *et al.* 2002; Steiner 2003). At the herbivore level, however, prey communities dominated by a single taxon create a limited resource base, whereas more equitable distribution of prey allows for more efficient use of resources. Therefore, our findings seem to support bottom-up regulation of ecosystem function, in which resource competition drives competitive exclusion at the primary producer level and resource heterogeneity drives trophic transfer efficiency at the herbivore level.

Alternatively, top-down regulation of phytoplankton community structure may be influencing BEF relationships observed in this study. Using the same continental-scale dataset used in our study, Yuan & Pollard (2018) found that cyanobacteria proportion explained a low amount of variance between RUE_{zp} models, indicating that both bottom-up and top-down processes determined zooplankton biomass in nutrient-rich lakes. There is a large body of literature demonstrating the importance of grazing pressure on shaping prey diversity, in which prey communities tend to be most diverse under moderate levels of grazing by promoting coexistence of competing prey (e.g. Paine 1966; McCauley & Briand 1979; Leibold 1996). Under high grazing pressure, phytoplankton communities can shift towards dominance by either grazing resistant taxa or by taxa with high resource-saturated growth rates (Sarnelle 2005), whereas prey can dominate through resource competition under low grazing pressure (resource-

Table 1 Analysis of covariance results for biodiversity–ecosystem functioning relationships by region with associated degrees of freedom (d.f.), sum of squares (SS), mean square error (MSE), *F* value and *P* values for the model

Model terms	d.f.	SS	MSE	*F* value	*P* value
Model 1: RUE_{pp} = richness × region					
Richness	1	144.79	144.79	68.65	**< 0.001**
Region	8	126.48	15.81	7.50	**< 0.001**
Richness × region	8	18.68	2.33	1.11	0.356
Error	1112	2345.44	2.11		
Model 2: RUE_{pp} = evenness × region					
Evenness	1	203.09	203.09	106.79	**< 0.001**
Region	8	247.21	30.90	16.25	**< 0.001**
Evenness × region	8	47.23	5.90	3.10	**< 0.010**
Error	1106	2103.30	1.90		
Model 3: RUE_{zp} = richness × region					
Richness	1	0.01	0.01	< 0.01	0.964
Region	8	120.08	15.01	4.61	**< 0.001**
Richness × region	8	17.92	2.24	0.69	0.703
Error	1102	3590.46	3.26		
Model 4. RUE_{zp} = evenness × region					
Evenness	1	360.13	360.13	123.63	**< 0.001**
Region	8	134.48	16.81	5.77	**< 0.001**
Evenness × region	8	23.33	2.92	1.00	0.433
Error	1096	3192.54	2.91		

Model terms included phytoplankton richness or evenness, region and an interaction term. Response variables were natural log-transformed prior to analyses. Significance was assessed at $\alpha = 0.05$ and significant values are in bold font.

ratio theory; McCauley & Briand 1979; Tilman 1982). Additionally, grazing by planktivorous fish can strongly regulate zooplankton biomass and composition, as well as nutrient recycling rates that can ultimately lead to trophic cascades on phytoplankton community structure (Vanni & Findlay 1990; Carpenter *et al*. 2001). Because the NLA dataset lacks fish data, we could not evaluate fish standing stocks as a covariate to help explain residual variance in BEF relationships. Although both bottom-up and top-down processes may be occurring, our findings provide support for bottom-up processes as strong forces regulating phytoplankton and zooplankton functioning in these lakes.

While we focused on evenness in this study due to its stronger effects on ecosystem functions, richness and phytoplankton biomass (measured as Chl-a) also had significant effects on RUE_{pp} and RUE_{zp}, thereby highlighting the complexity of biodiversity, productivity and ecosystem functioning relationships (Fig. 3; Cardinale *et al*. 2009; Hodapp *et al*. 2015). Compared to evenness, richness had weaker effects on RUE_{pp}, which supports findings from previous studies on natural and experimental phytoplankton communities (Ptacnik *et al*. 2008; Striebel *et al*. 2009). The saturating effect of phytoplankton richness on RUE_{pp} agrees with previous theoretical and empirical studies of richness–biomass relationships that have been attributed to functional redundancy of species in diverse communities (Fig. 3a; Cardinale *et al*. 2012). Richness effects did not translate to higher trophic levels, however, suggesting that it is the equitable distribution of biomass across prey species, not the number of prey species that drives trophic transfer efficiency (Fig. 3d; see resource capture hypothesis; Tilman *et al*. 1996; Cardinale *et al*. 2012).

Regional variation in BEF relationships

Although we anticipated that the direction of BEF relationships would be consistent for individual regions, we were surprised that the slopes of these relationships did not significantly differ among most regions (Fig. 4; Table 1). We anticipated that large gradients in climate, hydrogeology and land use across the entire study extent would lead to either regional or more localised effects that would modify BEF relationships. For comparison, previous studies have demonstrated that regional landscape characteristics can alter nutrient–primary producer relationships in lakes across broad spatial extents (e.g. Filstrup *et al*. 2014b; Fergus *et al*. 2016). The rate at which primary producer biomass changes in response to changes in limiting nutrient concentrations in these studies (i.e. relationship slopes), which is analogous to RUE_{pp} in our study, differs by region. While we found minimal differences in RUE among regions, these same regional landscape characteristics did not similarly modify BEF relationships in our study.

Consistent BEF relationship slopes should not be interpreted as increasing evenness having consistent effects on one measure of ecosystem functioning regardless of geographical setting or functional traits of the species pool. More likely, this finding suggests either that (1) factors influencing BEF relationships are more localised and are not adequately characterised at regional scales used in this study, (2) the random stratified design of the NLA masked regional landscape differences and therefore led to consistent BEF relationships or (3) differences in regional slopes were not large enough to be discerned by the statistical power of the sampling design. Future studies of BEF relationships at continental scales would need to consider these factors when determining sampling design and interpreting analyses.

Linking BEF studies across spatial scales

Whereas most previous BEF studies were conducted at local to regional scales, our study employed a distinctly macroscale approach. Macroecological approaches often seek emergent, general relationships using data-intensive empiricism, but typically at the cost of overlooking local, and potentially important, mediating variables (McGill 2019). Nonetheless, previous studies have demonstrated the importance of local (e.g. lake species composition) and regional (e.g. land use/cover) mechanisms in BEF and nutrient–primary producer relationships. Therefore, a challenge for future BEF studies is linking and quantifying the importance of processes operating across spatial scales (i.e. local to regional to continental). In our study, we were not surprised that phytoplankton richness and evenness explained little variance (1–10%) in ecosystem functioning across 1130 lakes in the continental US compared to previous local and regional studies because of large differences in climate, land use, hydrology and other ecological characteristics. While the variance explained (2–28%) by richness and evenness for individual regions was within the range of previous regional studies, there remained a substantial amount of unexplained variance in these relationships. Much of this unexplained variance may be attributable to local processes or cross-scale interactions or both that neither distinctly local-scale nor distinctly macro-scale studies are able to reveal (Soranno *et al*. 2014). Additionally, potential biases in detailed taxonomic identifications across laboratories or in counting methods applied to certain lake types, which may be inherent in similar large-scale monitoring programmes, may contribute to high amounts of unexplained variance in macro-scale research. In future work, we urge use of a macrosystems ecology framework (Heffernan *et al*. 2014) for integrating multi-scale processes in BEF relationships. Such an approach could lead to a more complete understanding of the drivers of BEF relationships across spatial scales and help provide a unifying conceptual framework for individual BEF studies conducted at local, regional or macro-scales.

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AUTHORSHIP

CTF and KBSK designed the study. CTF and KBSK performed analyses. IMM performed exploratory analyses. CTF, KBSK and IMM designed figures. CTF, KBSK and IMM wrote the manuscript. IMM prepared code for archiving.

DATA AVAILABILITY STATEMENT

Data and analysis scripts are available at https://doi.org/10.5281/zenodo.3440182 (Filstrup *et al*. 2019).

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SUPPORTING INFORMATION

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

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