

Herbivore regulation of plant abundance in aquatic ecosystems

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ABSTRACT

Herbivory is a fundamental process that controls primary producer abundance and regulates energy and nutrient flows to higher trophic levels. Despite the recent proliferation of small-scale studies on herbivore effects on aquatic plants, there remains limited understanding of the factors that control consumer regulation of vascular plants in aquatic ecosystems. Our current knowledge of the regulation of primary producers has hindered efforts to understand the structure and functioning of aquatic ecosystems, and to manage such ecosystems effectively. We conducted a global meta-analysis of the outcomes of plant–herbivore interactions using a data set comprised of 326 values from 163 studies, in order to test two mechanistic hypotheses: first, that greater negative changes in plant abundance would be associated with higher herbivore biomass densities; second, that the magnitude of changes in plant abundance would vary with herbivore taxonomic identity. We found evidence that plant abundance declined with increased herbivore density, with plants eliminated at high densities. Significant between-taxa differences in impact were detected, with insects associated with smaller reductions in plant abundance than all other taxa. Similarly, birds caused smaller reductions in plant abundance than echinoderms, fish, or molluscs. Furthermore, larger reductions in plant abundance were detected for fish relative to crustaceans. We found a positive relationship between herbivore species richness and change in plant abundance, with the strongest reductions in plant abundance reported for low herbivore species richness, suggesting that greater herbivore diversity may protect against large reductions in plant abundance. Finally, we found that herbivore–plant nativeness was a key factor affecting the magnitude of herbivore impacts on plant abundance across a wide range of species assemblages. Assemblages comprised of invasive herbivores and native plant assemblages were associated with greater reductions in plant abundance compared with invasive herbivores and invasive plants, native herbivores and invasive plants, native herbivores and mixed-nativeness plants, and native herbivores and native plants. By contrast, assemblages comprised of native herbivores and invasive plants were associated with lower reductions in plant abundance compared with both mixed-nativeness herbivores and native plants, and native herbivores and native plants. However, the effects of herbivore–plant nativeness on changes in plant abundance were reduced at high herbivore densities. Our mean reductions in aquatic plant abundance are greater than those reported in the literature for terrestrial plants, but lower than aquatic algae. Our findings highlight the need for a substantial shift in how biologists incorporate plant–herbivore interactions into theories of aquatic ecosystem structure and functioning. Currently, the failure to incorporate top-down effects continues to hinder our capacity to understand and manage the ecological dynamics of habitats that contain aquatic plants.

Key words: density-dependent effects, ecosystem structure and function, exclosure experiments, grazing impact, invasive non-native species, macrophyte standing crop, meta-analysis, resource–consumer interactions, trophic interactions.

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I. INTRODUCTION

Foraging by primary consumers on primary producers is a fundamental biotic process in nature. By controlling primary producer abundance, and regulating the flow of energy and nutrients between primary producers and higher trophic levels, interactions between primary producers and their herbivores play key roles in determining ecosystem structure, functioning and service provision (Hairston, Smith & Slobodkin, 1960; Huntly, 1991; Polis, 1999; Estes *et al.*, 2011). Globally, vascular plants are important primary producers across a range of ecosystems, and thus their regulation has important ecosystem-level consequences (Carpenter & Lodge, 1986; Engelhardt & Ritchie, 2001; Cronin, Lewis & Schiehsler, 2006).

The traditional view of ecologists has been that herbivore regulation of vascular plants did not occur in aquatic ecosystems. For example, Polunin (1984) considered that emergent macrophytes enter the food web only as detritus. Similarly, Gregory (1983, p. 161) concluded that 'living aquatic vascular macrophytes generally are not a major component of the diet of herbivores in lotic systems'. Furthermore, Wetzel (1983, p. 543) stated that herbivores typically remove less than 8% of total annual aquatic plant production. As a consequence, even recent aquatic ecology and food web texts omit mention of these interactions (e.g. Lampert & Sommer, 2007; Moore & de Ruiter, 2012). However, there is growing recognition that vascular aquatic plants are consumed by a range of taxa, principally birds (primarily waterbirds such as swans, geese, ducks, and rails), mammals, fish, crayfish, insects, echinoderms and molluscs (Prejs, 1984; Lodge, 1991; Newman, 1991; Lodge *et al.*, 1998). For example, Wood *et al.* (2012b) reported that, globally, there are 233 species of waterfowl that actively feed on plant tissues. Mammalian herbivores are particularly diverse in terms of foraging mode, as this group comprises true aquatic mammals (such as dugong *Dugong dugon*; Aragonés & Marsh, 2000), semi-aquatic diving species (such as beaver *Castor* spp.; Law, Jones & Wilby, 2014), and terrestrial species that wade into shallow waters to feed (such as moose *Alces alces*; Bergman & Bump, 2015). Interactions between herbivores and aquatic plants have been reported in a wide range of habitat types, including freshwater lakes, rivers, estuaries, wetlands, and shallow seas (Lodge *et al.*, 1998; Bakker *et al.*, 2016). Accordingly, interactions between herbivores and aquatic plants have a global distribution, having been observed from equatorial seas (de Iongh, Wenno & Meelis, 1995; Vonk, Pijnappels & Stapel, 2008) to Arctic wetlands (Gauthier *et al.*, 1995; Massé, Rochefort & Gauthier, 2001).

Indeed, it appears that herbivores are present wherever submerged, floating, or emergent plants are present. The only continent for which such interactions have not been reported is Antarctica, a region which lacks vascular aquatic plants.

There is a growing body of evidence that herbivores can regulate aquatic plant abundance (Cyr & Pace, 1993; Lodge *et al.*, 1998). However, the outcomes of plant–herbivore interactions appear to be highly variable across aquatic ecosystems. Numerous studies have experimentally excluded or enclosed herbivores in order to compare plant abundance with and without herbivores and quantified the outcomes of plant–herbivore interactions (e.g. Søndergaard *et al.*, 1996; Wass & Mitchell, 1998; Sarneel *et al.*, 2014). Such studies have reported a wide range of outcomes, such as strong negative effects of herbivores on aquatic plants (e.g. Stott & Robson, 1970; Silliman *et al.*, 2005; Law *et al.*, 2014), others report no effects (e.g. Roberts *et al.*, 1995), whilst some report positive effects of herbivory on aquatic plant abundance (e.g. Chambers *et al.*, 1990). Even within these broad outcomes, effect sizes are highly variable; across ecosystems reductions in plant abundance range from 0 to 100% (Cyr & Pace, 1993; Lodge *et al.*, 1998; Marklund *et al.*, 2002; Wood *et al.*, 2012b). However, such individual studies are typically limited in spatiotemporal and taxonomic extent, which raises doubts about how generally their conclusions apply. To allow us to understand the fundamental structure and functioning of ecosystems containing aquatic plants, as well as to manage such ecosystems under current and future conditions, we need to understand how the outcomes of plant–herbivore interactions are regulated.

The consistent methodology of the small-scale plant–herbivore studies allows a meta-analysis approach to be used to determine patterns across wide ranges of species and ecosystems (Poore *et al.*, 2012). Meta-analysis approaches have been used successfully to understand the factors which regulate the outcomes of plant–herbivore interactions in terrestrial ecosystems (Milchunas & Lauenroth, 1993; Hawkes & Sullivan, 2001) and for aquatic non-vascular primary producers (Hillebrand, 2002, 2009; Poore *et al.*, 2012). However, to date there have been no comprehensive studies of the factors which determine herbivore regulation of vascular primary producers in aquatic ecosystems.

In this study we address this deficit by conducting a global meta-analysis of the outcomes of plant–herbivore interactions, in order to test two mechanistic hypotheses. Previous studies have suggested that plant abundance appears to be negatively related to herbivore biomass density due to greater grazing pressure at high herbivore densities (Crivelli, 1983; Wood *et al.*, 2012b; Atkins *et al.*, 2015). Indeed,

Wood *et al.* (2012c) reported a significant linear relationship between mute swan (*Cygnus olor*) biomass density and the abundance of aquatic plants in shallow rivers. Therefore our first hypothesis was that greater negative changes in plant abundance would be associated with higher herbivore biomass densities. Similarly, small-scale studies have indicated that differences in herbivore taxonomic identity, linked to among-taxa differences in foraging ecology, physiology and behaviour, may be linked to variation in the magnitude of plant–herbivore interactions (Lodge *et al.*, 1998; Allcock & Hik, 2004). Thus, our second hypothesis was that the magnitude of changes in plant abundance would vary among different herbivore taxonomic groups.

II. METHODS

(1) Data collation

To locate suitable studies for our meta-analysis we performed a literature search using the following academic search engines: *ISI Web of Science*, *Scopus*, *JStor*, *PubMed* and *Google Scholar*. We used all 16 combinations of one herbivore search term ('herbivory', 'herbivore', 'grazing', 'grazer') together with one plant search term ('macrophyte', 'aquatic plant', 'aquatic vegetation', 'plant consumption') with the boolean operator 'AND'. The results of each search term were assessed for suitability for inclusion in our meta-analysis; we required studies to contain sufficient information to calculate change in plant abundance and the full range of explanatory variables. Additionally we searched previously published reviews and meta-analyses of aquatic herbivory for suitable studies (Lodge, 1991; Newman, 1991; Cyr & Pace, 1993; Lodge *et al.*, 1998; Valentine & Heck, 1999; Marklund *et al.*, 2002; Hughes *et al.*, 2004; Eklöf *et al.*, 2008; Poore *et al.*, 2012; Reeves & Lorch, 2012; Wood *et al.*, 2012b).

In order to conduct a comprehensive test of our two hypothesis it was necessary to account for a range of additional factors which previous individual studies have suggested may influence the outcomes of plant–herbivore interactions. For example, the classification of the herbivore and plant species as native or invasive (e.g. Stott & Robson, 1970; Parker, Burkepile & Hay, 2006; Korsten *et al.*, 2013), habitat type (Lodge *et al.*, 1998; Bergman & Bump, 2015), latitude (Schemske *et al.*, 2009; Morrison & Hay, 2012), phase of plant growth cycle (Cebrián & Duarte, 1994; Marklund *et al.*, 2002), size of experimental area and study length (Mitchell & Wass, 1996; Hillebrand, 2009), and herbivore and plant assemblage species richness (Lodge *et al.*, 1998), have each been suggested previously by localised studies to affect the outcome of interactions between primary consumers and vascular primary producers within aquatic ecosystems. Phases of the plant growth cycle comprised four possible classes, based on the phase in which the comparison between grazed and ungrazed treatments was reported by the study: growth, peak, winter, and transplant. We included transplant experiments as a distinct phase of the growth

cycle as transplanted plants may show different phenological and performance responses relative to locally adapted plants, and thus transplanted plants cannot be considered to occur under natural conditions in the growth cycle (Joshi *et al.*, 2001). Our approach also had the advantage of maximising data availability, by allowing us to include studies which used only transplant experiments.

We limited our meta-analysis to studies that used herbivore exclosure/enclosure or addition/removal experiments to measure vascular plant abundance both in the presence and absence of herbivores. To achieve maximum data availability we included studies of submerged, emergent, and floating vascular plant species, as such species have not been shown to differ in their responses to herbivory (e.g. Lodge *et al.*, 1998; Marklund *et al.*, 2002). We further limited our meta-analysis to studies where herbivore counts were made in a defined area over a defined period of time. The suitable studies categorised themselves as one or more of six aquatic habitat types: freshwater lakes, freshwater rivers, estuaries, wetlands, salt marshes, and marine habitats. We used the habitat type reported by each study to classify the habitat type for our analysis. As there is no universally accepted distinction between pond and lake (Sayer, 2014), for the purposes of our study we included ponds within the lake category. Whilst herbivore consumption rates may increase with body mass to a power of <1.0 (van Gils, Gyimesi & Van Lith, 2007; Wood *et al.*, 2012b), consumption is only one mechanism through which herbivores affect plant abundance, with others including trampling, and herbivore-induced changes in nutrient availability (e.g. through faecal deposition) and light climate (Mitchell & Wass, 1996; Hobbs & Searle, 2005). As the allometric scaling factors for non-consumptive mechanisms are typically unknown, we assumed a mass exponent of 1.0 in our conversion of individual to biomass densities as a conservative approximation.

We limited our analysis to studies that had measured plant abundance as fresh or dry mass biomass per unit area, and excluded those which reported only alternative measures of abundance such as percentage cover, volume or stem densities. We did this because different measures of plant abundance, whilst typically correlated, may not always show identical temporal trends in abundance (Wood *et al.*, 2012a) and may not show the same response to herbivory (Gayet *et al.*, 2011); including these could have introduced additional variance and limited our ability to detect changes in plant abundance due to our explanatory factors. We compared plant abundance with and without herbivores at the time of maximal standing crop in the 'without herbivores' treatment, after Wood *et al.* (2012b). Where studies contained multiple values of changes in plant abundance that were not statistically independent we calculated mean values for such changes and for herbivore density. Where data were presented in graphs, we extracted values from pdf versions using DataThief (Tummers, 2006). We calculated the percentage reduction in plant abundance (C) as: $C = -[(A_{\text{Herbivore Absent}} - A_{\text{Herbivore Present}})/A_{\text{Herbivore Absent}}] \times 100$, where $A_{\text{Herbivore Present}}$ and $A_{\text{Herbivore Absent}}$ are plant

abundance with and without herbivores present, respectively. The percentage change in plant abundance is the standard metric used in previous meta-analyses of herbivore effects on plants (Milchunas & Lauenroth, 1993; Lodge *et al.*, 1998; Marklund *et al.*, 2002). Similarly, following the approaches of these previous studies we did not consider statistical significance reported by individual studies, due to high levels of inter-study variance in test type and statistical power (Lodge *et al.*, 1998; Marklund *et al.*, 2002).

For each suitable study we also recorded the values of each predictor variable as given in the studies. Herbivore biomass density (g live mass m⁻²) was calculated as the total mass of herbivores (mean individual mass multiplied by the mean number of individuals present over the study period) divided by the study area size. Where information on sex and age ratios was presented, we used sex- and age-specific biomass values. Where no such information was presented we assumed an equal sex ratio and that all individuals were adults, and the mean mass of males and females was used in our biomass calculations. Herbivore taxa were recorded as Bird, Mammal, Crustacean, Mollusc, Insect, Fish, and Echinoderm. We limited our meta-analysis to studies that presented data for individual taxa, either where only one herbivore taxon was present or where the effects of different taxa were experimentally separated through careful enclosure design (e.g. Evers *et al.*, 1998; Wong, Kwong & Qiu, 2009).

(2) Statistical analyses

To meet the normality assumptions associated with our Gaussian linear models, values of *C* were rescaled between 0 and 1 and arcsine square-root transformed. Herbivore taxa, habitat type and herbivore–plant nativeness were treated as categorical factors. Herbivore density, latitude, size of experimental area, study length, herbivore assemblage species richness, and plant assemblage species richness were treated as covariates and were log₁₀-transformed to achieve linearity of relationship and normal distribution of residuals. To address our two hypotheses, we used linear models with Gaussian error structures to test the effects of (i) herbivore taxa; (ii) herbivore density; (iii) the nativeness of the herbivore and plant assemblage; (iv) habitat type; (v) latitude; (vi) phase of plant growth cycle; (vii) size of experimental area; (viii) study length; (ix) herbivore assemblage species richness; and (x) plant assemblage species richness, on percentage change in plant abundance (*C*). To identify issues with multicollinearity (Graham, 2003) we calculated the variance inflation factor (VIF), which measures the degree to which variances of regression coefficients are inflated relative to unrelated variables, associated with each of our continuous predictor variables (Aho, 2014). VIFs were calculated as $VIF = 1/(1 - R^2)$, based on the R^2 value associated with a linear regression of a predictor variable on all other predictor variables in our data set. Following the approach recommended by Aho (2014), we judged that multicollinearity was excessively influencing the efficiency and reliability of parameter estimation where $VIF > 5$.

We carried out full subset model selection in order to test all possible combinations of additive and two-way interaction terms using the *glmulti* package in R (Calcagno & de Mazancourt, 2010; R Development Core Team, 2015). For each candidate model we calculated the value of second-order Akaike's Information Criteria, corrected for small sample size relative to the number of predictor variables (AIC_c). The model with the lowest AIC_c value was judged to be our best-supported model, whilst any model with a ΔAIC_c value within 2.0 of the best-supported model was also considered to have substantial support in the data (*sensu* Burnham & Anderson, 2004). To facilitate detailed model comparison we also calculated the relative likelihood and Akaike weight associated with each candidate model, as indicators of relative strength of model support in the data (Aho, 2014). Furthermore, we used R^2_{adj} values to indicate the percentage of the variance in change in plant abundance explained by each model. *Post-hoc* differences between different levels of categorical factors were determined using Tukey's HSD. We present the 10 best-supported models in addition to a model comprised of the intercept alone. All statistical analyses were performed with R version 3.1.2 (R Development Core Team, 2015), with a significant effect attributed where $P < 0.05$.

III. RESULTS

From our meta-analysis we found 326 values for herbivore-induced changes in plant abundance from 163 published studies for the period 1961 to 2014 (see online Appendix S1). These studies exhibited large ranges in the values associated with our explanatory variables (see online Appendix S2). The variance inflation factors associated with each of our predictor variables were all < 5 (range = 1.79–4.35), indicating no issues with multicollinearity and thus there was no need to exclude any of our predictor variables from any candidate model (see online Appendix S3).

Across all studies we found a substantial range in observed herbivore-induced changes in plant abundance from –100 to +76% (see online Appendix S1), with a mean $\pm 95\%$ CI change of $-47.2 \pm 3.4\%$. The median change in abundance was -47.3% . Of the 326 experimental results, negative changes in plant abundance were reported in 300, positive changes in 21, and no change in five experiments (i.e. $\pm 0\%$). Complete elimination of plant above-ground standing crop (i.e. -100%) was reported in 11 experiments.

Variance in observed herbivore-induced change in plant abundance (*C*) was best explained by a model comprising herbivore biomass density, herbivore taxa, plant–herbivore nativeness, herbivore species richness, and an interaction between herbivore density and herbivore–plant nativeness (Tables 1 and 2). Across all taxa, herbivore biomass density exhibited a negative relationship with change in plant abundance (Fig. 1). Our best-supported model indicated an effect of herbivore taxa on mean reductions

Table 1. The 10 best-supported linear models (and null model) of change in plant abundance, as determined by corrected Akaike’s information criteria (AIC_c). *n* = 326 for all candidate models. The best-supported model is indicated in bold. Values of *k* refer to the number of fitted parameters in each candidate model

Model	<i>k</i>	AIC _c	ΔAIC _c	Relative likelihood	Akaike weights	<i>R</i> ² _{adj} (%)
<i>i</i>+<i>D</i>*<i>N</i>+<i>T</i>+<i>R</i>	23	−279.65	0.00	1.00	0.181	47.3
<i>i</i> + <i>D</i> * <i>N</i> + <i>T</i> + <i>R</i> + <i>S</i>	24	−279.55	0.10	0.95	0.172	47.4
<i>i</i> + <i>D</i> * <i>N</i> + <i>T</i> + <i>R</i> + <i>L</i>	24	−279.44	0.21	0.90	0.163	47.4
<i>i</i> + <i>D</i> * <i>N</i> + <i>T</i> + <i>R</i> + <i>S</i> + <i>L</i>	25	−278.85	0.80	0.67	0.122	47.5
<i>i</i> + <i>D</i> * <i>N</i> + <i>T</i> + <i>R</i> + <i>S</i> + <i>E</i>	25	−277.61	2.04	0.36	0.065	47.3
<i>i</i> + <i>D</i> * <i>N</i> + <i>T</i> + <i>R</i> + <i>P</i>	24	−277.31	2.35	0.31	0.056	47.1
<i>i</i> + <i>D</i> * <i>N</i> + <i>T</i> + <i>R</i> * <i>S</i>	25	−277.28	2.38	0.30	0.055	47.3
<i>i</i> + <i>D</i> * <i>N</i> + <i>T</i> + <i>R</i> * <i>L</i>	25	−277.14	2.51	0.28	0.052	47.3
<i>i</i> + <i>D</i> * <i>N</i> + <i>T</i>	22	−276.80	2.86	0.24	0.044	46.6
<i>i</i> + <i>D</i> * <i>N</i> + <i>T</i> + <i>S</i>	23	−276.59	3.07	0.22	0.039	46.8
<i>i</i>	1	−96.20	183.45	0.00	0.000	0.0

Predictor variables: *i*, intercept; *T*, herbivore taxa; *D*, herbivore density (g m^{−2}); *N*, nativeness of the herbivore and plant assemblages; *G*, stage of the plant annual growth cycle; *H*, habitat type; *R*, herbivore species richness; *P*, plant species richness; *L*, latitude (° from equator); *E*, size of experimental area such as enclosure or exclosure (m²); *S*, length of study (days).

in plant abundance (Table 2; Fig. 2). In particular, *post-hoc* comparisons indicated that insects were associated with lower reductions in plant abundance compared with all other taxa. Birds were associated with lower reductions in plant abundance than echinoderms, fish, and molluscs. Finally, crustaceans were associated with lower reductions in plant abundance compared with fish (Fig. 2). No other significant between-taxa differences were detected. We found evidence of an effect of herbivore–plant nativeness on changes in plant abundance (Table 2; Fig. 3). *Post-hoc* comparisons indicated that assemblages comprised of invasive herbivores and native plant assemblages were associated with greater reductions in plant abundance compared with invasive herbivores and invasive plants, native herbivores and invasive plants, native herbivores and mixed-nativeness plants, and native herbivores and native plants (Fig. 3; see online Appendix S4). By contrast, assemblages comprised of native herbivores and invasive plants were associated with lower reductions in plant abundance compared with both mixed-nativeness herbivores and native plants, and native herbivores and native plants (Fig. 3; see online Appendix S4). No other significant between-nativeness differences were detected. Furthermore, our best-supported model indicated a negative interaction between herbivore biomass density and herbivore–plant nativeness, such that the effect of nativeness on change in plant abundance was reduced at higher herbivore densities (Table 2). Across all studies, we found evidence of a positive relationship between herbivore species richness and change in plant abundance, with the strongest reductions in plant abundance reported for low herbivore species richness (Table 2; Fig. 4).

Our best-supported model explained 47.3% of the variance in changes in plant abundance (Table 1). The null model, comprised of an intercept alone, had a ΔAIC_c value of 183.5 relative to our best-supported model, effectively receiving no support in the data. Only two other candidate models were found to have an associated AIC_c value

within 2.0 of our best-supported model (Table 1). However, compared to our best-supported model, both alternative models were less parsimonious in terms of the number of fitted parameters, had higher AIC_c values, and lower relative likelihood and Akaike weights values, and thus were not considered further (Table 1).

IV. DISCUSSION

Our meta-analysis indicated that, in contrast to the traditional view of ecologists, herbivory is an important biotic process in aquatic ecosystems across a wide range of latitudes, habitat types and species assemblages. Despite the strong evidence for herbivore limitation of plant abundance presented here, herbivory as a structuring force in aquatic ecosystems has been poorly studied relative to bottom-up factors such as nutrient availability, light limitation and water temperature (Bornette & Puijalon, 2011). Our study is the first to yield a comprehensive understanding of how the outcomes of interactions between herbivores and vascular aquatic plants are regulated across a global range of aquatic ecosystems (all continents except Antarctica, spanning 3.3–73.3° from the equator). With 326 experimental results from 163 studies, our study represents the most comprehensive assessment to date of herbivore-induced changes in aquatic plants. Our study indicates that, in accordance with our two hypotheses, the magnitude of interactions between primary consumers and primary producers are determined by herbivore biomass density, herbivore species richness, and herbivore taxonomic identity, and that the nativeness of assemblages appears also to play a role.

The herbivore-induced changes in plant abundance identified in this meta-analysis were almost exclusively negative, with reductions reported for 300 of 326 experiments. The mean (±95% CI) change in plant

Table 2. The mean and S.E. effect sizes of the \log_{10} -transformed predictor variables in our best-supported linear model on the arcsine square-root transformed change in plant abundance

Variable	Parameter estimate	Parameter estimate S.E.
Intercept	0.362	0.043
Herbivore density	−0.077	0.023
Herbivore taxon (Birds)	—	—
Herbivore taxon (Mammals)	0.182	0.046
Herbivore taxon (Crustaceans)	0.323	0.045
Herbivore taxon (Molluscs)	0.316	0.053
Herbivore taxon (Insects)	0.165	0.039
Herbivore taxon (Fish)	0.275	0.043
Herbivore taxon (Echinoderms)	0.334	0.056
Herbivore species richness	0.091	0.041
Nativeness (II)	—	—
Nativeness (IM)	0.122	0.059
Nativeness (IN)	0.236	0.044
Nativeness (MM)	−0.051	0.648
Nativeness (MN)	0.065	0.080
Nativeness (NI)	0.134	0.046
Nativeness (NM)	0.167	0.061
Nativeness (NN)	0.112	0.035
Herbivore density : Nativeness (II)	—	—
Herbivore density : Nativeness (IM)	−0.108	0.037
Herbivore density : Nativeness (IN)	−0.152	0.027
Herbivore density : Nativeness (MM)	−0.053	0.530
Herbivore density : Nativeness (MN)	−0.066	0.050
Herbivore density : Nativeness (NI)	0.010	0.033
Herbivore density : Nativeness (NM)	−0.088	0.047
Herbivore density : Nativeness (NN)	−0.070	0.022

The table represents the best-supported model and had the form: C , intercept + herbivore density + herbivore taxon + herbivore species richness + herbivore–plant nativeness + (herbivore density \times nativeness). Nativeness of the herbivore and plant assemblages: NN, native herbivores and native plants; IN, invasive herbivores and native plants; MN, mixed herbivores and native plants; II, invasive herbivores and invasive plants; IM, invasive herbivores and mixed plants; MI, mixed herbivores and invasive plants; MM, mixed herbivores and mixed plants; NM, native herbivores and mixed plants; NI, native herbivores and invasive plants. The values for all other herbivore taxa are relative to birds, whilst the values for all other herbivore–plant nativeness groups were relative to II.

abundance of $-47 \pm 3\%$ represents a substantial loss of physical habitat and rerouting of energy and nutrients within food webs. We found that the magnitude of reductions in plant abundance in aquatic habitats exceeded those typically reported for terrestrial ecosystems. Cyr & Pace (1993) estimated that herbivores were responsible for the median removal of 18, 30, and 79% of primary productivity of terrestrial plants, aquatic macrophytes, and aquatic algae, respectively. Subsequent authors argued that these values represented reductions in abundance rather than removal of primary productivity (Mitchell & Wass, 1996), and so are comparable to our values of reduction in abundance. We found a median change in aquatic plant biomass of -47% , greater than both terrestrial ecosystems and previous estimates for aquatic plants. Similarly, Milchunas

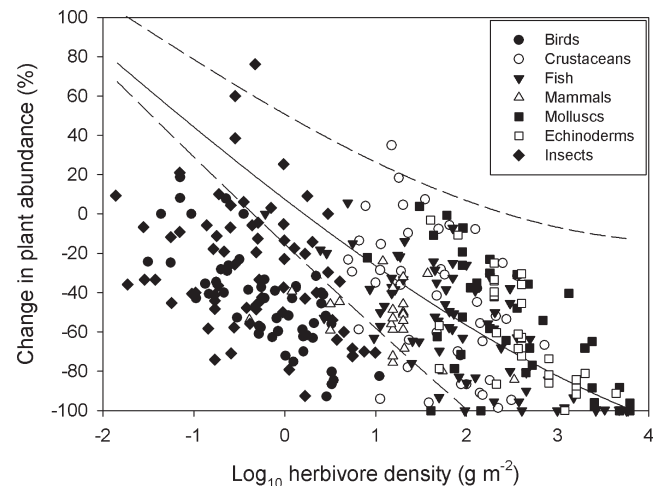


Fig. 1. The negative relationship between change in plant abundance and herbivore density across seven herbivore taxa. Data points represent observed values, while the fitted line represents the mean ($\pm 95\%$ CI; dashed lines) relationship based on our best-supported model (Table 2). Thus the fitted line does not match the data points perfectly as the fitted line also accounts for the effects of herbivore taxonomic identity, herbivore species richness, and herbivore–plant nativeness.

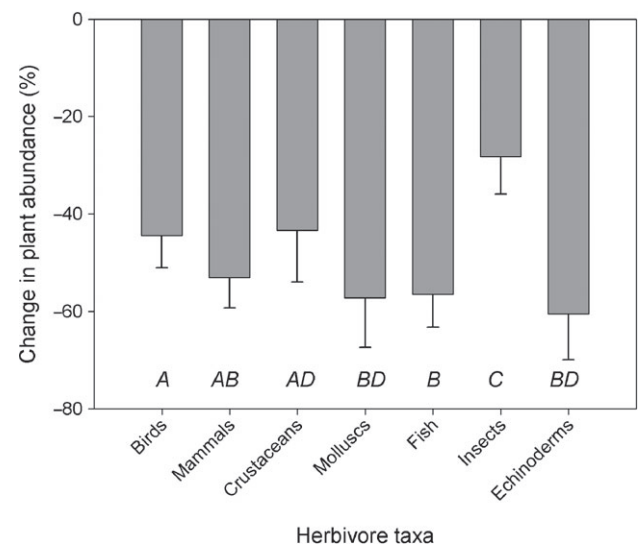


Fig. 2. Mean $\pm 95\%$ CI observed changes in aquatic plant abundance for each of our seven focal herbivore taxa. Different letters indicate significant *post-hoc* differences.

& Lauenroth (1993) reported a mean change in terrestrial plant abundance of -23% . Furthermore, Gruner *et al.* (2008) reported that herbivore removal typically led to increased primary producer abundance in freshwater and marine ecosystems, but no such pattern was detected for terrestrial ecosystems. However, our -47% median change in aquatic vascular plant abundance is still considerably less than those for algae within marine, brackish and freshwater ecosystems. For example, Hillebrand (2009) used a global meta-analysis to show a mean -59% change in periphyton abundance.

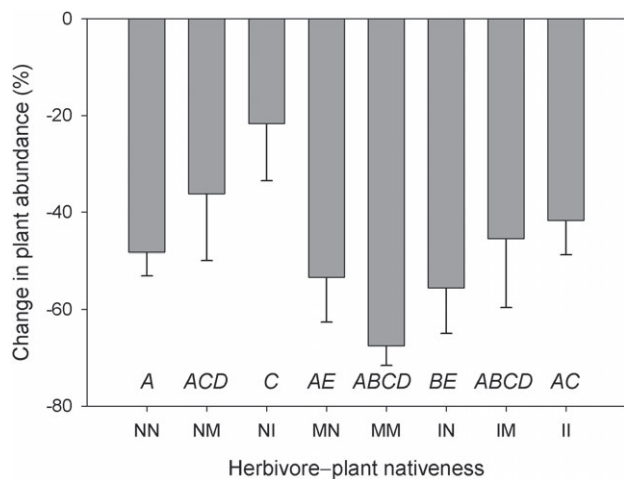


Fig. 3. Mean $\pm 95\%$ CI observed changes in aquatic plant abundance for each of our herbivore–plant nativeness groups. Group abbreviations: NN, native herbivores and native plants; NM, native herbivores and mixed plants; NI, native herbivores and invasive plants; MN, mixed herbivores and native plants; MM, mixed herbivores and mixed plants; IN, invasive herbivores and native plants; II, invasive herbivores and invasive plants; IM, invasive herbivores and mixed plants. No data were available for MI. Different letters below the columns indicate significant *post-hoc* differences between groups.

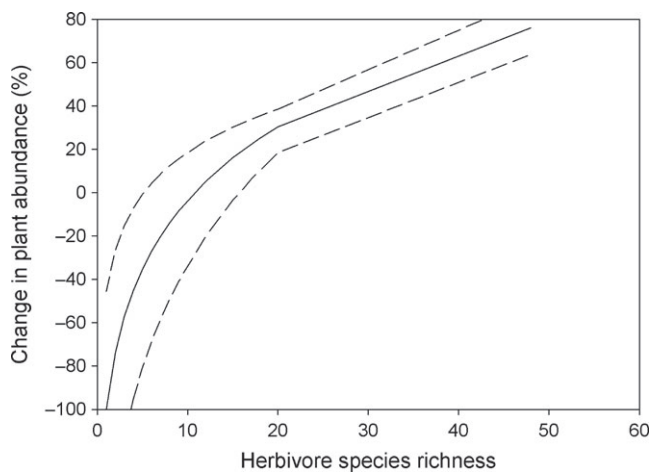


Fig. 4. The positive relationship between change in plant abundance and herbivore species richness. Data points represent observed values, while the fitted line represents the mean ($\pm 95\%$ CI; dashed lines) relationship based on our best-supported model (Table 2). The fitted line does not match the data points perfectly as it also accounts for the effects of herbivore density, herbivore taxonomic identity, and herbivore–plant nativeness.

Our findings highlight the need for a substantial shift in how ecologists incorporate plant–herbivore interactions into theories of aquatic ecosystem structure and functioning. We argue that, by regulating primary producer abundance, interactions between herbivores and vascular aquatic plants may play key roles in the maintenance of alternative stable states (e.g. Scheffer *et al.*, 2001). Furthermore,

we argue that changes in the relative abundance or composition of plant–herbivore assemblages may trigger trophic cascades that can shift ecosystems between alternative states (e.g. Carpenter, Kitchell & Hodgeson, 1985; Estes *et al.*, 2011). These mechanisms are equivalent to the previously documented interactions between phytoplankton and their zooplankton grazers (Scheffer *et al.*, 2001; Jones & Sayer, 2003). The failure to consider the importance of herbivory has been most acute among freshwater researchers (Lodge, 1991; Cebrián & Duarte, 1998; Klaassen & Nolet, 2007). By contrast, there has been greater appreciation of the roles of seagrass herbivores in estuaries and shallow seas (Thayer *et al.*, 1984; Heck & Valentine, 2006; Burkepile, 2013). Indeed, the similarities between plant–herbivore interactions within seagrass ecosystems, and those observed in terrestrial grazing lawns, have been highlighted recently (Burkepile, 2013; Bakker *et al.*, 2016). Such between-habitat differences were not supported by our finding of no effect of habitat type on the outcome of plant–herbivore interactions. Currently, key theories of aquatic ecosystem structure and functioning (e.g. Vannote *et al.*, 1980; Junk, Bayley & Sparks, 1989; Scheffer *et al.*, 2001) do not consider the possible role of herbivores in regulating vascular plant abundance, or the ecosystem consequences of such regulation. Our study builds on current evidence that aquatic herbivores can trigger shifts in ecosystem state, with losses of vascular plants and the ecosystem functions and services which they provide (Silliman *et al.*, 2005). Given the multiple roles of aquatic plants, the provision of goods and services in aquatic ecosystems is likely to be affected by herbivore-induced changes in plant abundance, in particular primary production which is a key supporting service. Annual primary productivity is positively related to peak biomass for aquatic plant communities (Duarte, 1989). Thus herbivore-induced losses in plant abundance can lead to substantial decreases in primary productivity, in particular where plants cannot regrow after herbivore damage (e.g. Silliman & Bertness, 2002). Furthermore, the loss of plant abundance will reduce their regulatory role on water movements, nutrient cycling and secondary production of animals (Eklöf *et al.*, 2008; Estes *et al.*, 2011).

Increased herbivore density represents greater grazing pressure on a plant community, with correspondingly higher quantities of plant tissues consumed and removed by non-consumptive mechanisms such as trampling (Hobbs & Searle, 2005; Wood *et al.*, 2012b). Thus it is unsurprising that changes in plant abundance were strongly negatively related to herbivore density, in accordance with our first hypothesis. Only at relatively low herbivore densities were positive changes in plant abundance reported, suggesting that in aquatic systems greater herbivore densities overwhelm plant compensatory growth responses. In support of our second hypothesis, we found substantial between-taxa differences in herbivore effects on plant abundance, with echinoderms, molluscs, and fish having relatively large impacts on plants, whilst insects and birds had relatively low impacts. Our findings concur with the recent research by Bakker *et al.*

(2016), which concluded that among herbivores the obligate aquatic species that live within water permanently have the greatest impacts on aquatic plants. The between-taxa differences we identified may be linked to differences in herbivore individual movement ability and foraging ecology. The observed result that bird herbivory was associated with smaller changes in plant abundance relative to most other taxa may be linked to inequalities in the movement ability of these taxa. Birds are highly mobile consumers which can, and frequently do, move between foraging sites in response to changes in site profitability (Nolet *et al.*, 2001; Gyimesi *et al.*, 2012; Wood *et al.*, 2013). At foraging sites where plant abundance becomes substantially depleted birds, unlike the other taxa in our study, can abandon the site and fly elsewhere. Thus bird-induced reductions in plant abundance may be lower than for other taxa which cannot easily move away from the foraging site. Similarly, adult insects capable of flight could move between foraging areas to avoid severe depletion. However, many studies in our meta-analyses concerned flightless life stages of insects which could not move between waterbodies. Here, the relatively low impact of insect herbivores may be explained by their high specificity for certain plant species and tissues, which means that only part of a heterogeneous plant community will be affected (Newman, 1991). This contrasts with the bulk-grazing strategies of many other herbivore taxa, such as echinoderms, molluscs and crayfish, which will consume multiple tissue types and species and will thus affect a greater proportion of a plant community (Lodge *et al.*, 1998). Whilst taxa other than birds and adult insects can also exhibit movements between habitats in response to food availability (e.g. crayfish; Grey & Jackson, 2012), such movements are typically over much shorter distances than birds; for example herbivorous waterfowl can undertake daily movements of up to 20 km between foraging and roosting sites (Newton, Thom & Brotherston, 1973). Another reason for the relatively low impact of bird herbivores may be that many aquatic bird species also consume seeds and animal matter, and thus the vegetative plant tissues which make up the majority of plant above-ground biomass comprises only a small part of their diet (Wood *et al.*, 2012b). Indeed, Wood *et al.* (2012b) showed that birds which were more herbivorous had a greater *per capita* effect on plant abundance than those that were more omnivorous. By contrast, the greatest reductions in plant abundance for a given herbivore density were reported for echinoderms and molluscs which are entirely herbivorous and cannot move quickly to new feeding areas in response to plant depletion. However, changes in plant abundance caused by birds and insects could still be substantial. For example, birds were associated with a mean and a maximum change of -44 and -93% respectively. Such high reductions may be expected to occur where alternative feeding areas are unavailable, or birds ability to move between sites is constrained, for example during their annual flightless moulting period (Dos Santos *et al.*, 2012).

Whilst some localised studies have documented large impacts of invasive herbivores on aquatic plants (e.g.

Stott & Robson, 1970; Carlsson, Brönmark & Hansson, 2004; Tatu *et al.*, 2007), we have shown for the first time that plant–herbivore nativeness is a key factor affecting the magnitude of herbivore impacts on plant abundance across a wide range of species assemblages. In particular, compared with native plants we found that invasive plants experience relatively small losses in biomass due to native herbivores, which may aid the establishment of invasive plants beyond their native range. The mean change in plant abundance associated with assemblages of native herbivores and invasive plants found in our study (-22%) was similar to that reported by Parker *et al.* (2006) for all ecosystems. However, the impacts of invasive herbivores were not consistently greater than native herbivores across all assemblages. Furthermore, the effect of nativeness on change in plant abundance was reduced at higher herbivore densities, perhaps because at high herbivore densities the opportunities for selective feeding on preferred species will be diminished because of competition among individuals (Schoener, 1971). Recent decades have seen an increased spread of both invasive herbivores and macrophytes, which suggests that the magnitude of plant–herbivore interactions may be varying over time in many invaded aquatic ecosystems in response to changes in the nativeness of species assemblages (Jackson & Grey, 2013; Evangelista, Thomaz & Umetsu, 2014).

Previous research has shown that greater diversity of the herbivore assemblage increased damage to primary producers (Duffy, Richardson & Canuel, 2003). However, in this study we found evidence for a positive relationship between herbivore species richness and change in plant abundance, with the strongest reductions in plant abundance reported for low herbivore species richness. The effect of herbivore species richness was not apparent in the observed data, and was only identified once the other key factors in our best-supported model (herbivore density, herbivore taxa, and herbivore–plant nativeness) had been accounted for. Indeed, many studies in our meta-analysis reported substantial reductions in plant abundance, of up to 100% , associated with only a single species of herbivore (e.g. Pípalová, 2002; Ip *et al.*, 2014; but see Coetzee, Byrne & Hill, 2007). By contrast, we found no effect of plant species richness on the size of the outcome of plant–herbivore interactions.

Our finding of no latitudinal gradient in herbivore effects on primary producers is consistent with other recent meta-analyses conducted for marine and terrestrial ecosystems (Gruner *et al.*, 2008; Hillebrand, 2009; Moles *et al.*, 2011; Poore *et al.*, 2012). Finally, we found no strong support for consistent differences in herbivore impact among different habitat types; reductions in plant abundance were equivalent across lake, river, estuary, wetland, salt marsh, and shallow-sea habitat types. Variation among habitat types identified in previous localised studies (Lodge *et al.*, 1998) may reflect differences in other factors, such as herbivore densities, rather than effects of habitat *per se*. Our habitat-type categories were broad, due to the limited information presented by individual studies that could be

used to classify habitats, and so future work should examine whether key habitat characteristics, such as productivity and nutrient status, can modulate plant–herbivore interactions. In particular, evidence from terrestrial ecosystems has suggested that differences in habitat productivity can affect plant–herbivore interactions (Bakker *et al.*, 2006). We were unable to consider habitat productivity in the current study as few of the studies we identified presented quantitative information on productivity.

We have shown here that herbivory is an important force in the control of plant abundance across aquatic systems, as has long been recognised for terrestrial plants and aquatic algae. However, herbivory is unlikely to be the sole driver of plant dynamics in most ecosystems. In particular, a range of bottom-up processes are known to influence plant abundance such as nutrient availability, light limitation, and temperature (Barko, Adams & Clesceri, 1986; Bornette & Puijalon, 2011). Therefore a key future challenge is to integrate our understanding of the regulatory effects of top-down (e.g. herbivory), bottom-up (e.g. nutrient availability), and competitive processes on plant abundance and ecosystem primary productivity (Hughes *et al.*, 2004; Gayet *et al.*, 2011; Wood *et al.*, 2012c; Sarneel *et al.*, 2014). Currently, our limited knowledge of multifactorial regulation of primary producers hinders efforts to manage aquatic ecosystems effectively (Chambers *et al.*, 1999; Bakker *et al.*, 2013).

V. CONCLUSIONS

(1) The traditional view of biologists has been that herbivore regulation of vascular plants did not occur in aquatic ecosystems, and thus even recent aquatic ecology and food web texts omit mention of these interactions (e.g. Lampert & Sommer, 2007; Moore & de Ruiter, 2012). By contrast, the role of herbivory in terrestrial ecosystems, and primary consumer–phytoplankton interactions in aquatic ecosystems, have long been recognised by researchers (McNaughton *et al.*, 1989; Milchunas & Lauenroth, 1993; Hillebrand, 2002; Estes *et al.*, 2011; Poore *et al.*, 2012). Despite the traditional view that herbivory played no significant role in aquatic plant dynamics, we found a growing literature on plant–herbivore interactions in aquatic ecosystems. The availability of numerous localised studies of herbivore effects on plant abundance, using comparable methodologies, allowed us to carry out a comprehensive meta-analysis of herbivore-induced changes in plant abundance across a wide range of species assemblages, geographic regions, and habitat types.

(2) We have demonstrated that herbivores are an important structuring force affecting aquatic plant abundance. In accordance with our two hypotheses, we found evidence that herbivore-induced changes in plant abundance varied between herbivore taxa and herbivore–plant nativeness, decreased with herbivore diversity, and increased with herbivore biomass density. We argue that the issue of whether herbivores can affect aquatic

plant abundance is increasingly well understood, and there is now overwhelming evidence that herbivores can reduce (and in some cases increase) plant abundance. Researchers should now focus on understanding the conditions under which herbivores exert such effects on aquatic plant abundance. We have shown here that both herbivore density and herbivore species richness, as well as the nativeness of the herbivore–plant assemblage, are key factors in understanding the magnitude of herbivore-induced changes in aquatic plant abundance.

(3) For aquatic ecosystems, the current failure to incorporate top-down effects continues to hinder our fundamental understanding of the functioning of ecosystems that contain aquatic plants. Furthermore, fundamental knowledge of the roles of such trophic interactions will help us to understand how aquatic ecosystems will respond to the sustained environmental change these systems are experiencing (Moss, 2015). If not accounted for, herbivory will confound our attempts to understand and predict responses in plant dynamics and the interactions of plants with other organisms, ecosystem processes and the physico-chemical environment (Reader, 1992). Furthermore, efforts to restore aquatic ecosystems to plant-dominated states require detailed understanding of how plant communities respond to multiple perturbations in space and time; we argue that herbivory must be considered as one such perturbation. Unaccounted for impacts on primary producers and the wider ecosystem due to herbivory may limit our ability to manage and restore aquatic ecosystems through targeted schemes such as the European Union's Water Framework Directive (Hering *et al.*, 2010). Indeed, it has been acknowledged that such schemes must account for key biotic interactions in order to be effective (Logan & Furse, 2002). By providing a quantitative relationship between herbivore densities and changes in plant abundance, our findings should aid managers in determining when herbivore impacts on aquatic plants may affect restoration attempts. The results of our global meta-analysis highlight the need for greater recognition among biologists of the role of different herbivore assemblages in regulating aquatic plant dynamics.

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VIII. SUPPORTING INFORMATION

Additional supporting information may be found in the online version of this article.

Appendix S1. Data extracted from all suitable studies in the meta-analysis.

Appendix S2. The distribution of values within the 10 explanatory variables used in the meta-analysis.

Appendix S3. A summary of the Variance Inflation Factors (VIFs) associated with the predictor variables.

Appendix S4. A summary of the post-hoc comparisons between herbivore taxa and herbivore–plant nativeness groups.

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