



# Ecological impacts of invading seaweeds: a meta-analysis of their effects at different trophic levels

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## ABSTRACT

**Aim** Biological invasions are among the main threats to biodiversity. To promote a mechanistic understanding of the ecological impacts of non-native seaweeds, we assessed how effects on resident organisms vary according to their trophic level.

**Location** Global.

**Methods** We performed meta-analytical comparisons of the effects of non-native seaweeds on both individual species and communities. We compared the results of analyses performed on the whole dataset with those obtained from experimental data only and, when possible, between rocky and soft bottoms.

**Results** Meta-analyses of data from 100 papers revealed consistent negative effects of non-native seaweeds across variables describing resident primary producer communities. In contrast, negative effects of seaweeds on consumers emerged only on their biomass and, limited to rocky bottoms, diversity. At the species level, negative effects were consistent across primary producers' response variables, while only the survival of consumers other than herbivores or predators (e.g. deposit/suspension feeders or detritivores) decreased due to invasion. Excluding mensurative data, negative effects of seaweeds persisted only on resident macroalgal communities and consumer species survival, while switched to positive on the diversity of rocky-bottom consumers. However, negative effects emerged for biomass and, in rocky habitats, density of consumers other than herbivores or predators.

**Main conclusions** Our results support the hypothesis that seaweeds' effects on resident biodiversity are generally more negative within the same trophic level than on higher trophic guilds. Finer trophic grouping of resident organisms revealed more complex impacts than previously detected. High heterogeneity in the responses of some consumer guilds suggests that impacts of non-native seaweeds at higher trophic levels may be more invader- and species-specific than competitive effects at the same trophic level. Features of invaded habitats may further increase variability in seaweeds' impacts. More experimental data on consumers' response to invasion are needed to disentangle the effects of non-native seaweeds from those of other environmental stressors.

## Keywords

Biological invasions, effect size, mensurative and experimental data, non-native seaweeds, systematic review, trophic groups.

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## INTRODUCTION

Biological invasions are globally acknowledged among the major threats to biodiversity (Parker *et al.*, 1999; Simberloff *et al.*, 2005). Concerns over their potential ecological, social and economic consequences have resulted in a plethora of studies aiming to estimate the direction and magnitude of the effects of non-native plants on resident species and communities (e.g. Britton-Simmons, 2004; Vilà *et al.*, 2006; Liao *et al.*, 2007; Bulleri *et al.*, 2010). Despite such a large research effort, a comprehensive framework for understanding the impacts of invaders is still lacking, likely as a consequence of the difficulties in distilling generalities from disparate case studies (Vilà *et al.*, 2011; Blackburn *et al.*, 2014; Jeschke *et al.*, 2014). In the last few years, some progress has however been made through qualitative syntheses and quantitative meta-analyses of available information (Schaffelke & Hewitt, 2007; Williams & Smith, 2007; Gaertner *et al.*, 2009; Thomsen *et al.*, 2009, 2014; Powell *et al.*, 2011; Vilà *et al.*, 2011).

Some of these syntheses suggest a tendency for the effects of non-native plants on resident plant communities to be consistently negative, while their effects on animal communities are more variable (Gaertner *et al.*, 2009; Thomsen *et al.*, 2009, 2014; Powell *et al.*, 2011; Vilà *et al.*, 2011). A recent meta-analysis by Thomsen *et al.* (2014) has shown that marine invaders generally have negative effects on biodiversity at the same trophic level, but less negative, or indeed positive effects on biodiversity at higher trophic levels. These patterns suggest that competition would prevail in interactions between resident and non-native species within a trophic level, while processes such as habitat formation and food provision would ultimately result in neutral to positive effects towards higher trophic levels (Thomsen *et al.*, 2014).

The meta-analysis by Thomsen *et al.* (2014) was, to our knowledge, the first to assess how the effects of invaders vary with trophic level. In that study, local communities were categorized as plant, animal or mixed. Often, a finer trophic resolution of animal communities cannot be extracted from published data because studies typically group species with disparate life history traits and different trophic levels together. In contrast, the trophic level of individual consumer species can be generally established. Specific hypotheses formulated to explain differences in the effects of non-native plants on species at different trophic levels can be, thus, formally tested, promoting a mechanistic understanding of invaders impacts on resident biodiversity and ecosystem functioning.

To address this issue, we undertook a global meta-analytical comparison of the effects of non-native seaweeds within and on higher trophic guilds. We focused on seaweeds as they play a key role in providing habitat and represent a substantial component in the primary productivity of marine environments (Mann, 1973). Anthropogenic activities have greatly facilitated the global spread of seaweeds, causing more than 400 cases of introduction to non-native locations world-wide (Williams & Smith, 2007). A relatively large proportion of these introduced seaweeds have been successful in

becoming invasive and establishing large populations in the invaded range. Over the last two decades, non-native seaweeds have catalysed the attention of marine ecologists, producing a large body of literature describing their impacts on extant communities.

Importantly, there are indications that non-native seaweeds have notable effects on resident species throughout the food chain. For instance, generalist herbivores (including gastropods, isopods, polychaetes, sea urchins, fishes) have been observed to consume non-native seaweeds in the majority of feeding experiments (e.g. Dumay *et al.*, 2002; Britton-Simmons, 2004), suffering, in some cases, physiological damage (Trowbridge & Todd, 2001; Box *et al.*, 2009; Terlizzi *et al.*, 2011; Tomas *et al.*, 2011). Non-native seaweeds can, on the other hand, indirectly affect organisms at higher trophic levels through the modification of the abiotic environment. For example, the invasive epiphyte *Lophocladia lallemandii* can cause oxidative stress in a filter-feeding bryozoan living within *Posidonia oceanica* meadows, by generating water anoxia (Deudero *et al.*, 2010). In contrast, the intricate web of stolons formed by the invasive *Caulerpa racemosa* provides small crustaceans with a refuge from predators (Pacciardi *et al.*, 2011). In other cases, non-native seaweeds have been shown to decrease the density of dominant mesofauna (important to higher level consumers), likely through a reduction in habitat complexity (Janiak & Whitlatch, 2012). Thus, the spread of non-native seaweeds represents an ideal model system to assess how the effects of an invasion can propagate through different trophic levels of resident communities.

Here, we provide the results of a systematic review and meta-analyses (Pullin & Stewart, 2006; Lortie, 2014) of the published literature on the effects of non-native seaweeds on resident organisms. In addition to previous meta-analyses investigating the impacts of primary producers on resident communities at different trophic levels (Thomsen *et al.*, 2009, 2014; Vilà *et al.*, 2011), we explored variations in the effects of non-native seaweeds among consumer species characterized by marked differences in life traits. In particular, our aim was to assess how the effects of non-native seaweeds on resident species and communities vary (1) according to their trophic level (for species-level responses: primary producers versus herbivores versus predators versus other consumers; for community-level responses: primary producers versus consumers) and (2) among habitats. In addition, in order to assess to which extent study selection criteria may account for contrasting results generated by previous works (Thomsen *et al.*, 2009, 2014), we compared the results of analyses performed on the whole dataset (i.e. both mensurative and experimental data) with those of analyses on experimental data only.

## METHODS

### Literature search

We searched the 'ISI Web of Science' database for relevant literature in June 2012, with no restriction on publication

year, using the following search term combinations: (alga\* OR macroalga\* OR seaweed\*) AND (alien\* OR invasi\* OR introduced OR allochthonous OR non-indigenous OR non-indigenous OR 'non-native\*' OR non-native\* OR exotic\*) AND (marine OR brackish OR estuar\* OR coastal OR shallow OR sea\* OR aquatic OR maritime OR lagoon\* OR pelagic OR benth\* OR demersal OR shore\* OR intertidal OR subtidal OR ocean\* OR bay OR cove) AND (impact\* OR effect\* OR influence OR consequence\* OR food web\* OR 'food web\*' OR ecosystem\* OR biomass OR biodiversity OR 'biological diversity' OR communit\* OR richness OR diversity OR abundance OR evenness OR cover OR density OR 'reproductive capacity' OR mortality OR growth OR assemblage\* OR producti\* OR decomposition OR 'nutrient cycl\*' OR oxygen OR carbon OR flux OR respiration OR 'ecosystem metabolism' OR 'sediment stabilization' OR epiphyte\* OR 'sediment mixing' OR resilience OR stability OR resistance OR invasibility). Reference lists from all the retrieved articles were then screened for further relevant publications.

Assessment of references obtained through the search was performed through a 3-step process as follows: (1) scanning of article titles (mostly to exclude articles dealing with completely unrelated topics); (2) reading of the abstract and (3) reading of full text. We required studies to quantitatively compare relevant response variables between invaded and non-invaded units (with the term 'unit' meaning organisms/individual/plots/treatments/areas/sites/locations/regions), invaded versus invader removal units or control (no invader) versus invader-transplanted units. This resulted in an initial set of 144 papers that were evaluated against the following criteria for data inclusion:

- (1) Papers without replication or appropriate controls were excluded. We evaluated whether controls and invaded units were sufficiently similar but spatially and temporally independent.
- (2) Studies were excluded when manipulation (generally the removal) of the non-native seaweed was not carried out independently from that of resident species. For example, the manipulation of canopy stands including both non-native and resident seaweeds (Farrell & Fletcher, 2004).
- (3) Studies were excluded when non-invaded sites were characterized by the presence of other non-native species. For example, sites invaded by *Caulerpa racemosa* compared to sites heavily colonized by *Wormesleyella setacea* (Klein & Verlaque, 2009).
- (4) Studies were excluded when variations in response variables could not be unambiguously interpreted as positive or negative effects (e.g. relative proportion of individuals exhibiting a certain colouring; Arigoni *et al.*, 2002).
- (5) In the case of mensurative studies reporting time series, the first and last time of sampling were used, to account for variation through time. In contrast, for experimental studies, only the last time of sampling was extracted, assuming that the effects of experimental manipulations (removal or addition of the invader) are more likely to manifest on longer temporal scales.

- (6) When data could not be directly extracted from papers, the authors of the original study were asked to provide either raw data or relevant information (e.g. means, standard deviation/variance, sample size). Studies were not included when this procedure did not allow us to obtain estimates of variation in the effect sizes, necessary for weighted analyses.

## Data extraction and effect sizes

We extracted means, measures of variability (i.e. standard errors, standard deviations, confidence intervals) and sample sizes for units where the non-native species was present or absent. Data extraction from graphs was carried out by means of the image analysis software IMAGEJ (Schneider *et al.*, 2012). We retained variables accounting for the response to invasion of either single species or communities. Our operative definition of community includes the presence of more than one species or any taxonomic group higher than species, including morphological or functional groups. We analysed data on variables related to density/cover, biomass, growth and survival of individual species and density/cover, biomass, diversity (including both richness and diversity indices) and evenness of communities (see Table 1 for the detailed list of variables included within each category). Density and cover constitute somewhat different estimates of abundance; however, data on percentage cover came almost exclusively from studies on plants, so that no analyses could be run separately for this variable. Instead of losing a large amount of data on plants, we, therefore, decided to merge density and cover data (Vilà *et al.*, 2011). Studies reporting data on species fitness variables different from growth or survival were not considered, and a total of 100 studies were finally included in the analyses (see Appendix S1 and Table S1 in Supporting Information).

We calculated Hedges'  $g^*$ , which measures the unbiased, standardized mean difference between invaded and non-invaded means (Borenstein *et al.*, 2009). Negative and positive Hedges'  $g^*$  values indicate, respectively, negative and positive effects of non-native species on resident communities or species. Hedges'  $g^*$  was calculated as:

$$g^* = gJ \text{ where}$$

$$g = \frac{x_{\text{Invaded}} - x_{\text{Not invaded}}}{SD_{\text{pooled}}}$$

$$\text{with } SD_{\text{pooled}} = \sqrt{\frac{(n_{\text{Invaded}}-1)SD_{\text{Invaded}}^2 + (n_{\text{Not invaded}}-1)SD_{\text{Not invaded}}^2}{n_{\text{Invaded}} + n_{\text{Not invaded}} - 2}}$$

$$\text{and } J = 1 - \frac{3}{4(n_{\text{Invaded}} + n_{\text{Not invaded}} - 2) - 1}$$

Effect sizes for primary producers and consumers were estimated from the dataset and its subsets (experimental data only, rocky bottom or soft-bottom data only) by means of mixed-effects models (Borenstein *et al.*, 2009). In mixed-effects models, a fixed effect was used to model among groups variability (trophic level in this case), while a random effect was used to model within-group variability. The effect sizes of individual comparisons were weighted by the inverse

**Table 1** Summary of the ecological impacts due to non-native seaweeds classified by ecological levels, impact types and response variables analysed

Level	Impact type	Variables
Primary producer species (e.g. macroalgae or phanerogams)	Density/cover	Density or cover of adults/recruits
	Biomass	Above-/below-ground biomass of leaves/roots/rhizomes; biomass primary productivity/production
	Growth	Size/change in size of whole organisms or parts
	Survival	% survival, mortality, longevity
Primary producer community	Density/cover	Density or cover of adults/recruits
	Biomass	Biomass of plants, biomass production
	Diversity	Number of species/taxa, Shannon diversity index
	Evenness	Pielou's evenness
Consumer species	Density/cover	Density or cover of adults/recruits/ juveniles/colonies
	Biomass	Biomass of whole organisms or parts
	Growth	Size/change in size of whole organisms or parts
	Survival	% survival, mortality rates, predation rates
Consumer community	Density/cover	Density or cover of individuals/ colonies
	Biomass	Biomass
	Diversity	Number of species/taxa, diversity indices (Shannon, Margalef)
	Evenness	Pielou's evenness

of within-study variance plus between-study variance, the latter being calculated within levels of the moderator (i.e. trophic levels). Effect sizes were first calculated using all the data available in the dataset or in the subsets, including multiple estimates from each study, when available. However, this procedure does not take into account potential autocorrelation among observations within studies, thus violating the assumption of independence in the data (Borenstein *et al.*, 2009). In addition, when computing summary effects across studies, it assigns more weight to studies with multiple outcomes. One approach to solve this issue is to average within studies across sources of independence (e.g. multiple sites, different times of sampling, comparison of the same invasive species with several native species) to generate one single effect size per response variable per study. However, unless the degree of autocorrelation among observations being averaged is known and explicitly incorporated into calculations, the estimates of variances associated with the means are based on the assumption of a zero correlation (Borenstein *et al.*, 2009). This is likely to lead to over- or underestimation of variance and underestimation of the precision of the difference (Borenstein *et al.*, 2009). For the

reasons explained above and following Gibson *et al.* (2011) and He *et al.* (2013), median effect sizes and 95% confidence intervals were calculated by resampling one observation per publication, using 10,000 bootstrap samples, generated with replacement. Median effect sizes were considered significantly different from zero when their 95% confidence intervals do not overlap zero.

For analyses focusing on variables at the species level, resident consumers were categorized as 'predators' (parasites were excluded), 'herbivores' or 'other consumers' (such as suspension feeders, deposit feeders and/or detritivores) based on information obtained from MarLIN (The Marine Life Information Network; <http://www.marlin.ac.uk/>) and FishBase (<http://www.fishbase.org/>) databases and expert opinion when information on feeding habit was not available. Predators and herbivores included also species that, in addition to either herbivory or predation, may exhibit other lower order feeding habits.

The null hypothesis (no difference in the effect size between primary producers and consumers) was tested through the Q statistic, a weighted sum of squares following a  $\chi^2$  distribution describing variation in the effect size between groups (Borenstein *et al.*, 2009; Viechtbauer, 2010). To test for the significance of differences between trophic levels (primary producers versus consumers for community-level variables; primary producers versus predators versus herbivores versus other consumers for species-level variables), we used the between-group heterogeneity of the mixed-effect models (a weighted sum of squares describing variation in effect size between groups; Borenstein *et al.*, 2009; Viechtbauer, 2010). The effects of the moderator (i.e. the trophic level) were deemed as significant when the median  $Q_M$ , generated by data permutations, exceeded the critical value (corresponding to  $\alpha = 0.05$ ) obtained from the null distribution generated by permutations with reshuffling of labels (trophic levels). The exact significance level ( $P_{\text{Between}}$ ) was estimated as the proportion of times out of 10000 permutations in which the median  $Q_M$  was smaller than the critical Q value from the null distribution [i.e.  $(Q_{M\text{Null}} \geq \text{median}Q_M)/10000$ ].

### Tests for publication bias

To assess publication bias, we visually examined funnel plots of effect size standard errors against residuals (based on mixed-model effect size calculations) and tested their asymmetry through a rank correlation test (Viechtbauer, 2010). Asymmetry in funnel plots emerged for community density/cover ( $\tau = -0.21$ ,  $P < 0.0001$ ) and diversity ( $\tau = -0.34$ ,  $P < 0.01$ ), but not for the other variables (Table S2, Fig. S1 in Supporting Information). Asymmetry emerged as a consequence of some data with large residual values and high variances. Following He *et al.* (2013), these data were removed to adjust for potential publication bias (Fig. S1). Adjusting for publication bias did not change the outcomes of the analyses on resident community density/cover (Tables S3),



suggesting that publication bias did not have a severe effect on our results. In contrast, adjusting for potential bias in the diversity data caused the difference in effect sizes between the two trophic levels to be not significant (see 'Mensurative and experimental studies' in Table S3). We conducted analyses using the *METAFOR* package (Viechtbauer, 2010), in R v2.15 (R Development Core Team, 2013).

## RESULTS

Among the 100 papers we retained, experimental data (both from field or laboratory studies) were extracted from a total of 48 papers, and mensurative data were extracted from 65 papers. Data related to the effects of 12 seaweeds, which were generally described as invasive in the study regions (Parker *et al.*, 1999; Ricciardi & Cohen, 2007): *Caulerpa racemosa*, *Caulerpa taxifolia*, *Codium fragile* spp., *Fucus evanescens*, *Fucus serratus*, *Grateloupia turuturu*, *Gracilaria vermiculophylla*, *Lophocladia lallemandii*, *Neosiphonia harveyi*, *Sargassum muticum*, *Undaria pinnatifida* and *Wormesleyella setacea*. Experimental data were available for only eight non-native seaweeds (*C. racemosa*, *C. taxifolia*, *C. fragile* spp., *F. evanescens*, *G. vermiculophylla*, *N. harveyi*, *S. muticum* and *U. pinnatifida*). Studies had been performed in the Mediterranean Sea (34), along the coasts of Atlantic Europe (27), Australia (16), Atlantic (16) and Pacific (4) North America and Argentina (3).

### Effects on communities

Non-native seaweeds had significant negative effects on the density/cover (median effect size:  $-1.18$ , CI:  $-1.76/-0.62$ ), biomass (median:  $-0.4$ , CI:  $-0.63/-0.18$ ), diversity (median:  $-1.7$ , CI:  $-2.28/-1.24$ ) and evenness (median:  $-1.26$ , CI:  $-2.18/-0.63$ ) of native primary producer communities and on the biomass of consumer communities (median:  $-0.64$ , CI:  $-1.47/-0.02$ ) (Fig. 1). Effects on consumer communities were statistically different from those on primary producer communities for density/cover ( $P_B = 0.014$ ) and diversity ( $P_B = 0.023$ ) (Table S3).

Following the exclusion of mensurative studies from the dataset, significant negative effects on density/cover and diversity of resident primary producers persisted (density/cover: median:  $-1.04$ , CI:  $-1.61/-0.42$ ; diversity: median:  $-1.45$ , CI:  $-1.71/-1.2$ ). Lack of a sufficient number of studies prevented analyses on community biomass and evenness. Exclusion of mensurative studies also reduced differences between trophic levels, which did not differ significantly for any of the response variables investigated (Fig. 1, Table S3).

In rocky-bottom habitats (intertidal and subtidal), non-native seaweeds had significant negative effects on the diversity of both resident primary producers (all data: median:  $-1.90$ , CI:  $-2.55/-1.40$ ; experimental data only: median:  $-1.40$ , CI:  $-1.69/-1.12$ ) and consumers (all data: median:  $-0.57$ , CI:  $-1.07/-0.11$ ). Negative effects on the diversity of consumers switched to positive when analyses were per-

formed on experimental data only (median:  $0.63$ , CI:  $0.20/1.22$ ). The effects on the diversity of consumer communities did not, however, statistically differ from those on primary producers (Fig. 2, Table S4).

Lack of a sufficient number of studies prevented us to repeat the analyses on other community variables or on soft-bottom habitats data (i.e. intertidal and subtidal soft bottoms, soft vegetated habitats and seagrasses).

### Effects on species

Non-native seaweeds had significant negative effects on the density/cover of resident primary producer species (median:  $-0.7$ , CI:  $-1.24/-0.14$ ). These effects were evident in soft (median:  $-1.40$ , CI:  $-2.46/-0.33$ ), but not in rocky-bottom habitats. In contrast, effects on density/cover of higher trophic groups were always neutral (Fig. 3) (Tables S5 and S6).

Following the exclusion of mensurative data, negative effects on density/cover of resident primary producer species disappeared when all data or soft-bottom habitats only were analysed. In contrast, they changed to significantly negative in rocky-bottom habitats (median:  $-0.58$ , CI:  $-0.98/-0.15$ ) (Fig. 3) (Tables S5 and S6).

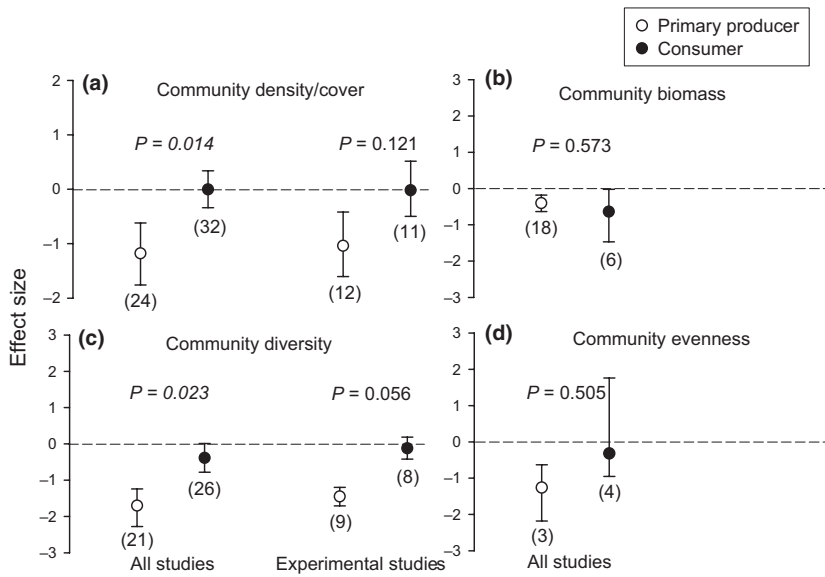
A significant negative effect on density/cover of other consumers was detected when all experimental data (median:  $-0.63$ , CI:  $-1.43/-0.06$ ) or only those from rocky-bottom habitats (median:  $-0.42$ , CI:  $-0.79/-0.08$ ) were included. Effects on herbivores and predators remained neutral in all cases (Fig. 3) (Tables S5 and S6).

Differences in the effects of non-native seaweeds on density/cover between primary producers and higher trophic levels were not significant for any dataset examined (Fig. 3) (Tables S5 and S6).

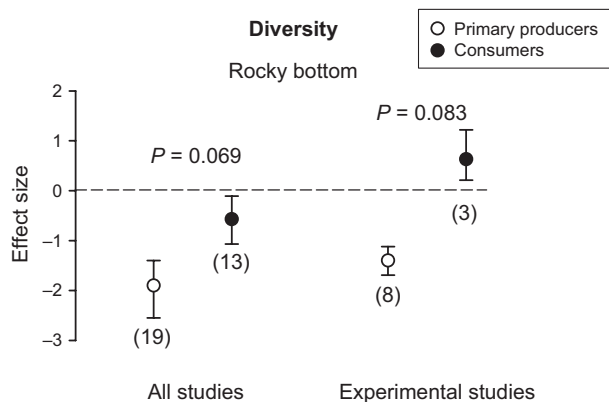
Non-native seaweeds had significant negative effects on the biomass (median:  $-0.39$ , CI:  $-0.95/-0.09$ ), growth (median:  $-0.6$ , CI:  $-0.82/-0.41$ ) and survival (median:  $-1.04$ , CI:  $-1.75/-0.76$ ) of resident primary producer species. In contrast, significant negative effects on consumers emerged only for the survival of suspension feeder/deposit feeder/detritivore species (other consumers; median:  $-1.11$ , CI:  $-1.68/-0.52$ ) (Fig. 4) (Table S5).

Following the exclusion of mensurative data, the analyses did not detect any significant effect on primary producer species or herbivores. In contrast, negative effects remained significant on the survival of other consumer species (median:  $-1.12$ , CI:  $-1.68/-0.52$ ) and emerged for their biomass (median:  $-0.85$ , CI:  $-2.61/-0.09$ ) (Fig. 4) (Table S5).

Differences in the effects of non-native seaweeds between primary producers and higher trophic levels were not significant for any of the response variables examined (Fig. 4) (Table S5). Lack of a sufficient number of studies prevented us from running additional analyses on data of biomass, growth or survival from experimental data only. Likewise, it was not possible to assess variations in these



**Figure 1** Effects of non-native seaweeds on (a) density/cover, (b) biomass, (c) diversity (including both species/taxa richness and diversity indices) and (d) Pielou's evenness of communities of primary producers and consumers, calculated using the entire dataset or experimental studies only. Symbols report median effect size calculated using 10000 bootstrap samples and 95% confidence intervals. Probabilities refer to the comparison of effect sizes between primary producers and consumers for all studies and experimental studies only, separately. Number of studies in parentheses.



**Figure 2** Effects of non-native seaweeds on diversity of communities of primary producers and consumers living on rocky bottoms (intertidal and subtidal), calculated using the entire dataset or experimental studies only. Symbols report median effect size calculated using 10000 bootstrap samples and 95% confidence intervals. Probabilities refer to the comparison of effect sizes between primary producers and consumers for all studies and experimental studies only, separately. Number of studies in parentheses.

variables at the level of predators or to focus on specific habitats.

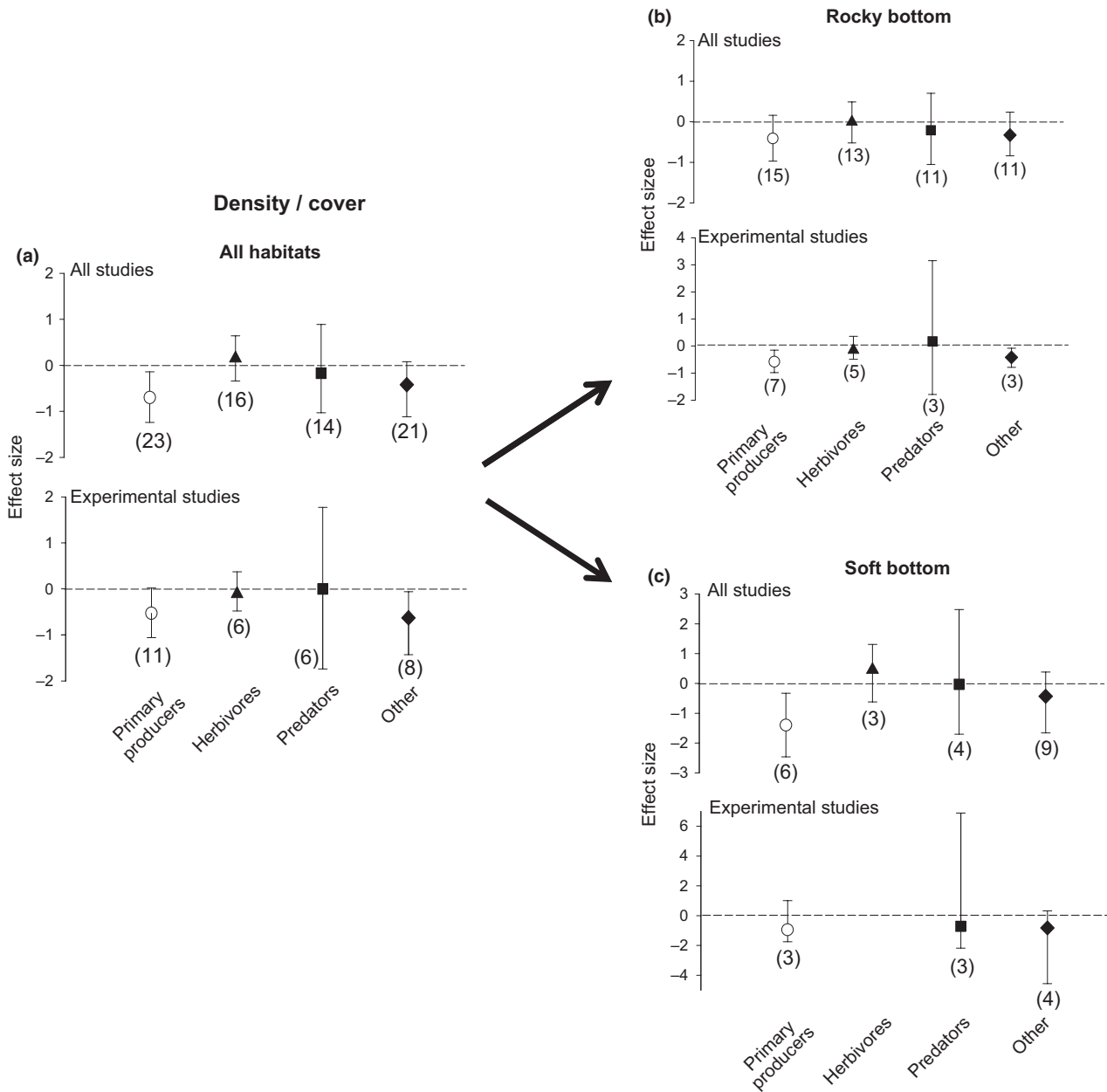
## DISCUSSION

Negative effects of non-native seaweeds on resident plant communities were consistent across the response variables we examined (i.e. density/cover, biomass, diversity and evenness), supporting previous findings of strong negative impacts of plant invaders on resident primary producer assemblages (Gaertner *et al.*, 2009; Thomsen *et al.*, 2009, 2014; Powell *et al.*, 2011; Vilà *et al.*, 2011). A significant negative effect of non-native seaweeds on resident consumer

communities was, in contrast, detected only on their biomass. Despite the fact that effects on native producers were significantly different from those on consumers only for density/cover and diversity of communities, our results generally support the relative trophic position hypothesis of Thomsen *et al.* (2014), which proposed that invaders' effects on resident biodiversity might be more negative within the same than on higher trophic levels.

Thomsen *et al.* (2014) found significant positive effects of invading seaweeds on resident consumer biodiversity. Apparent discrepancies between the present study and that of Thomsen *et al.* (2014) likely arise from the use of different study inclusion criteria (both mensurative and experimental in this study versus experimental data only in that of Thomsen *et al.*), as well as the inclusion of more recent studies in our meta-analyses (for a total of 100 papers versus 29 papers included by Thomsen *et al.*, 2014). Interestingly, on rocky bottoms, the exclusion of mensurative studies caused the effects of non-native seaweeds on the diversity of consumers to switch from negative to positive. These results suggest that, in the marine environment, effects of invading plants on resident consumer communities might be the outcome of different mechanisms in different habitats.

In particular, the provision of a complex habitat by non-native seaweeds (such as *S. muticum*, *C. fragile* and *U. pinnatifida*), offering shelter and/or food (Britton-Simmons, 2004; Schmidt & Scheibling, 2007; Irigoyen *et al.*, 2011), is of major importance in rocky-bottom habitats, where consumers dwell above ground. In contrast, consumer communities in soft sediments may be affected negatively by non-native seaweeds also through the modification of below-ground conditions, for example through the release of secondary metabolites into the detritus (Taylor *et al.*, 2010). This may, to some extent, explain the lack of effects on diversity of consumers when all habitats were included. Thus, mensurative studies, being not able to correctly disentangle the effects



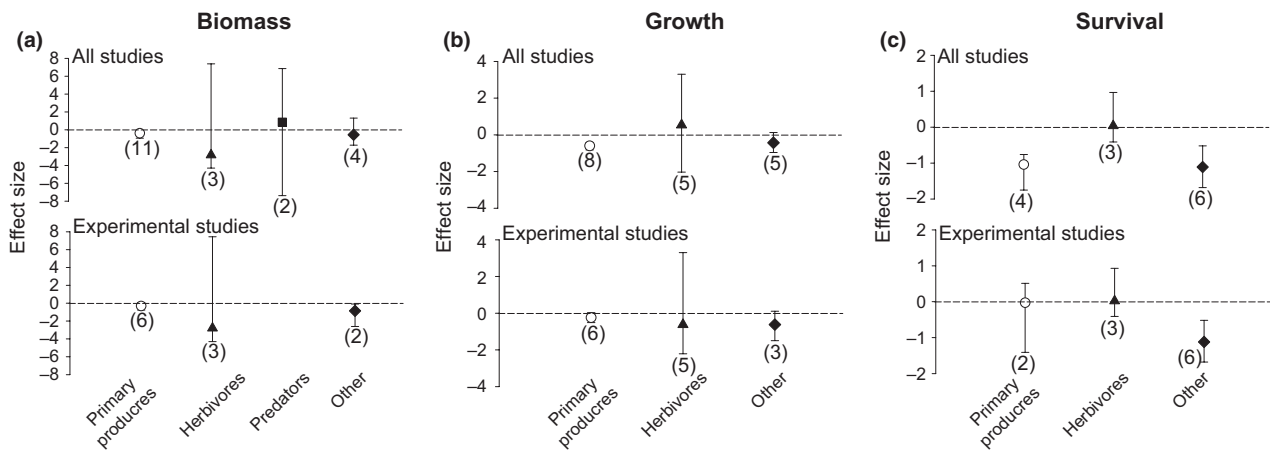
**Figure 3** Effects of non-native seaweeds on species-level density/cover of primary producers, herbivores, predators and other consumers in all (a), rocky-bottom (b) or soft-bottom (c) habitats, calculated using the entire dataset or experimental studies only. Symbols report median effect size calculated using 10000 bootstrap samples and 95% confidence intervals. Comparisons of effects sizes between primary producers and consumers were never significant. Number of studies in parentheses.

of non-native seaweeds from other stressors, may overestimate negative effects on consumers diversity (Lotze *et al.*, 2006).

As emerged at the community level, there was a trend for the effects of non-native seaweeds on resident primary producer species to be negative. Analyses including both mensurative and experimental data showed that non-native seaweeds depressed the density/cover, biomass, growth and survival of local plant species. The magnitude of these effects was, however, reduced by the exclusion of mensurative data

from the analyses. In addition, analyses on density/cover data ran separately for soft-bottom or rocky-bottom habitats yielded contrasting results, likely due to differences between target species in the two habitats (i.e. seagrasses versus macroalgae, respectively).

Seagrass meadows, characterized by low taxonomic diversity and unique physiological characteristics, are globally threatened by alterations to abiotic conditions (Orth *et al.*, 2006). Again, mensurative studies might have overestimated invaders' impact on seagrass density (Lotze *et al.*, 2006; Orth



**Figure 4** Effects of non-native seaweeds on species-level (a) biomass, (b) growth and (c) survival of primary producers, herbivores, predators and other consumers, calculated using the entire dataset or experimental studies only. Symbols report median effect size calculated using 10000 bootstrap samples and 95% confidence intervals. Comparisons of effects sizes between primary producers and consumers were never significant. Number of studies in parentheses.

*et al.*, 2006). In fact, analyses of experimental data only, although characterized by lower statistical power (i.e. they were based on a small number of studies), did not show significant effects of invading seaweeds on seagrass density, suggesting a trade-off between negative (e.g. competition for light availability, Drouin *et al.*, 2012) and positive (e.g. enhanced reproductive shoot density; Ceccherelli & Campo, 2002) effects of invaders.

In contrast, there is high variability in physiological and ecological traits among macroalgae; for example, several macroalgal species are weak competitors that can opportunistically take advantage of degraded environmental conditions (e.g. filamentous species forming turfs; Benedetti-Cecchi *et al.*, 2001). In this case, mensurative studies might have underestimated the competitive effects of invaders on density/cover of resident macroalgae in degraded environments.

Competition for resources with non-native seaweeds is likely to underpin the changes observed in resident plant communities (Thomsen *et al.*, 2014). The heterogeneity of invaders' traits (e.g. including siphonous species, such as *C. racemosa*, *C. taxifolia* and *C. fragile* spp., filamentous species, such as *W. setacea*, and canopy formers, such as *C. fragile* spp., *Fucus* spp., *U. pinnatifida*, *S. muticum* and *G. turuturu*) may translate into a wide range of mechanisms through which these seaweeds compete with resident primary producers, and macroalgae in particular. For example, *Caulerpa* species produce three-dimensional networks of stolons that generate adverse physical/chemical conditions for native plants, by enhancing sediment retention and reducing water flow (Piazzi *et al.*, 2007). The same species can release allelochemicals against macroalgal competitors (Raniello *et al.*, 2007). In contrast, mechanisms underpinning negative effects of canopy-forming non-native species, such as *U. pinnatifida* or *S. muticum*, are linked to pre-emption of resources (light, nutrient, space availability; Britton-Simmons, 2004; Casas *et al.*, 2004).

The lack of significant effects of non-native seaweeds on herbivore species suggests that alterations caused to resident primary producer communities did not imply detrimental changes to their value as food or habitat (i.e. they serve as an alternative food or habitat source in the invaded system). The response of individual herbivore species was, however, highly variable, indicating that some species were influenced negatively and others positively. Some studies clearly indicate that some siphonous green invading seaweeds, if ingested, can induce physiological damage to herbivorous fish through production of chemical defences (Box *et al.*, 2009; Terlizzi *et al.*, 2011), or reduce growth and reproductive rates of resident sea urchins as a consequence of their low nutritional value (Lyons & Scheibling, 2007; Tomas *et al.*, 2011). In other cases, non-native seaweeds are preferred over the resident macroalgal species, either as habitat or as food (Trowbridge & Todd, 2001; Siddon & Witman, 2004).

The lack of effects of non-native seaweeds on predator species density/cover and biomass (the only two variables that could be analysed) may partly reflect the absence of effects on their prey (herbivores or other consumers). However, predator species might be also indirectly affected by habitat modifications caused by non-native seaweeds (Vazquez-Luis *et al.*, 2009; Janiak & Whitlatch, 2012). Non-native macroalgae may largely influence resident predators through this mechanism, but effects can be either negative or positive. For example, small predators may be disadvantaged by the loss of habitat complexity, as it is the case of *G. turuturu* replacing *Chondrus crispus* (Janiak & Whitlatch, 2012), or favoured by an increase in refuges created by the invading alga (e.g. Vazquez-Luis *et al.*, 2009). A similar positive effect has been shown for recruits/juveniles of larger predators (e.g. *G. vermiculophylla*, *C. fragile* spp. *tomentosoides* on crabs, sea-stars, fish) (Schmidt & Scheibling, 2007; Thomsen, 2010). It is worth stressing that the small number of studies available



for this group could have limited the statistical power of our analyses.

Non-native seaweeds decreased the survival of other consumers. This group was mainly composed of suspension and deposit feeders, for which anoxic- and sulphide-rich sediments usually found in presence of some habitat-forming non-native seaweeds (e.g. *C. taxifolia*; Chisholm & Moulin, 2003) can be toxic (Shumway *et al.*, 1985; Laudien *et al.*, 2002). Non-native seaweeds may also increase post-settlement mortality of epiphytic species, possibly through the release of chemicals (e.g. effects of *Fucus evanesceus* on *Balanus improvisus*, Wikstrom & Pavia, 2004).

The removal of mensurative data caused effect sizes of density/cover and biomass of other consumers to be more (and significantly) negative. When density/cover data were analysed separately between habitats, significant negative effects from experimental studies emerged only in rocky-bottom habitats (e.g. Wikstrom & Pavia, 2004). Lack of effects in soft bottoms might suggest the existence of positive below-ground effects of non-native seaweeds on this group of consumers, likely able to counterbalance negative ones. For example, Olabarria *et al.* (2010) have suggested that decomposition of wrack of *S. muticum* might act as a source of organic matter, thus facilitating the opportunistic worm *Capitella capitata*. However, results from these analyses must be interpreted with caution, due to the relatively small number of studies.

Overall, despite large variability in the effects of non-native seaweeds among different groups of consumers, a negative effect emerged on whole consumer community biomass when both mensurative and experimental data were analysed. More data from experimental studies are, however, needed to provide unambiguous estimates of the effects of non-native seaweeds on consumer communities.

Context dependency has prevented the identification of simple empirical rules for predicting invasion impacts (Parker *et al.*, 1999). Matching the attributes of invading and resident species has resulted in broad conceptual frameworks, such as the distinctiveness hypothesis, predicting larger impacts if non-native and resident species are functionally and/or taxonomically different from each other (Diamond & Case, 1986; Ricciardi, 2003). Building on this concept, Thomsen *et al.* (2014) have recently evaluated the effects of invading species belonging to different trophic groups (i.e. marine plants, mobile consumers or sessile filter feeders) on the biodiversity of both resident plants and animals. Their results highlight that matching the trophic position between invading and resident species can contribute to explain some of the variability in effect sizes usually observed. However, as a novel finding of our study, taking into account key features of resident species, such as the trophic level and habitat-specific life traits, can reveal greater complexity in the outcome of invasion (e.g. Vilà *et al.*, 2011; Thomsen *et al.*, 2014).

In summary, our results support the view of a generalized competitive effect of non-native plants within the same

trophic level (Thomsen *et al.*, 2014). Large heterogeneity in invader effects on herbivores and predators suggests, on the contrary, that impacts on resident species belonging to higher trophic levels could be more invader- and species-specific, due to the diversity and complexity of paths through which bottom-up effects can take place. Features of invaded habitats may further increase the variability in the effects on consumer species.

As clearly emerged from this study, the inclusion of data from mensurative studies can greatly influence estimates of the direction and intensity on the effects of invaders on resident species or communities. Gaining more data through experimental studies able to correctly disentangle the effects of non-native species from those of other stressors (Gurevitch & Padilla, 2004; Didham *et al.*, 2005; Bulleri *et al.*, 2010) should be thus considered a priority if we are to develop a robust theoretical framework for predicting the ecological impacts of plant invaders across trophic levels.

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## SUPPORTING INFORMATION

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

**Appendix S1** List of retained papers

**Appendix S2** Datasets

**Figure S1–S2** Funnel plots for community and species level variables

**Table S1** Excluded papers and reasons for exclusions

**Table S2** Rank correlation tests

**Table S3** Summary of mixed-effect models\_communities

**Table S4** Summary of mixed-effect models\_community diversity\_rocky bottom

**Table S5** Summary of mixed-effect models\_species

**Table S6** Summary of mixed-effect models\_species density/cover\_rocky and soft bottom

## BIOSKETCH

The authors of this article (except for AC) are partners within the project VECTORS (Vectors of Change in Oceans and Seas Marine Life, Impact on Economic Sectors) (FP7/2007–2013). Interests of authors cover the fields of marine ecology, biological invasions, biodiversity and ecosystem functioning, phycology and zoology.

Author contributions: Main ideas have been conceived by F.B. and L.B.C. and discussed with E.M., E.C., T.C., J.K., D.L. and G.R. within project meetings; E.M., F.B., C.R., G.G. and J.K. collected the data; AC greatly contributed to information on feeding habits of consumers; E.M., F.B. and L.R. analysed the data; E.M. and F.B. led the writing. All authors commented on drafts of the manuscript.

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