CONCEPTS & SYNTHESIS

EMPHASIZING NEW IDEAS TO STIMULATE RESEARCH IN ECOLOGY

Consumer control as a common driver of coastal vegetation worldwide

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Abstract. Rapid, global, anthropogenic alteration of food webs in ecosystems necessitates a better understanding of how consumers regulate natural communities. We provide a global synthesis of consumer control of vegetation in coastal wetlands, where the domineering role of physical factors such as nutrient and salinity, rather than consumers, has been emphasized for decades. Using a data set of 1748 measures of consumer effects reported in 443 experiments/observations on all continents except Antarctica, we examine the generality of consumer control in salt marshes and mangroves globally. Our analyses show that salt marsh herbivores, including insects, snails, crabs, waterfowl, small mammals, and livestock, generally and often strongly suppress plant survival, aboveground biomass, and height, while their effects on plant density, belowground biomass, reproduction, and cover are more variable. These effects occur in forbs, grasses, and shrubs, and in both seedlings and adult plants. Herbivores additionally affect plant nutrient stoichiometry, and mediate plant interactions, though their effects on plant diversity are less consistent. Higher trophic levels also affect plants, as predators facilitate plant growth through trophic cascades that suppress grazer abundance and grazing rate. In mangroves, there are also signs of consumer control, though the relatively few studies available have often focused on mangrove propagules and seedlings rather than adults. Our analyses further reveal that the strength of consumer control is regulated by many physical factors. Nutrient, disturbance, and flooding, for example, amplify the negative effects of herbivores. Along latitudinal gradients, increased temperature enhances the negative effects of ectothermic herbivores, but has no effect on those of endothermic herbivores. Consumer control of coastal plants is also apparent across study methodologies: in field and laboratory settings, in observational studies, in consumer exclusion and addition experiments, in natural and transplanted plants, and in experiments of various durations. The role of consumer control in coastal vegetation worldwide highlights the need to better recognize and theoretically conceptualize both top-down and bottom-up forcing and their interactions in coastal wetlands. Improved understanding and conservation of coastal wetlands will only occur if we incorporate what the science has revealed: trophic feedbacks are an important and pervasive determinant of coastal plant communities.

Key words: climate change; coastal wetlands; food webs; global warming; mangroves; meta-analysis; plant–herbivore interactions; predators; salt marsh; top-down control; trophic cascade.

INTRODUCTION

Accelerating human activities are substantially impacting Earth's ecosystems, not only by altering carbon, nitrogen, and hydrological cycles and the physical environment of living organisms, but also by directly modifying the species composition and diversity of biological communities (Vitousek et al. 1997). Populations of consumers, such as predators and herbivores, are modified by human activities in multiple ways. Humans can decrease wild consumer populations through

overharvesting, pollution, or habitat loss (Jackson et al. 2001, Estes et al. 2011). Humans can also increase consumer abundance by introducing novel consumers, such as livestock and invasive animals, to ecosystems (Pimentel et al. 2001). Such alterations of consumer populations often skew food webs in ecosystems, disrupting their functioning, and in extreme situations, causing ecosystem collapse (Jackson et al. 2001, Duffy 2003, Bertness and Silliman 2008, Estes et al. 2011, Silliman et al. 2013). Rapid, global, anthropogenic alteration of food webs necessitates a better understanding of consumer control in natural communities for predicting and mitigating impacts. However, important gaps remain in current understanding of the roles consumers play in natural communities.
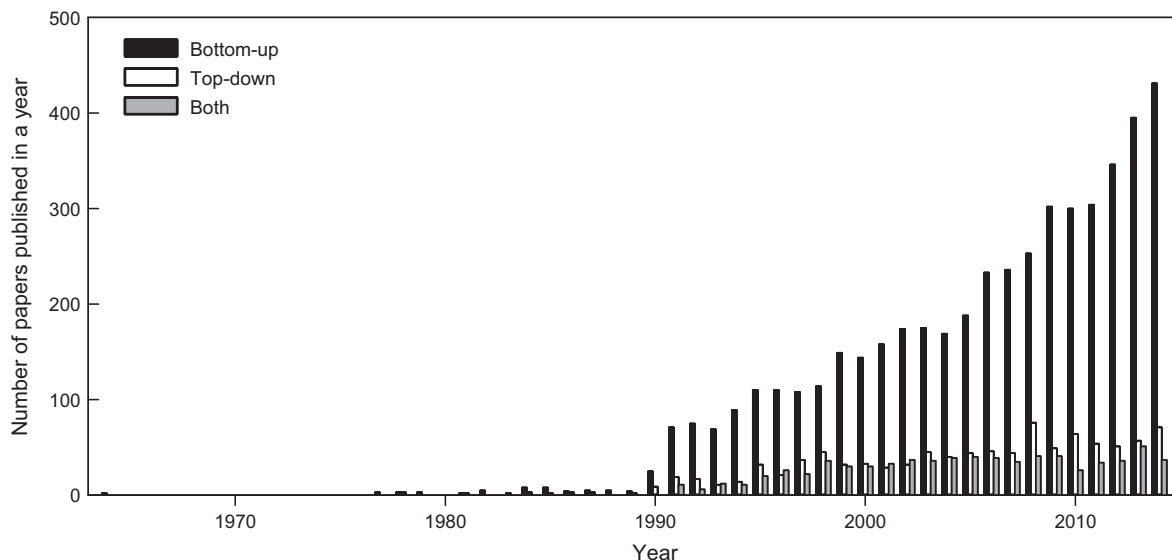
Fig. 1. Number of publications on consumer and physical control of coastal vegetation in each year between the 1960s and 2014. The number of publications was obtained by searching Web of Science using the search item TS = (salinity* OR physical stress* OR nutrient* OR flooding* OR abiotic stress* OR bottom-up* OR inundation OR fertiliz* OR nitrogen) for physical control, and TS = (top-down* OR herbivor* OR grazing* OR predat* OR consumer* OR trophic cascade*) for consumer control, in combination with TS = (salt marsh* OR mangrove* OR coastal wetland*) and TS = (plant* OR vegetation* OR mangrove* OR grass* OR forb* OR shrub*). These searches resulted in 4786, 994, and 732 papers in total on physical control, consumer control, and both, respectively.

A major void in the understanding of trophic feedbacks is whether consumer control is general across different types of ecosystems. In the marine realm, consumer control has long been believed to be strong in algae- or sessile-animal-dominated ecosystems (such as rocky shores or coral reefs; Strong 1992, Shurin et al. 2002, Cebrian and Lartigue 2004, Poore et al. 2012). In contrast, in vascular-plant-dominated marine ecosystems, such as salt marshes and mangroves, plant growth is widely thought to be constrained primarily by physical factors including salinity, anoxia, and nutrients. Indeed, the number of studies on consumer control in salt marshes and mangroves is less than one-third of that of pure bottom-up control studies (Fig. 1). This asymmetry likely reflects the fact that, for nearly 60 yr, bottom-up, physical factors have been thought to be the primary regulator of plant communities in coastal wetlands (Morris et al. 2002, Mendelssohn and Batzer 2006, Mitsch and Gosselink 2015). This idea of the predominance of bottom-up control emerged from early observational salt marsh studies in the southeastern United States (Odum and Smalley 1959, Teal 1962) and from the influence of classical systems ecology studies on early salt marsh researchers, such as H. T. Odum and E. P. Odum (see Bertness et al. 2014b).

However, there also has been a long history of studies investigating top-down control of coastal vegetation by livestock grazing (Ranwell 1961, Bakker 1985). In Europe, where salt marshes have been used for livestock grazing for several millennia, livestock grazing has been widely shown to regulate the growth, structure, and diversity of coastal plant communities (Bakker 1985, Kiehl et al. 2001, Olsen et al. 2011). In addition, there have been several decades of studies on geese grazing in European and North American salt marshes, where geese have been shown to exert strong control on plants, and in some cases, denude marshes to bare mudflats (Smith and Odum 1981, Cargill and Jefferies 1984, Srivastava and Jefferies 1996, Olff et al. 1997). These early studies on both livestock and geese highlight that coastal plant communities may be more vulnerable to consumer control than generally assumed.

Early observational studies in salt marshes (e.g., Crichton 1960) suggested that small invertebrate consumers, such as crabs, could also damage vegetation and maintain bare, unvegetated substrate. Decades later, experimental studies in the southeastern and eastern United States revealed that snails could substantially limit the growth of marsh grasses (Silliman and Zieman 2001, Silliman et al. 2005) and that both insect predators and herbivores could exert strong top-down control on marsh plants (Denno et al. 2002, Finke and Denno 2004). Since then, many more consumer control studies have been conducted in salt marshes worldwide (Fig. 1), suggesting that top-down control by invertebrate consumers, including crabs, snails, and insects, may be widespread (e.g., Silliman and Bortolus 2003, Alberti et al. 2008, Bertness et al. 2008, Daleo et al. 2009, Holdredge et al. 2009, He et al. 2015). Despite these findings, ~80% of studies investigating controls of coastal vegetation over the recent 5 yr (2010–2014) did not mention top-down effects of consumers (Fig. 1; this asymmetry between

consumer control and physical control studies does not exist in rocky shore and reef studies; see Appendix S1: Fig. S1). Likewise, a cross-ecosystem meta-analysis, which included a limited number of studies on coastal vegetation, suggests an insignificant role of consumers in regulating marine vascular plants (Poore et al. 2012). Whether consumer control is weak in coastal wetlands, or is strong and pervasive and should be better incorporated into our understanding of coastal wetlands is primed to be tested in a comprehensive global meta-analysis.

Another major gap in current understanding of consumer control is whether top-down effects of consumers will be amplified or weakened under environmental change (Silliman et al. 2013). Theory suggests that predation and herbivory vary predictably along natural environmental gradients (Menge and Sutherland 1987, Silliman et al. 2013), but will anthropogenic modifications of the physical environment of ecosystems affect consumer control? Recent studies have shown that climate warming, eutrophication, drought, and sea-level rise can alter consumer–resource ratios by differentially affecting the abundance of species at different trophic levels (Petchey et al. 1999, Ledger et al. 2013), or by affecting consumption rates of consumers via modification of plant palatability or consumer behavior (O'Connor 2009, Gilbert et al. 2014, He and Silliman 2015). However, the generality and predictability of such effects of environmental change are not well understood, especially for coastal wetlands. Because coastal wetlands are intensely affected by nutrient input, sea-level rise, and overfishing among other anthropogenic impacts (Lotze et al. 2006, Bromberg Gedan et al. 2009, He et al. 2014), understanding how environmental change affects consumer control in these ecosystems is critical to improving conservation strategies.

Current understanding of consumer control of vegetation is also constrained by a lack of studies examining effects of consumers across multiple plant response variables, consumer and plant species, and study methodologies. The lack of understanding in this area could contribute to present inconsistencies on the importance of consumer control. First, past studies or syntheses often considered only one, two, or three plant response variables (mostly aboveground biomass or species richness). However, plant demography, growth, physiology, interactions, and diversity can have contrasting responses to consumer grazing. Furthermore, consumer effects can be highly variable depending on consumer and plant species. Among herbivores in coastal wetlands, differences in abundance, size, and feeding habits can affect their top-down regulation of plants (Coverdale et al. 2012, Poore et al. 2012). Similarly, plants of different growth forms and of different life stages may respond to consumers differently (Burkepile and Hay 2006). In addition, the observed effects of consumer control can differ between field and laboratory studies, among studies of observations, consumer exclusions, and consumer additions, among studies of natural, transplanted and seeded plants, and among experiments of different durations. Despite these potential variations, holistic analyses of consumer control of vegetation in coastal wetlands, as well as in other ecosystems, are few.

Here, we synthesize consumer control studies in salt marshes and mangroves, and thereby provide a global perspective on consumer control of coastal wetland vegetation. Using a data set of 1748 measures of consumer effects reported in 443 experiments/observations from 22 coastal countries on all continents (except Antarctica; Fig. 2), we examine whether consumer control of coastal vegetation is evident across a diversity of consumer and plant species, across a variety of plant response variables, and in studies with different methodologies. We also examine if environmental factors operating at local and global scales, such as nutrient, disturbance, flooding, temperature, and precipitation, affect the strength of consumer control. Specifically, we test the following hypotheses: (1) herbivores generally affect the demography, growth, and chemistry of plants in
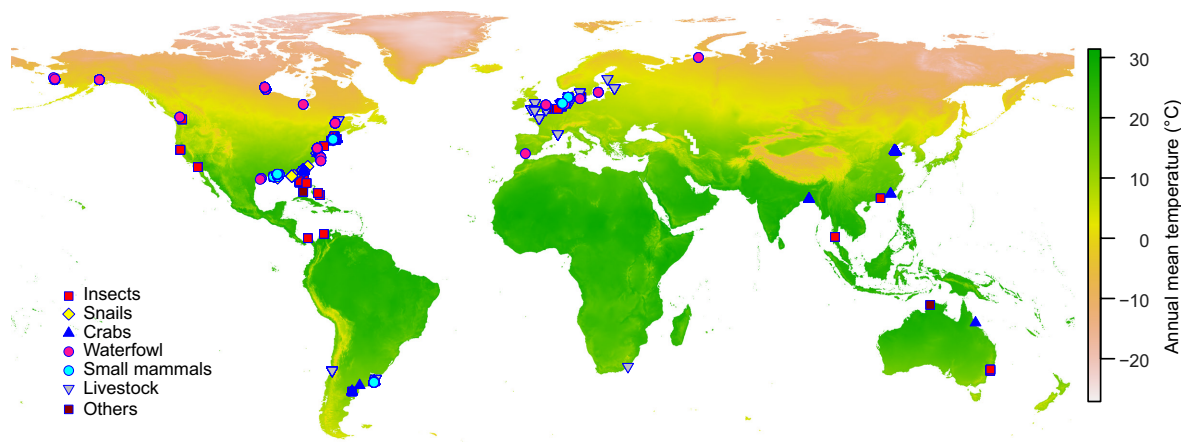

Fig. 2. Global distribution of consumer control studies included in this synthesis.

salt marshes and mangroves; (2) herbivores decrease the strength of plant competition and increase plant diversity; (3) predators and omnivores generate trophic cascades and thereby enhance plant performance by suppressing herbivore abundance and grazing rate; and (4) consumer control of coastal vegetation is generally observed independently of study methodologies (i.e., observational vs. experimental studies, field vs. laboratory studies, low vs. high tidal zones, natural, transplanted vs. seeded plants, and different study durations).

METHODS

Data set

To compile a list of publications on consumer control in coastal wetlands, we searched Web of Science in April 2015, using the following query: TS = (top-down* OR herbivor* OR grazing* OR predat* OR consumer* OR trophic cascade*) AND TS = (salt marsh* OR mangrove* OR coastal wetland* OR coastal marsh*) AND TS = (plant* OR vegetation* OR mangrove* OR grass* OR forb* OR shrub*). This resulted in 1808 publications. We also included 28 other published and unpublished studies that were known to be relevant. We examined each publication and retained those that (1) examined the effects of herbivores, omnivores, or predators (including parasitoids) on plants in observational studies and field or laboratory experiments (studies of omnivores or predators without examining their effects on plants or herbivory were excluded); (2) measured the effects of consumers on variables related to plant demography, growth, chemistry, or diversity (see the following paragraph); and (3) reported mean values of the data with sample sizes and some measure of variance (e.g., standard deviations/errors) in both consumer present and absent treatments. The literature selection procedure is provided in Appendix S1: Fig. S2 as a PRISMA flow diagram. Some publications included experiments (or observations) at multiple sites, tidal zones, or years, or included both laboratory and field experiments; these were treated as separate experiments, as they possessed independent controls (Poore et al. 2012). Multiple exclusions of different consumers that shared a control in a few publications were also treated as separate experiments. Finally, 443 experiments/observations reported in 178 published and unpublished studies (Appendix S2) were retained. Of these, 412 experiments from 163 publications were on salt marshes, and 31 experiments from 15 publications were on mangroves.

For each experiment/observation, we extracted data on different plant response variables in consumer absent and present treatments from text, tables, or by digitizing figures in the publication. For plant demographic responses, we considered survival, density, and reproduction; for plant growth responses, we considered aboveground biomass, belowground biomass, height, and cover; for plant chemical responses, we considered nitrogen concentration, and carbon:nitrogen ratio; and for plant diversity responses, we considered species richness, Shannon diversity, and evenness. Other plant response variables existed, but were often too few for meaningful syntheses. When multiple response variables were reported in an experiment, they were considered in separate analyses to reduce autocorrelation. Some experiments reported the responses of different plant species separately, which were included in our data set, but potential autocorrelation among these data did not affect our results (see Appendix S3). For experiments on predators and omnivores, besides plant responses (aboveground biomass, height, and growth rate), we also extracted data on herbivore responses (herbivore abundance and herbivory) in consumer-absent and consumer-present treatments. For experiments that crossed consumer presence with one or two other factors, such as competition, nutrient, disturbance (those that physically damaged vegetation in part or in full using herbicide, cutting or burning), flooding, or salinity, data were collected from each of the four or eight treatment combinations. When data were reported for multiple dates, those reported at the end of the experiment (mostly in late summer or fall) were used. When consumer treatments in a study included exclusion and addition (highest density treatments were considered), both were included in our data set. When multiple levels of an environmental factor were available, to reduce autocorrelation, we used data from only the ambient and highest levels of treatment.

We also recorded the following variables for each study: (1) author(s) and year; (2) study venue (field vs. laboratory), latitude, longitude, and tidal zone (e.g., low vs. high zone); (3) habitat (marsh vs. mangrove); (4) annual mean temperature, annual precipitation; (5) name, growth form (forb, grass vs. shrub), and life history stage (seedling vs. adult) of the study plant species; (6) name, type 1 (herbivore, omnivore, or predator), type 2 (vertebrate vs. invertebrate), and type 3 (insect, snail, crab, waterfowl, small mammal, or livestock) of the study consumer species; (7) source (natural, transplanted, or seeded) of the study plant species, method of consumer manipulation (observation, exclusion, or addition), and experimental duration (months); and (8) other factors manipulated (e.g., competition or nutrient) and their treatment level (ambient vs. treated). If unavailable in the paper, latitude and longitude data were determined by locating the study site on Google Earth, and plant growth forms by searching the Plants Database (*available online*)[2] or other scholarly records on Google. Consumers were classified as herbivores, omnivores, or predators, following the original study. Although this type of consumer classification is widely used, it might be debatable in some cases, and future studies on consumer diet are needed to improve this understanding. Long-term annual mean temperature and annual precipitation data were obtained from Worldclim (5 arc-minutes

[2] http://plants.usda.gov

resolution; *available online*),[3] which is a set of global climate grids widely used in macroecological studies (Hijmans et al. 2005).

Effect size metrics

To estimate effect sizes of consumers on each of the above plant demographic, growth, chemical or diversity variables, we used Hedges' *g**, a widely used effect size metric that measures the unbiased, standardized difference (Borenstein et al. 2009) in mean performance between consumer-present and consumer-absent treatments divided by the combined standard deviation of the two treatments. Hedges' *g** effect sizes were calculated using the following equation (Gurevitch et al. 2000):

$$g_C^* = \frac{m_P - m_A}{S_C} \times J_C$$

where g_C^* denotes the effect size of consumers, *m* the mean of a response variable, *P* and *A* the consumer present and absent treatments, respectively, J_C a correction factor for small sample bias, and S_C the pooled standard deviation (equations for J_C and S_C are available in Gurevitch et al. [2000]). For studies of predators and omnivores, their effect sizes on herbivore abundance and herbivory were calculated similarly. For binomial survival and reproduction data, effect sizes were estimated by computing the natural log of the ratio of the odds of survival/reproduction in consumer present and absent treatments and converting log odds ratios to Hedges' *g** (Borenstein et al. 2009). Positive and negative g_C^* indicate positive and negative impacts of consumers, respectively.

For studies that examined effects of consumers on plant-plant interactions, we first calculated Hedges' *g** in mean plant performance between neighbor present and absent treatments in without and with consumers treatments, respectively, using the above equation, where *P* and *A* then denote neighbor present and absent treatments, respectively. Positive and negative g_C^* indicate facilitation and competition, respectively. We also estimated the effect sizes of consumers on plant-plant interactions, g_I^*, using the following equation (Gurevitch et al. 2000):

$$g_I^* = \frac{(m_{Pp} - m_{Ap}) - (m_{Pa} - m_{Aa})}{S_I} \times J_I$$

where *m* denotes the mean of a response variable, *Pp*, *Ap*, *Pa* and *Aa* the four treatment combinations of neighbors (present, *P*; absent, *A*) and consumers (present, *p*; absent, *a*), respectively, J_I a correction factor for small sample bias, and S_I the pooled standard deviation (equations for J_I and S_I are available in Gurevitch et al. 2000). Positive g_I^* indicate that consumers increase plant facilitation and decrease competition, and vice versa. Similarly, for studies that crossed consumer presence treatments with an environmental factor, we first estimated the effect sizes of consumers in low- and

[3] http://www.worldclim.org

high-level treatments of that environmental factor, respectively, and then estimated the interaction effect sizes of consumers and the environmental factor, where *Pp*, *Ap*, *Pa*, and *Aa* then denote the four treatment combinations of consumers (with, *P*; without, *A*) and the environmental factor (high level, *p*; low level, *a*), respectively. A positive g_I^* indicates that an environmental factor increases the positive effects of consumers and decreases their negative effects, and vice versa.

Meta-analysis

Using random-effects models (Borenstein et al. 2009), we first estimated mean g_C^* and 95% confidence intervals (95% CIs) on each plant demographic and growth variable available for salt marsh and mangrove studies, respectively. We used random-effects models instead of fixed-effects models, as the fixed-effects model assumption that all observed variation in effect size among studies is due to sampling error was unlikely to be met across the broad range of studies included in our data set and random-effects models can address variation in effect size among studies (Borenstein et al. 2009). Similarly, using random-effects models, we estimated mean g_C^* on each plant chemistry and diversity variable, as well as on competitive effects in herbivore-present and herbivore-absent treatments. Mean values of g_I^* on the interactive effects of herbivores and competition were also estimated. For studies on predators and omnivores, we estimated mean g_C^* on herbivore abundance, herbivory, and plant growth in salt marshes and mangroves (when available), respectively. In these analyses, heterogeneity was estimated using the *Q* statistic, a measure of weighted squared deviations, and mean effect sizes are considered significant if their 95% CIs do not overlap zero (Borenstein et al. 2009). All analyses were conducted using R 3.1.2 (R Core Team 2014) and its metafor package.

For salt marsh studies (mangroves studies were excluded due to low sample size), we also estimated mean g_C^* on each plant demographic and growth variable available for each type (type 3) of herbivores and for each plant growth form, using mixed-effects models that included herbivore type 3 and plant growth form as the moderators, respectively, in random-effects models (Viechtbauer 2010). We grouped herbivores by taxon and plants by growth form, as (1) these groups have been widely studied and are representative of main plant and herbivore functional groups in salt marshes and (2) classifying species into these groups was straightforward and feasible with species information available (see *Data set*). Other grouping factors, such as herbivore feeding mode (Moon and Stiling 2002), existed, but most studies available examined chewing herbivores, and those that examined gall-making, boring, or sucking herbivores were rare. Similarly, mixed-effects models (with plant life stage as the moderator) were used to estimate mean g_C^* on plant survival and aboveground biomass for seedling and adult plants across the entire data set and also within a

subset of studies that simultaneously examined seedlings and adult plants. In these analyses, we used the between-group heterogeneity statistic Q_M to assess if effect sizes differ among different types of herbivores, different plant growth forms, and different plant life history stages.

To examine if environmental factors (including nutrient, disturbance, flooding, and salinity) affect the strength of herbivore effects on plants, we estimated mean g_C^* on plant aboveground biomass and 95% CIs in low and high levels of an environmental factor, respectively, and also mean g_I^* for the interactive effects between herbivores and the environmental factor. We considered only plant aboveground biomass in this analysis, as well as in the following analyses, as aboveground biomass was the most widely quantified plant response variable (see *Results*). Few studies have examined interactions between herbivores and other environmental factors, or between predators (or omnivores) and environmental factors, and thus they were not analyzed. Furthermore, to examine if herbivore effects vary as a function of latitude, temperature or precipitation, we analyzed the relationships between g_C^* and latitude, temperature, and precipitation, respectively, using meta-regression (Borenstein et al. 2009). This analysis was conducted separately for all ectotherms and endotherms, and also for each type of herbivores (type 3), respectively. To reduce methodological variation across studies, we included in this analysis only data from field exclusion experiments at ambient conditions (data from field studies that manipulated local environmental factors, such as nutrient and disturbance, were excluded). To account for potential autocorrelation, we repeated this analysis by pooling all the same effect size metrics within each experiment by conducting a meta-analysis of these effect sizes, and also within each 0.5 latitude and 0.5 longitude, because consumer effects at some sites were examined in multiple experiments (see He and Silliman 2015). The amount of heterogeneity explained by the meta-regression models was estimated using the Q_M statistic.

To examine if herbivore effects are general in studies of different methodologies, we used mixed-effects models and estimated mean g_C^* and 95% CIs on plant aboveground biomass for field and laboratory studies and for low and high tidal zone studies, respectively. For field studies, we also estimated mean g_C^* for observational studies, consumer-exclusion, and consumer-addition experiments, and also for studies of natural, transplanted, and seeded plants, respectively, using mixed-effects models. Additionally, for field experiments, we examined if g_C^* varies with experimental duration using meta-regression.

To examine the robustness of our results, we supplemented our effect size estimations in multiple ways by accounting potential autocorrelation in the data set and by examining if temporal variation affects our results. To examine the potential influence of publication bias, we examined funnel plot asymmetry for each effect size metric using the trimfill method and Rosenthal's fail-safe number. Detailed methods and results of these supplementary
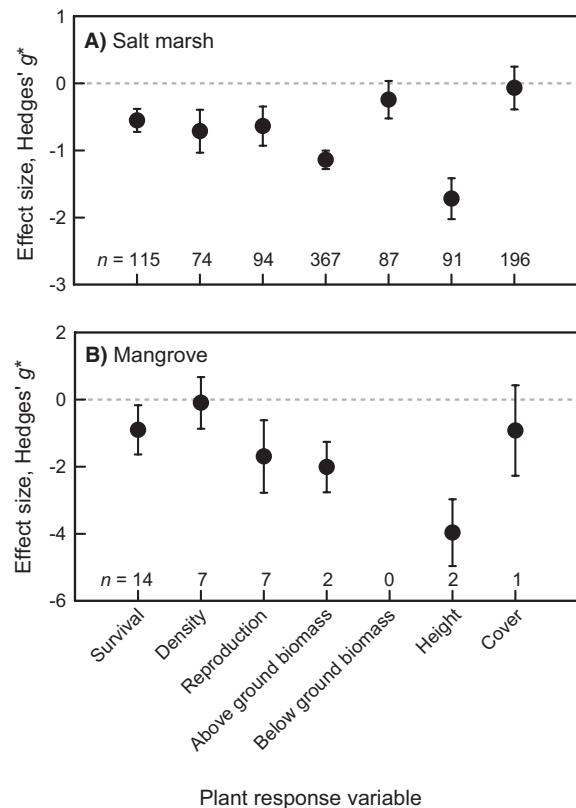

FIG. 3. Overall effect sizes of herbivores on different plant performance measures in coastal wetlands: (A) salt marshes and (B) mangroves. Shown are mean effect sizes and 95% confidence intervals. Effect sizes are considered significant if their 95% CIs do not overlap zero. Sample sizes are indicated with *n*.

analyses are presented in Appendix S3. These analyses suggest that our results are generally robust.

RESULTS

Effects of herbivores

For salt marshes, across the entire data set, herbivores strongly decreased plant survival, density, and reproduction, as well as plant aboveground biomass and height, although their effects on plant belowground biomass and cover (Fig. 3A) were insignificant. These effects of herbivores were generally observed in the few mangrove studies available (mostly on mangrove propagules and seedlings), although herbivore effects on mangrove density were insignificant (Fig. 3B).

The effects of herbivores on plants varied significantly with herbivore taxon (Fig. 4; Appendix S1: Table S1). For the three plant demographic variables, all types of herbivores included in our data set consistently decreased plant survival, though the strength of their effects differed (Appendix S1: Table S1), with crabs having more negative effects than insects, waterfowl, and others (Fig. 4A). Different types of herbivores had variable
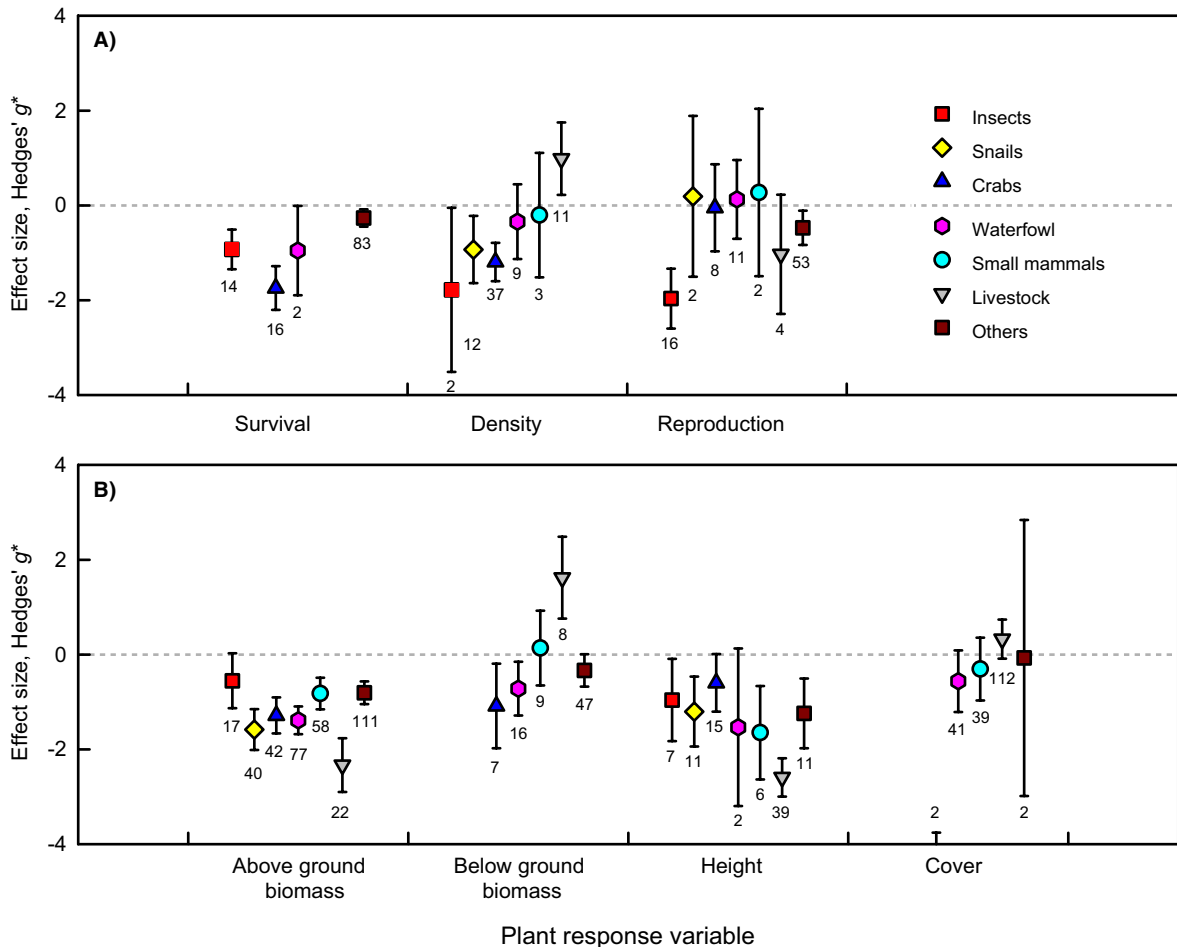
FIG. 4. Effects of different types of herbivores on plant performances in salt marshes. (A) Demographic variables included survival, density, and reproduction, and (B) growth variables included aboveground biomass, belowground biomass, height, and cover. Sample sizes are given below each point. Other details follow Fig. 3.

effects on plant density and reproduction (Fig. 4A). Insects, snails, crabs, and other herbivores significantly decreased, waterfowl and small mammals did not significantly affect, and livestock increased plant density (Fig. 4A). Insects and other herbivores significantly decreased, while snails, crabs, waterfowl, and small mammals did not affect reproduction (Fig. 4A). For the four plant growth variables, in general, different types of herbivores consistently decreased plant aboveground biomass and height (Fig. 4B). Different types of herbivores had contrasting effects on plant belowground biomass, however. Crabs, waterfowl, and other herbivores significantly decreased, small mammals did not significantly affect, and livestock significantly increased plant belowground biomass. Crabs also significantly decreased plant cover, though the effects of all other types of herbivores were insignificant (Fig. 4B).

The effects of herbivores also varied with plant growth form and life history stage (Fig. 5; Appendix S1: Table S1). For plant demographic variables, herbivores most strongly decreased the survival, density, and reproduction of forbs.

While herbivores also negatively affected the survival, density, and reproduction of grasses, they did not for shrubs (Fig. 5A). For plant growth variables, herbivores consistently decreased the aboveground biomass and height of all plant growth forms (except that the effects on the height of forbs were insignificant), but their effects on belowground biomass and cover were insignificant for most plant growth forms (Fig. 5B). Furthermore, herbivores often had stronger negative effects on the survival of plant seedlings than adults, but weaker negative effects on the aboveground biomass of plant seedlings than adults, results that were consistent between analyses across the entire data set and within studies that simultaneously examined seedlings and adults (Fig. 5C, D; Appendix S1: Table S1).

Herbivores additionally affected other attributes of plants including plant chemistry, interactions, and diversity in salt marshes (few studies on mangroves were available). For plant chemistry, herbivores significantly increased plant nitrogen concentration (Hedges' $g^* = 0.66$; 95% CI 0.39–0.93) and decreased plant carbon:nitrogen ratio (Hedges' $g^* = -0.92$; 95% CI −1.47 to −0.37). For plant interactions,
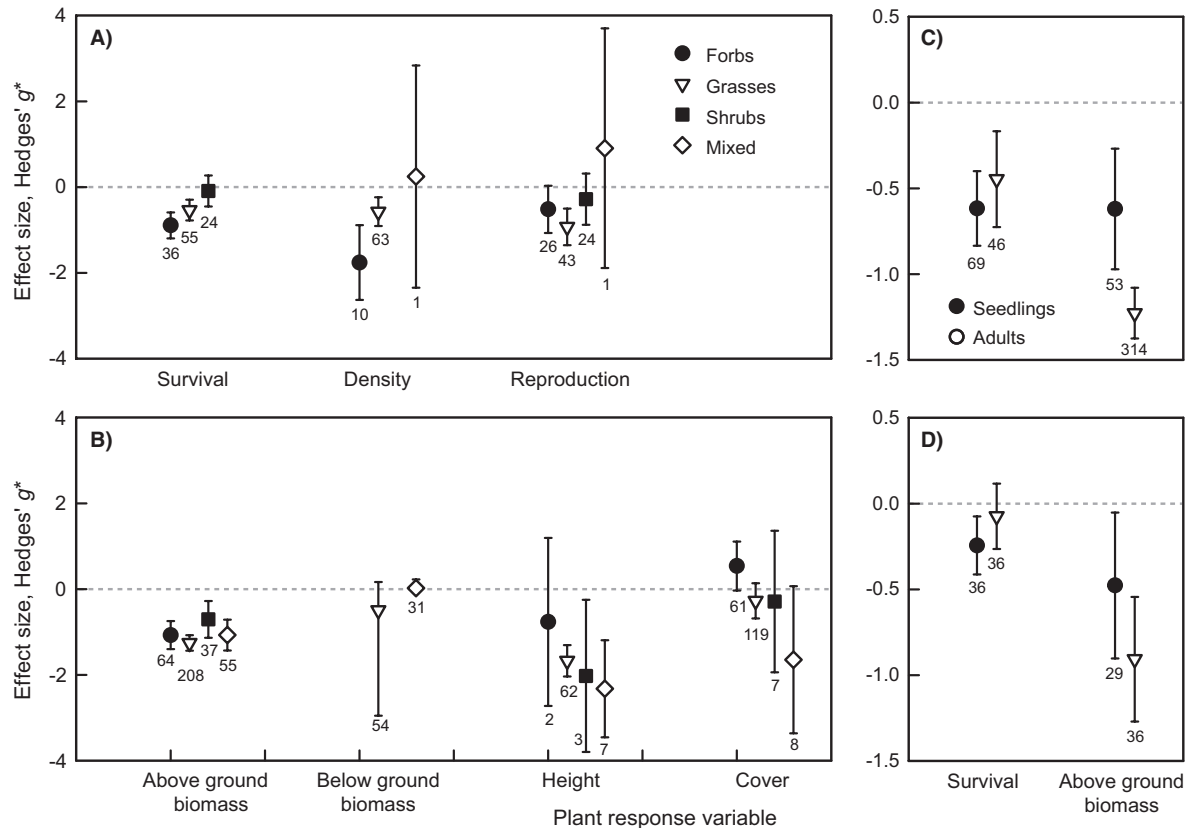
FIG. 5. Effects of herbivores on plants of (A, B) different growth forms (forbs, grasses, shrubs, and mixed) and of (C, D) different life history stages in salt marshes. Sample sizes are given below each point. Other details follow Fig. 3.

herbivores significantly decreased the intensity of competition: plant interactions were significantly competitive without herbivores, but became neutral or less competitive when herbivores were present (Fig. 6A). Although herbivores significantly affected plant interactions, their effects on plant species richness, Shannon diversity, and evenness were insignificant (Fig. 6B).

Effects of predators and omnivores

In salt marshes, predators generally decreased herbivore abundance and herbivory, and had significantly positive cascading effects on plant growth (Fig. 7A). While omnivores consistently decreased herbivore abundance and herbivory, their cascading effects on plants were insignificant (Fig. 7B). In mangroves, predators significantly decreased herbivory, but their effects on herbivore abundance and plant growth were insignificant, where only very few studies were available (Fig. 7A).

Mediation by environmental factors

Across site-scale studies, the effects of herbivores were significantly affected by nutrient, disturbance, and flooding, but not by salinity (Fig. 8). The interactions between nutrient and herbivores were significantly

negative, indicating that nutrient enrichment amplified the negative effects of herbivores on plants (Fig. 8A). Similarly, disturbance and flooding significantly amplified the negative effects of herbivores on plants (Fig. 8). Although the effects of herbivores shifted from negative to neutral with increased salinity, their interactions were insignificant (Fig. 8B), but only three studies were available.

Along global gradients, the effects of ectothermic herbivores varied significantly with latitude and mean annual temperature (Fig. 9A, B), but not with annual precipitation (Fig. 9C). The effects of ectothermic herbivores significantly increased with decreasing latitude and increasing mean annual temperature (Fig. 9A, B), trends generally consistent in crabs, insects, and snails. The effects of crabs (but not others) also significantly increased with increasing annual precipitation (Fig. 9C). In contrast, the effects of endothermic herbivores did not vary with latitude or annual mean temperature or annual precipitation, results that were consistent between waterfowl and small mammals (Fig. 9D–F).

Generality across methodologies

The impacts of herbivores on plants were generally observed in studies with different methodologies, including site setting, consumer manipulation method,
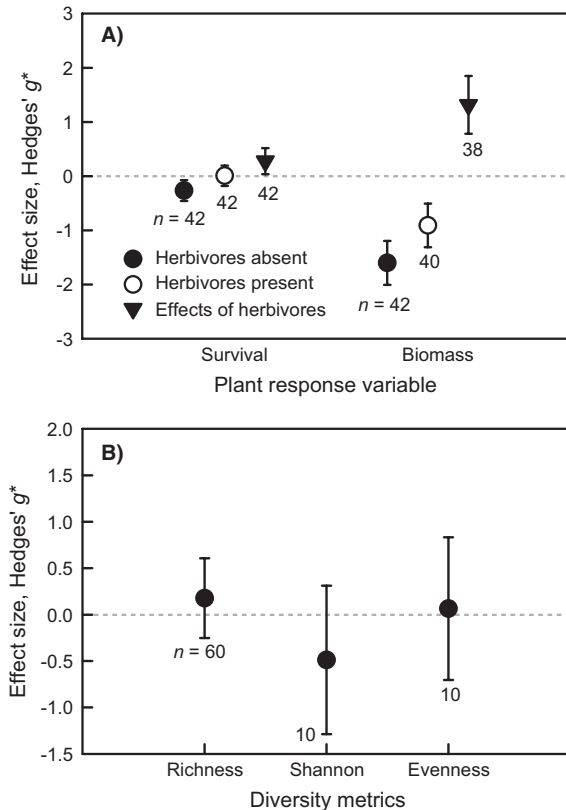
FIG. 6. Effects of herbivores on plant interactions and diversity in salt marshes. (A) Effects on plant interactions. Shown are mean effect sizes (and 95% confidence intervals) on the effects of plant competition with and without herbivores and on the interactions between plant competition and herbivores. (B) Effects on plant species richness, Shannon diversity, and evenness. Other details follow Fig. 3.

chemistry, and interactions of plants in coastal wetlands, and that the top-down role of consumers is evident across a wide range of consumers and locations globally. Thus, coastal vegetation is widely mediated not only by bottom-up, physical factors (Odum and Smalley 1959, Teal 1962, Morris et al. 2002, Mendelssohn and Batzer 2006), but also by top-down, consumer factors. Although the relative strength of top-down control is generally weaker in vascular-plant-dominated systems than in algal-based systems (e.g., intertidal and subtidal rocky reefs; Cebrian and Lartigue 2004, Poore et al. 2012), our results highlight that top-down control of vascular plants by consumers in coastal wetlands globally is evident and significant. As shown in our work, the relative strength of consumer impacts on coastal vegetation also varies with consumer type and plant characteristics (including plant growth form and life stage), and is mediated by bottom-up, physical factors operating at both local and global scales, such as nutrient availability and temperature, suggesting that global environmental change may have important consequences for consumer–vegetation interactions.

Effects of herbivores

The long-held view that coastal vegetation is primarily controlled by bottom-up factors is challenged by our finding that a variety of herbivores strongly suppress the

source of study plants, and experimental duration (Fig. 10). First, the effects of herbivores were observed in both field and laboratory studies, and were observed in field studies located in both low- and high-tidal zones (Fig. 10A). Second, the effects of herbivores were observed across observational studies, consumer exclusion and consumer addition experiments, though consumer addition experiments typically found stronger herbivore effects than did consumer exclusion experiments (Fig. 10B). Third, the effects of herbivores were observed not only in studies of natural plants, but also in studies of transplanted plants, though few studies of seeded plants were available (Fig. 10C). Finally, the effects of herbivores were observed in field experiments of varying duration, and did not vary significantly with experimental duration (Fig. 10D).

DISCUSSION

Our work provides a unique global perspective on how consumers affect coastal vegetation, showing that consumers substantially regulate the demography, growth,
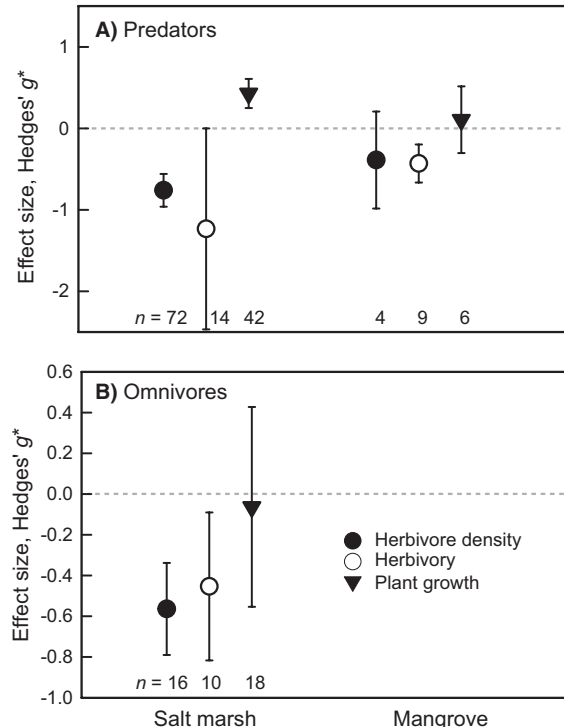

FIG. 7. Effects of (A) predators and (B) omnivores on herbivore abundance, herbivory, and plant growth in mangroves and salt marshes. Note that no studies on omnivores in mangroves were available. Other details follow Fig. 3.
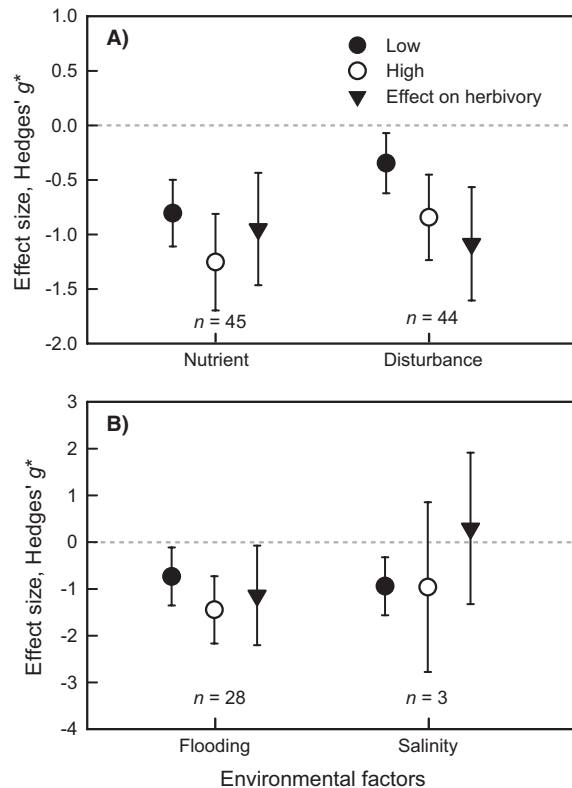
Fig. 8. Regulation of consumer control by environmental factors: (A) nutrient and disturbance and (B) flooding and salinity. Other details follow Fig. 3.

survival, aboveground biomass, and height of plants in coastal wetlands. The worldwide distribution of studies included in our analyses reveals that a wide range of coastal wetlands are systems controlled by strong rather than weak and localized top-down forces. While Poore et al. (2012) found no significant effects of herbivores in salt marshes, their work primarily focused on marine algal studies and included only a limited number of salt marsh studies (see Koricheva and Gurevitch [2014] for methodological issues and recommendations for meta-analysis). A lack of significant herbivore effects in Poore et al. (2012) may also be due to that it mixed studies of plant aboveground biomass, density, and cover responses into a single analysis. However, as shown here, the effects of herbivores strongly depend on the measure of plant response. To our knowledge, this is the first quantitative synthesis that has compared the effects of herbivores across multiple plant demographic, growth, and chemical components, though studies of plant–plant interactions have consistently shown that the effects of neighbors vary with the measure of target plant response (Goldberg et al. 1999, He et al. 2013).

Additionally, Poore et al. (2012) included only field herbivore exclusion experiments, while our work included studies of different methodologies: field and laboratory studies, and consumer exclusion and addition

experiments. Although the effects of herbivores were significant in both exclusion and addition studies in our analysis (Fig. 10B; also see Fig. 2b in He and Silliman 2015), the effects were found to be generally stronger in addition experiments. Consumer addition experiments are often done at high densities, or even above natural densities, which may not represent typical conditions in coastal wetlands. However, herbivore addition experiments may indicate top-down control in future scenarios of predator decline. In contrast, exclusion studies may be more appropriate for testing top-down control in natural conditions (Luck et al. 1988), but could underestimate top-down control due to incomplete exclusion or recolonization. Furthermore, laboratory studies can be more artificial than field studies, but have advantages such as allowing more mechanistic experimentation under repeatable experimental settings. Our work highlights the value of synthesizing results from a combination of studies that employ different methodologies to gain an enhanced understanding of the effects of consumers in coastal wetlands, as well as in other ecosystems.

Our results not only confirm the top-down effects of large-bodied herbivores such as livestock and geese, as generally recognized in coastal vegetation studies across Europe, Canada, the United States, and South America (Fig. 2), but also reveal that those by smaller herbivores such as crabs, insects, and snails, as shown in recent studies, are general and widespread. Classic studies on top-down control of salt marsh plants by small herbivores have been criticized for focusing on one or a few marsh sites with highest herbivore abundance (i.e., study bias) and for lacking spatial generality. However, as shown in our synthesis, crab herbivory has been found to significantly regulate salt marsh plant performance not only in New England, but also in South America (Alberti et al. 2008, Daleo et al. 2009) and China (He et al. 2015). Similarly, strong top-down effects of both snails (Silliman et al. 2005, Hughes 2012) and insects (Finke and Denno 2004, Bertness et al. 2008, Johnson and Jessen 2008) on salt marsh plants have been reported by independent researchers across a large spatial extent in the eastern United States. The generality of top-down control of plants by herbivores shown in our synthesis is further corroborated by the prevalence of herbivores documented in large-scale surveys of coastal wetlands (e.g., Farnsworth and Ellison 1997, Silliman and Bortolus 2003, Alberti et al. 2007). Importantly, it should be recognized that, while strong top-down control of plants by herbivores in coastal wetlands has been documented in studies from Asia, Australia, South America, and Africa (Fig. 2), studies from those regions are often far fewer than those from Europe and North America, and are thus less represented in our synthesis.

Our finding that different types of herbivores may differentially affect plants is likely influenced by herbivore body size, grazing habit, and abundance. For example, burrowing marsh crabs (Coverdale et al. 2012) and grubbing waterfowl (Gauthier et al. 1995) strongly
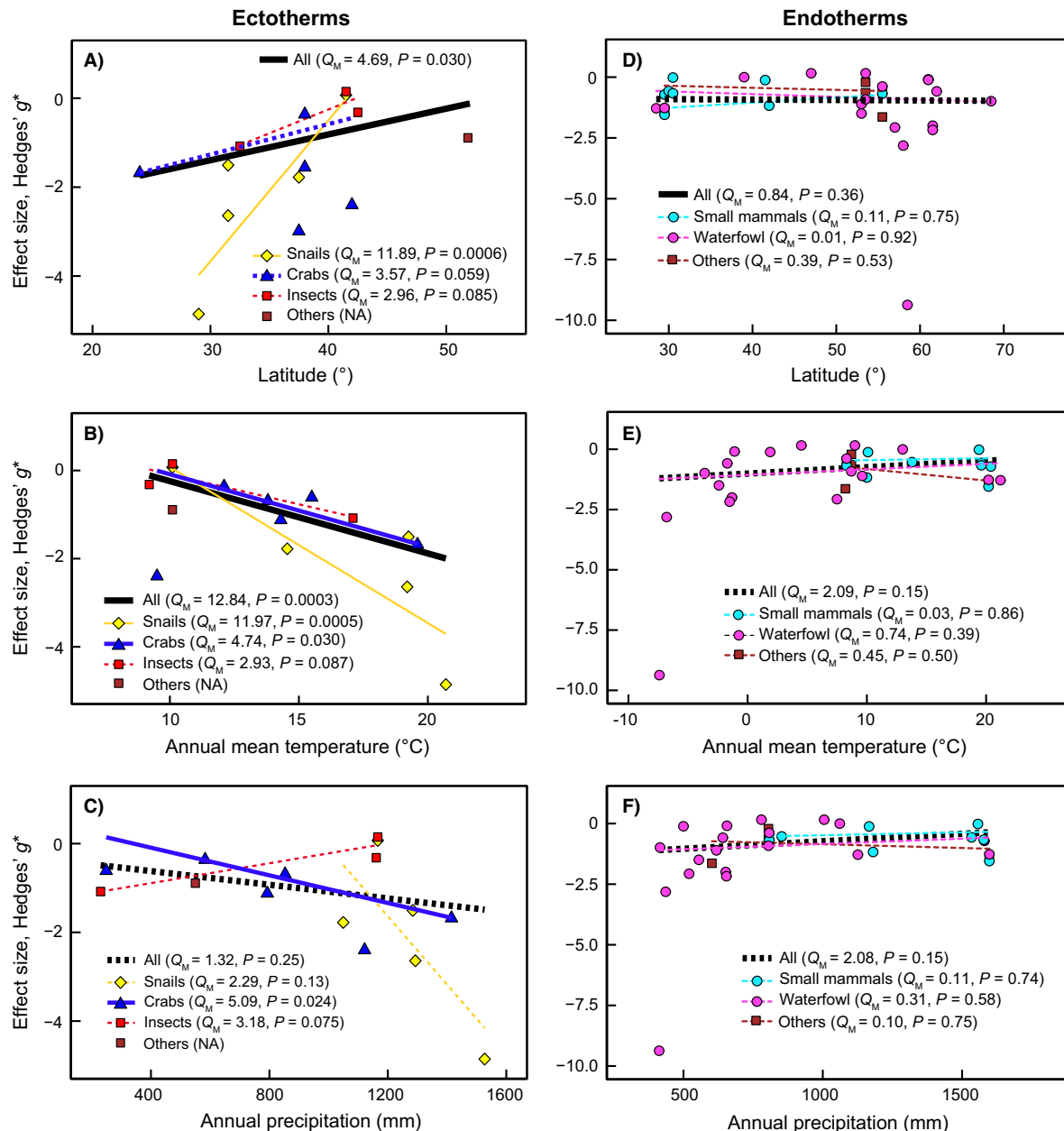
FIG. 9. Consumer control as a function of climatic factors. (A, B, C) Effects of ectothermic herbivores as a function of latitude (A), annual mean temperature (B), and annual precipitation (C). (D, E, F) Effects of endothermic herbivores as a function of latitude (D), annual mean temperature (E), and annual precipitation (F). Test statistics of the meta-regression models (Q_M and P) are shown. NA indicates not available. Significant ($P < 0.05$) and insignificant ($P > 0.05$) relationships are shown with solid and dashed lines, respectively.

decrease plant belowground biomass, flower-attacking insects (Bertness et al. 1987) more negatively affect plant reproduction, while aboveground grazing small mammals and livestock primarily decrease plant aboveground biomass and height. Livestock more strongly suppress plant aboveground biomass than do small mammals, likely because of their larger body size (higher consumption; also see Poore et al. 2012), while crabs and snails have stronger effects on plant aboveground

biomass than do small mammals, likely because they are more abundant. Other factors such as feeding mode can also mediate the top-down effects of herbivores (e.g., Moon and Stiling 2002), but studies that specifically examine the top-down effects of gall-making, boring, or sucking herbivores (rather than chewing herbivores) have yet to be done to further this understanding. Additionally, herbivores can also affect plants through pathways other than consumption, such as trampling (Jónsdóttir 1991,
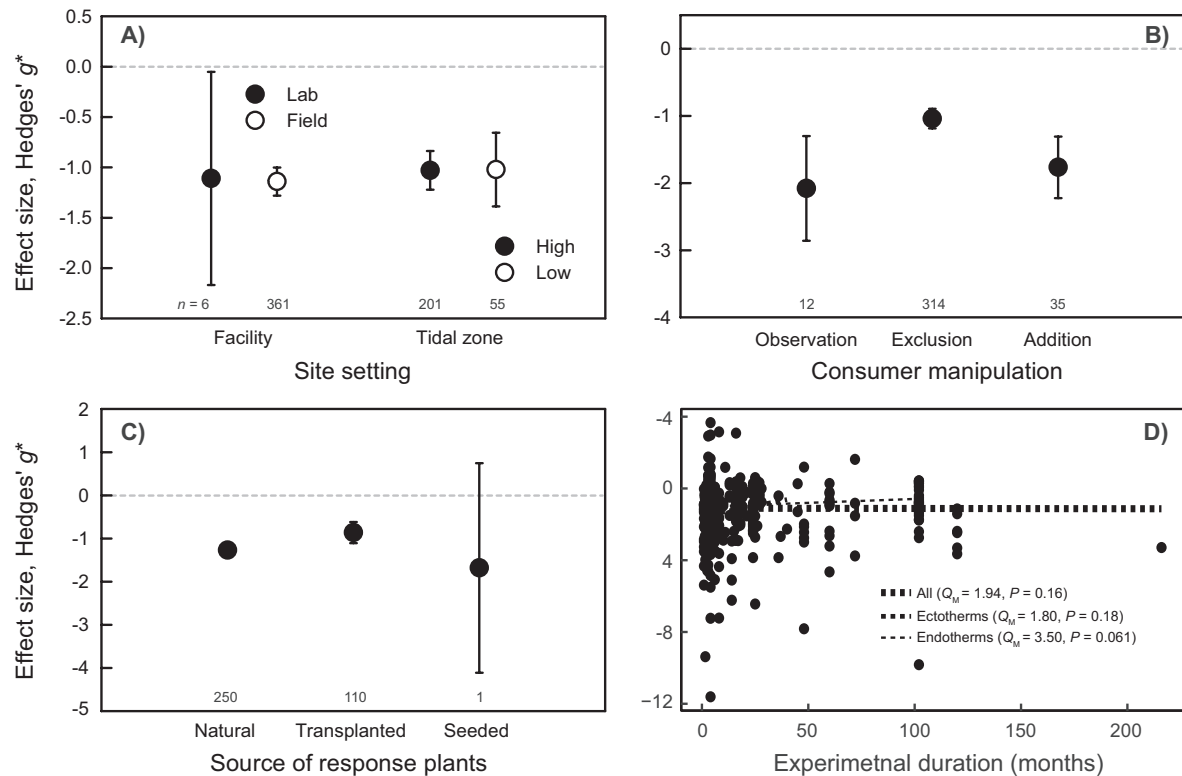
FIG. 10. Methodological variables and consumer control. (A) Site setting: field vs. laboratory studies and low vs. high tidal zone studies. (B) Consumer manipulation methods: observation, exclusion vs. addition. (C) Sources of response plants: natural, transplanted vs. seeded. (D) Experimental duration. Panels A, B, and C, show mean effect sizes and 95% confidence intervals. Panel D shows data points of effect sizes and test statistics of the meta-regression models (Q_M and P).

Schrama et al. 2013), fecal deposition (Ruess et al. 1989), or facilitation of microbial infection (Silliman and Newell 2003). While it was not an objective of our analysis to disentangle the relative importance of these different pathways in regulating the strength of herbivore effects, our analyses, by contrasting the overall effects of different herbivores, suggest that different mechanisms may underlie the variable effects of different herbivores.

Our study results further highlight the importance of plant growth form and life stage in mediating the strength of herbivore effects. Although classic studies investigating the effects of herbivores in coastal wetlands often focused on grasses, in particular *Spartina* spp. (likely because *Spartina* spp. are often among the most spatially dominant plants in salt marshes), our results show that herbivores also strongly affect salt marsh forbs (e.g., *Salicornia europaea* and *Suaeda salsa*, He et al. 2015) and shrubs (e.g., *Artemisia maritima*, Dormann et al. 2000; *Iva frutescens*, Crain 2008). These results suggest that top-down control of plants by herbivores, as shown in classic studies on grasses, is also evident in other plants, although the acting herbivores may or may not vary. However, herbivores have generally weaker effects on the survival and reproduction of shrubs in comparison to grasses and forbs, potentially because shrubs are generally more resistant to herbivores (Perelman et al. 1997).

For mangroves, which are comprised of shrubs or trees, nevertheless, our analyses suggest that herbivores primarily affect their survival and reproduction. Our results of herbivore impacts on mangroves should be interpreted with caution due to low sample size, and the generality of these results should be examined in future studies (see *Looking to the future*). Also, most of the mangrove studies available measured impacts of consumers on survival of propagules or seedlings (e.g., Clarke and Myerscough 1993). The survival of plant seedlings is indeed more vulnerable to herbivory in comparison to adult plants, as shown in our analyses of salt marsh studies (also see Strauss and Agrawal 1999).

Our synthesis additionally provides insight on herbivore effects on plant chemistry and plant-plant interactions in coastal wetlands. Herbivory increases plant nitrogen concentration and decreases plant carbon:nitrogen ratio, likely because when large amounts of biomass are removed by herbivores, plants respond by regrowing with new leaves that are low in structural material and high in photosynthetic enzymes. Studies from other habitats also support these effects of herbivores (Jaramillo and Detling 1988). However, most of the studies available investigated the effects of relatively large chewing herbivores, such as crabs, waterfowl, or mammals, while sucking, gall making, and boring insects may have different effects on plant N

concentration (see Daehler and Strong [1997] for a study on sap-feeding grasshoppers). Furthermore, our finding that herbivores decrease the intensity of plant competition supports the stress-gradient hypothesis that plant–plant interactions will be less competitive and more facilitative with increasing biotic stress (Bertness and Callaway 1994, He et al. 2013). However, weakened plant competition by herbivores does not consistently lead to higher plant diversity, even though livestock grazing can promote plant diversity in some European salt marshes (Esselink et al. 2000) and many terrestrial grasslands (Borer et al. 2014). In contrast to highly species-diverse terrestrial grasslands, salt marsh plant communities are often comprised of one or a few species (Pennings and Bertness 2001), suggesting that not finding impacts on diversity is not surprising. Nevertheless, altered plant–plant interactions and preferential grazing by herbivores may ultimately change species composition, having community-level consequences for coastal vegetation (He et al. 2015).

Effects of predators and omnivores

Our synthesis of salt marsh studies provides support for the trophic cascade theory that predators can enhance the growth of primary producers by suppressing herbivores, and agrees with experimental and observational studies that predator depletion (either natural or human-driven) can intensify herbivory, which, in extreme cases, can denude marshes (Silliman and Bertness 2002, Silliman et al. 2013, Bertness et al. 2014a). In contrast, the overall effects of omnivores on plant growth were insignificant, even though omnivores significantly decreased herbivore abundance and herbivory. Because omnivores consume both plants and animals, their effects on plants may be more variable (Polis and Strong 1996, Ho and Pennings 2008). However, we caution that while omnivores are prevalent in salt marshes, studying the effects of omnivory on plants has not been a major effort (Ho and Pennings 2008), nor has been the trophic cascade effects of predators and omnivores in mangroves (Fig. 8), indicating an important knowledge gap.

Environmental change and consumer control at local and global scales

A novel finding of our study is that environmental factors at both local and global scales mediate the strength of consumer control in coastal wetlands, having important implications for understanding environmental change impact. At local scales, our results suggest that environmental change can amplify top-down control of plants by herbivores. Our finding that nutrient enrichment amplifies top-down control expands generality of our past work synthesizing field herbivore removal experiments on natural vegetation (He and Silliman 2015) to synthesizing experiments on both natural and planted vegetation. Our results further show that top-down control by herbivores may be amplified by other

environmental change factors such as disturbance (i.e., vegetation removal and fire) and flooding—two factors that are expected to increase with increasing human disturbance of coastal wetlands and sea-level rise (Bromberg Gedan et al. 2009). Silliman et al. (2005) suggested that drought, by elevating salinity stress, can trigger snail grazing fronts that kill salt marsh vegetation, but our analysis was limited by sample size (only a couple of studies were available) to confirm its generality. However, given that drought is expected to intensify in many regions with climate warming (Dai 2013), studies should further explore whether drought and/or increased salinity affects consumer control of coastal vegetation.

At global scales, our results show that top-down control of plants by ectothermic rather than endothermic herbivores increases with increasing annual mean temperature, resulting in stronger top-down control at lower latitudes. Warming has been shown to strengthen plant-herbivore interactions in some cases (i.e., O'Connor 2009). Our finding that temperature mediates plant–herbivore interactions across global latitudinal gradients supports the metabolic theory of trophic interactions that predicts trophic interactions will be strengthened with elevated temperature (Gilbert et al. 2014). Interestingly, however, top-down control of plants by endothermic herbivores such as small mammals and waterfowl does not vary with latitude or temperature, and can even be higher at colder temperatures. Studies of hares in the High Arctic also suggested that grazing could be more intense in winter than in summer (Klein and Bay 1994). These results appear inconsistent with some warming experiments where top-down control by mammalian herbivores was found to be magnified at elevated temperatures (Brodie et al. 2012). The causes of these differences are unclear, but warming experiments have often been conducted at scales that are smaller than typical habitat sizes of large-bodied mammals (thus experimental warming may have only directly affected plants but not the energetics of mammals). Moreover, unlike ectotherms, energetic costs of thermoregulation for endotherms often decrease with increasing temperature (Lindstedt and Boyce 1985, Swihart and Bryant 2001). Our study thus highlights the value of incorporating thermoregulation pathway into future models predicting the impact of rising temperature on trophic interactions.

Looking to the future

While our global synthesis clearly demonstrates the widespread role of consumer control in coastal wetlands, our work also highlights important gaps in current studies, and our findings may serve as the basis for new hypotheses that stimulate further empirical tests at local, regional and global scales. Specifically, future studies are required to improve understanding in the following areas.

First, as discussed in *Discussion: Effects of herbivores*, consumer control in mangroves, particularly for the

growth of adult mangrove trees (e.g., Anderson and Lee 1995), has not been well examined in consumer manipulation experiments. Current studies of consumer control in mangroves have largely focused on seedlings and propagules, or observations of herbivory (e.g., percentage of leaf area consumed by herbivores; Erickson et al. 2004) or predation (Farnsworth and Ellison 1997). However, to understand the actual impacts of consumers on mangroves, consumer exclusion or addition experiments are required. Regrettably, while mangrove ecosystems globally are habitats for abundant herbivores and predators (Farnsworth and Ellison 1997, Hogarth 1999) and theory suggests that consumer pressure should be strong in tropical zones (Gaines and Lubchenco 1982), an advanced understanding of consumer control in mangroves is lacking.

Second, a greater understanding of the impacts of trophic cascades, top predators and predator diversity in coastal wetlands is sorely needed. The predators that have been investigated in previous studies and included in our analyses are all small, primary predators such as insects, crabs or fish, but the cascading effects of predators depend on body size and food chain length (Fretwell 1987). Many coastal wetlands are habitats for large-bodied top predators such as alligators, birds, sharks, and sea otters, and recent studies show that they regulate populations of predatory or herbivorous marsh animals (Xiong et al. 2010, Nifong and Silliman 2013). Thus, future studies should expand investigation into impacts of complex food web structure on wetland vegetation structure and function.

Third, experimental studies on the impact of global change on consumer control in coastal wetlands have been lacking. A variety of global change drivers have been forecasted to impact the functioning and stability of coastal wetlands, and one possible impact mechanism is altered consumer control of vegetation (Silliman et al. 2013). While we now understand that eutrophication, disturbance, and increased flooding amplify consumer control in coastal wetlands, studies on other global change drivers such as climate warming, drought, and rising CO_2 are few. Past experiments, often from other ecosystems, suggest that these factors can magnify consumer control (e.g., O'Connor 2009), sometimes to a level that causes entire loss of vegetation and ecosystem collapse (Silliman et al. 2013). Future experiments testing these possibilities in coastal wetlands will be crucial to furthering understanding of biophysical coupling.

Fourth, future studies are needed to examine whether and to what extent the effects of consumers on coastal vegetation scale up to affect the functioning of coastal wetlands. Because consumers strongly regulate vegetation that is the foundation species of coastal wetlands (Altieri and van de Koppel 2014), it is likely that the effects of consumers on vegetation will scale up to impact the functioning of coastal wetlands. Studies are beginning to show that consumers affect multiple ecosystem functions such as carbon storage, decomposition, water purification, and coastal erosion (Kirwan et al. 2008, Hensel and Silliman 2013), but such studies are uncommon, and the generality and variability are uncertain. Studies should further investigate the consumer–ecosystem function link and how this interaction may be altered under global change.

Finally, more studies should be conducted on other types of consumers, including parasites and fungal pathogens, and in understudied regions. While our syntheses included the majority of the most conspicuous animal consumers in coastal wetlands, we highlight the need to study the sometimes-unseen consumers that include parasites and fungal pathogens, both of which, as shown in relatively few studies (Pennings and Callaway 1996, Silliman and Newell 2003, Grewell 2008, Altman and Byers 2014), may play a powerful role in mediating coastal vegetation directly or indirectly by affecting the behavior of their hosts. We also note that a large proportion of consumer control studies available by far were conducted in a few intensely studied regions such as the East Coast of North America and Europe, and more studies from understudied regions should be especially encouraged to reduce geographical bias in current studies and further the generality of our findings. When possible, future studies should locate study sites in a fully random manner (so bias towards studying consumer effects in sites where consumers are known to be strong can be minimized), and should be coordinated across multiple sites and geographic regions (Fraser et al. 2013), to better testify the findings and hypotheses emerged from our synthesis.

This global perspective on the roles of consumers play in regulating coastal vegetation thus not only provides much needed synthesis and impetus for better incorporating consumer control in coastal wetland ecology but can also serve as a stimulator for new discoveries that can further our ecological understanding and inform coastal wetland conservation in a rapidly changing era.

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CONCEPTS & SYNTHESIS

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Supporting Information

Data Availability

Concepts & Synthesis