

EVIDENCE FOR IMPACTS OF NONINDIGENOUS MACROALGAE: A META-ANALYSIS OF EXPERIMENTAL FIELD STUDIES¹

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Invasions by nonindigenous macroalgal species (NIMS) potentially cause severe impacts on native species. We conducted a meta-analysis of 18 field-based manipulative experiments to quantify the direction and magnitude of impacts (Hedges effect size d , hereafter ES). We found significant small-to-medium negative effects on “macrophyte abundance” (cover, biomass of native taxa; $ES_{\text{cumulative}} = -0.30$) and medium-to-large negative effects on “macrophyte assemblages” (richness, diversity, total abundance; $ES_{\text{cumulative}} = -0.70$). In contrast, $ES_{\text{cumulative}}$ were not significant for “macrophyte processes” (growth, mortality; $ES_{\text{cumulative}} = -0.39$), “animal abundance” (densities; $ES_{\text{cumulative}} = -0.13$), or “animal assemblages” (richness, diversity; $ES_{\text{cumulative}} = 0.75$). The nonsignificant effect sizes were characterized by low sample sizes and should be interpreted with caution. Three study-specific effect sizes were particularly large (<-2.0), showing that, in specific cases, impacts can be highly negative. From a conservation perspective, focus could be on such worst-case scenarios. Still, the reported $ES_{\text{cumulative}}$ are likely biased toward larger effects because only the most conspicuous NIMS have been tested and because nonsignificant results are less likely to be published. To better understand the impacts of NIMS, more manipulative experiments are needed, testing more species and under contrasting environmental conditions. Future studies should include procedural control treatments and report the abundance of the NIMS to avoid ambiguous interpretations. In conclusion, current experimental evidence shows that

NIMS have, on average, small-to-large negative impacts on native plant species and assemblages. It is possible that these effects can result in severe consequences when accumulated over long time periods and large spatial scales.

Key index words: field experiments; impacts; meta-analysis; nonindigenous macroalgal species

Abbreviations: ES, Hedges effect size d for individual response variables within a study; ES_{average} , average d per study; $ES_{\text{cumulative}}$, cumulative d for all studies; NIMS, nonindigenous macroalgal species

The spread of nonindigenous species (NIS) by human activity potentially causes dramatic ecological impacts, and it is considered a major threat to biodiversity conservation (Parker et al. 1999, Simberloff 2005). Nonindigenous macroalgal species (NIMS) are represented by several invasive species (NIS with fast spread to many new regions and establishing large populations, Parker et al. 1999, Ricciardi and Cohen 2007) that have received considerable attention for their possible ecological impacts in coastal ecosystems (Schaffelke and Hewitt 2007, Williams and Smith 2007). Two NIMS, *Undaria pinnatifida* (Harv.) Suringar and *Caulerpa taxifolia* (M. Vahl) C. Agardh, have been included on a list of the 100 worst invasive species in the world (Lowe et al. 2000). Intense public attention and funds for study and eradication have been allocated to NIMS, and a conservative estimate of management costs exceeds US\$50 million (Schaffelke and Hewitt 2007). Given that several NIMS are considered high-impact pests that are impossible or costly to eradicate, it is pertinent to review the scientific evidence and provide standardized quantitative estimates of their impacts.

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Two reviews on the impacts of NIMS were published recently (Schaffelke and Hewitt 2007, Williams and Smith 2007). These reviews summarized, respectively, 60 and 68 correlative field studies and field and laboratory experiments, either qualitatively (table 1 in Schaffelke and Hewitt 2007) or semiquantitatively (table 1 in Williams and Smith 2007, vote-counting, “-” = negative, “+” = positive, “0” = none, and “Δ” = nondirectional effects). To supplement these two reviews, we here address the assessment of impact from a quantitative meta-analytic perspective. We focus only on field experiments where NIMS abundance was manipulated to provide a causal link to response variables (native species). For our purpose, we excluded laboratory and correlative studies as well as clearance experiments where all species, not only NIMS, were removed. We decided on these limitations because correlative studies cannot separate “driver from passenger effects” (Didham et al. 2005), laboratory studies are difficult to extrapolate to complex processes in nature, and because experimental manipulations in the field have been heralded as a strong method to establish cause-effect relationships with high realism (Hairston et al. 1960, Connell 1961, 1983, Gurevitch et al. 1992). Our main objective was to analyze field-based NIMS impact experiments to test if NIMS have significant negative effects on native species and assemblages. We also added statistical tests of the vote counts reported by Williams and Smith (2007) to indicate if the different types of

effects were significant for correlative and/or manipulative studies (i.e., to test if negative results were reported more often than expected by chance).

MATERIALS AND METHODS

Peer-reviewed studies, where the abundance of NIMS was manipulated and the responses of native species quantified, were located by searching ISI databases (Web of Science, Current Contents), reviews, and back-/cross-referencing. For each study, we tabulated the NIMS, response variables, the spatiotemporal context, experimental design, and key results (Table S1 in the supplementary material). A total of 18 manipulative field studies were located. Mean values and measures of dispersion were extracted for all reported response variables (an all-inclusive data selection criterion, which assumes that the experimenter solely chooses and reports appropriate variables). A few variables reported without measures of dispersion were excluded from meta-analysis but still tabulated in Table S1. Separate spreadsheets were prepared for five groups of responses: “macrophyte abundance” (cover or biomass of native species or form-functional group, including both macroalgae and seagrasses), “macrophyte assemblages” (total abundance, richness, diversity), “macrophyte processes” (percent mortality, survival, or growth), “animal abundance” (densities of associated fauna), and “animal assemblages” (total abundance, richness, diversity). The tests of animal variables only targeted mobile species; hence, impacts on sessile animals could not be evaluated here. Control groups were defined as plots without NIMS, based on either removal from already invaded plots or untouched noninvaded plots. In contrast, test groups were defined as plots with NIMS, based on either additions to noninvaded plots or on presence in already invaded plots. This way, if NIMS cause a reduction in a response variable, effect sizes are negative. Hedges effect sizes d corrected for small sample sizes (hereafter ES) were calculated

TABLE 1. Study-specific average effect sizes ($ES_{\text{average}} = \text{Hedges } d$, corrected for small sample sizes) for five groups of response variables extracted from manipulative field studies on impacts of nonindigenous macroalgal species (NIMS). Abundance = cover or biomass for plants and density for animals. Assemblages = richness, diversity, or total abundance. Processes = growth or mortality. v = variance of ES_{average} . n = number of reported impacts per test group per study. NA = not available (the study did not measure this variable and/or did not report measures of dispersion). A total of 200 individual effect sizes were extracted (=sum of all n).

Study	NIMS	Macrophytes									Animals					
		Abundance			Assemblages			Processes			Abundance			Assemblages		
		ES_{average}	v	n												
Ceccherelli and Campo 2002	<i>Caulerpa racemosa</i>	0.89	0.45	10	NA	NA	0									
Piazzi et al. 2005	<i>Caulerpa racemosa</i>	-1.04	0.44	14	-2.73	0.78	4	NA	NA	0	NA	NA	0	NA	NA	0
Piazzi and Ceccherelli 2006	<i>Caulerpa racemosa</i>	-1.44	0.45	3	-2.06	0.52	2	NA	NA	0	NA	NA	0	NA	NA	0
Ceccherelli and Sechi 2002	<i>Caulerpa taxifolia</i>	0.25	0.40	4	NA	NA	0									
Ceccherelli and Cinelli 1997	<i>Caulerpa taxifolia</i>	-0.12	0.17	4	NA	NA	0									
Gribben and Wright 2006	<i>Caulerpa taxifolia</i>	NA	NA	0												
Chavanich and Harris 2004	<i>Codium fragile</i>	NA	NA	0	NA	NA	0	NA	NA	0	-0.05	0.25	4	NA	NA	0
Bulleri et al. 2006	<i>Codium fragile</i>	0.17	0.25	4	NA	NA	0									
Levin et al. 2002	<i>Codium fragile</i>	NA	NA	0	NA	NA	0	-0.32	0.17	3	-0.47	0.37	4	NA	NA	0
Scheibling and Gagnon 2006	<i>Codium fragile</i>	-1.17	0.44	14	NA	NA	0									
Schmidt and Scheibling 2007	<i>Codium fragile</i>	-0.02	0.25	4	NA	NA	0	NA	NA	0	0.00	0.25	11	1.58	0.33	1
Sánchez and Fernández 2005	<i>Sargassum muticum</i>	-0.06	0.35	8	0.40	0.34	5	NA	NA	0	NA	NA	0	NA	NA	0
Viejo 1997	<i>Sargassum muticum</i>	-0.19	0.51	15	-0.73	0.58	3	NA	NA	0	NA	NA	0	NA	NA	NA
Britton-Simmons 2004	<i>Sargassum muticum</i>	-0.82	0.49	10	-1.01	0.48	2	-2.55	0.73	2	-0.26	0.45	5	-0.28	0.41	2
Ambrose and Nelson 1982	<i>Sargassum muticum</i>	-0.69	0.88	1	NA	NA	0									
Casas et al. 2004	<i>Undaria pinnatifida</i>	-0.56	0.21	28	-1.07	0.23	3	NA	NA	0	NA	NA	0	NA	NA	0
Valentine and Johnson 2005	<i>Undaria pinnatifida</i>	0.20	0.25	14	0.44	0.27	4	NA	NA	0	NA	NA	0	NA	NA	NA
Airoldi 2000	<i>Womersleyella setacea</i>	-0.56	0.12	6	NA	NA	0	-0.11	0.11	6	NA	NA	0	NA	NA	0

ES, Hedges effect size d for individual response variables within a study; ES_{average} , average d per study.

for all individual response variables (Rosenberg et al. 2000). This effect size was preferred over the log response ratio because of many “zero” values, which resulted in undefined log response ratios. Each study contributed a single average ES (hereafter ES_{average}) for each measured independent test and therefore a single degree of freedom. Thus, ES from non-independent response variables were averaged into a single ES per species (e.g., if both cover and biomass were reported for same species), per test group (e.g., if both richness and diversity were calculated), and per experiment (e.g., if the experiment was repeated at different locations or seasons or with orthogonal multifactorial manipulations). Averaging within-study ES is a common approach, but strong nonindependence within a study may still bias P -values (Marin-Martinez and Sanchez-Meca 1999). However, data were inadequate for autocorrelation weighing procedures, and we argue that other types of nonindependence probably provide more pressing problems to meta-analysis in general (e.g., between researchers, choice of NIMS and response variables, various types of spatial, temporal, and taxonomic autocorrelations). A total of 200 ES were extracted from the 18 studies and converted, as described above, into 15 ES_{average} for “macrophyte abundance,” seven for “macrophyte assemblages,” three for “macrophyte processes,” four for “animal abundance,” and two for “animal assemblages” (Table 1, the sum of all $n = 200$). Finally, cumulative ES ($ES_{\text{cumulative}}$), total sample heterogeneity (Q_T), and 95% confidence levels were calculated for each group of responses in MetaWin 2.0 (Rosenberg et al. 2000). We use Cohen’s conventional interpretation of the magnitude of effect sizes; that is, 0.2, 0.5, 0.8, and 1 represent “small,” “medium,” “large,” and “very large” effects, respectively (equivalent to Pearson’s product-moment correlation coefficient r of 0.10, 0.24, 0.37, and 0.45, Rosenberg et al. 2000, Gurevitch and Hedges 2001).

RESULTS AND DISCUSSION

Effect sizes and test results. We found experimental field data for six species of NIMS: *Codium fragile* ssp. *tomentosoides* (Goor) P. C. Silva (five studies), *Sargassum muticum* (Yendo) Fensholt (four studies), *C. taxifolia* and *C. racemosa* (Forssk.) J. Agardh (three studies each), *U. pinnatifida* (two studies), and *Womersleyella setacea* (Hollenb.) R. E. Norris (one study; assuming that all turf-algae are NIMS, as in Williams and Smith 2007) (Table 1). Given that 277 NIMS have been recorded worldwide (Williams and Smith 2007), impacts have only been tested experimentally for 2.1% of all possible species. With the exception of *W. setacea*, these species represent the most well-known and conspicuous NIMS, which have established large populations at numerous localities around the world (Schaffelke and Hewitt 2007, Williams and Smith 2007). All studies but one (Sánchez and Fernández 2005) reported at least one significant effect (Table S1), supporting the general notion that NIMS do affect native species and assemblages at some level. Still, it is equally important to note that almost all studies also reported nonsignificant results, suggesting that impacts may not be detected at all levels of organization. $ES_{\text{cumulative}}$ values were -0.30 , -0.70 , -0.39 , -0.13 , and 0.75 for macrophyte abundance, macrophyte assemblages, macrophyte processes, animal

abundance, and animal assemblages, respectively (Fig. 1). However, only the two first groups of response variables, characterized by the highest number of samples, were significant (95% CL that do not bracket zero). Thus, competitors of NIMS (i.e., the macrophytes) were clearly more negatively affected than users (i.e., the mobile animals), likely because many algal-associated animals are generalists with little or no habitat specificity (Bell 1991, Wernberg et al. 2004). In addition, macrophyte assemblages, macrophyte processes, and animal assemblages showed significant sample heterogeneity (Table 2), suggesting that other explanatory variables should be investigated. However, the low sample sizes for these variables exclude a “structured” meta-analysis (Rosenberg et al. 2000), which will have to await the publication of many more field-based ES. Note that none of the $ES_{\text{cumulative}}$ values was > -0.8 (i.e., large effect), although 29% of the ES_{average} values were indeed large and negative (9 out of 31, cf. Table 1). The three most negative ES_{average} values reported were < -2.0 (Table 1, corresponding to correlation coefficients $r > 0.7$), detected on macrophyte assemblages (two studies on *C. racemosa*) and macrophyte processes (one study on *S. muticum*). Such “extreme” ES_{average} values provide a warning against only focusing on $ES_{\text{cumulative}}$; from a conservation perspective, it could be argued that management should focus on these

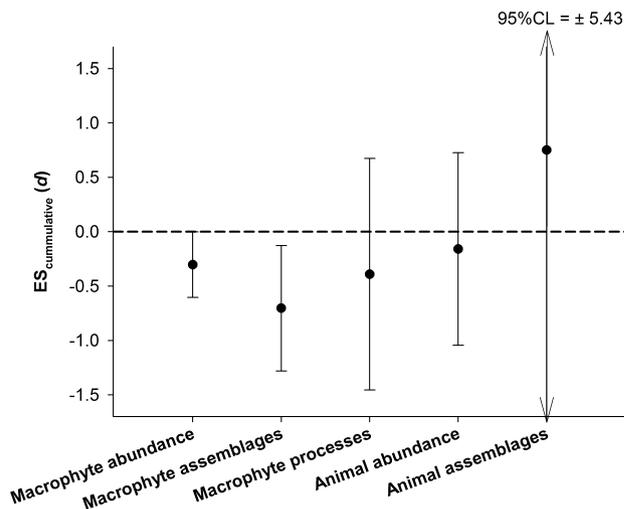


FIG. 1. Cumulative effect sizes ($ES_{\text{cumulative}}$) of nonindigenous macroalgal species impacts on five groups of responses ($\pm 95\%$ CL): “macrophyte abundance” (cover or biomass of native macroalgae and seagrass, $n = 15$), “macrophyte assemblages” (total abundance, richness, diversity, $n = 7$), “macrophyte processes” (percent mortality, survival, or growth, $n = 3$), “animal abundance” (densities of associated fauna, $n = 4$), and “animal assemblages” (total abundance, richness, diversity, $n = 2$). Variables where CL do not bracket zero are significant. Data are based on 200 individual ES extracted from 18 manipulative field studies (Table 1 and Table S1 in the supplementary material). Note that CL extends beyond the figure for “animal assemblages.” ES, Hedges effect size d for individual response variables within a study; $ES_{\text{cumulative}}$, cumulative d for all studies.

TABLE 2. Meta-analysis of impact of nonindigenous macroalgal species (NIMS) on five groups of response variables. Abundance = cover or biomass for plants and density for animals. Assemblages = richness, diversity, or total abundances. Processes = growth or mortality. $ES_{\text{cumulative}}$ = Hedges d cumulative effect size, corrected for small sample sizes. Q_T = total heterogeneity. Tests were performed in MetaWin 2.0 (Rosenberg et al. 2000).

Variable	Macrophyte		Processes	Animal	
	Abundance	Assemblages		Abundance	Assemblages
$ES_{\text{cumulative}}$	-0.30	-0.70	-0.39	-0.16	0.75
95% CL	-0.60 to -0.01	-1.28 to -0.12	-1.45 to 0.67	-1.04 to 0.73	-4.68 to 6.18
Q_T	13.941	18.051	7.133	0.433	4.683
df	14	6	2	3	1
$P(\chi^2)$	0.454	0.006	0.028	0.933	0.031
Sqrt. pooled variance	<0.001	0.896	0.753	<0.001	1.166
Mean study variance	0.377	0.457	0.337	0.330	0.370

worst-case scenarios, and implementation of extreme statistics (Gaines and Denny 1993) could be a future statistical approach to detect and focus on the most negative values.

On the basis of ratings of Williams and Smith (2007), we calculated the frequency of occurrence of different effects and tested if they were significantly different from each other (Table 3). These calculations and χ^2 -tests demonstrated that negative effects (“-”) were reported significantly more often than positive effects (“+”), no effects (“0”), or non-directional effects (“ Δ ”), for all studies pooled, and for correlative and experimental studies separately ($P < 0.05$, Table 3). Interestingly, experimental studies showed the greatest proportion of negative effects (59%). We also applied our stricter data selection criteria (excluding laboratory experiments and general clearance experiments) to the experimental studies tabulated by Williams and

Smith 2007 and repeated the calculations. Again, there was a large proportion of negative effects (58%), but the results were only near significant ($P = 0.065$), probably because of low power due to the fewer included studies. Although the vote-counting data were in agreement with our calculated $ES_{\text{cumulative}}$, with more negative than positive effects, the latter near-significant result demonstrates a typical problem associated with vote counting: all near-significant results are classified as “no effects.” This is problematic because manipulative field studies generally are characterized by few replicates and high variability and therefore may not have the power to detect weak effects. For example, Levin et al. (2002) and Ceccherelli and Campo (2002) both reported $P = 0.06$ for effects of NIMS on kelp recruitment and seagrass female flower density, respectively (but note that researchers may choose to increase α ; e.g., Levin et al. interpreted kelp recruitment as being negatively affected by NIMS). In contrast, the meta-analytical approach incorporates the ES in a quantitative manner, and repeated near-significant results will, therefore, be detected as weak but significant impacts as power increases with the inclusions of more studies.

Specific NIMS impacts. *S. muticum* was shown to decrease kelp recruitment (Ambrose and Nelson 1982), abundance of canopy-forming species (Britton-Simmons 2004), and the native fucoid *Bifurcaria bifurcata* (Viejo 1997). In contrast, Sánchez and Fernández (2005) found no impacts on *B. bifurcata*. In the study by Britton-Simmons (2004), kelp growth and species richness were also reduced by the invader. However, all of these studies also showed that many species and assemblage variables were unaffected by the NIMS. Impacts of *C. fragile* have been experimentally tested in kelp beds and on artificial structures. However, *C. fragile* probably more often invades shallow estuaries (Trowbridge 1998), where it may compete for space with economically important shellfish; Neill et al. (2006) estimate a loss of >US\$1.2 million \cdot year⁻¹ for the aquaculture industry in Canada. Surprisingly, we found no manipulative experiments documenting an impact on shellfish. *C. fragile* has been shown to

TABLE 3. Tests on vote counts of impacts of nonindigenous macroalgal species (NIMS). Counts of negative, positive, multidirectional or no effects were extracted from table 1 in Williams and Smith (2007). Counts were tested with χ^2 to examine if negative results were reported more often than expected by chance, based on, respectively, (a) all studies: χ^2 (df = 3) = 4.44, $P < 0.001$; (b) correlative studies: χ^2 (df = 3) = 11.87, $P = 0.008$; (c) experimental studies; χ^2 (df = 3) = 27.36, $P < 0.001$; and (d) experimental field studies: χ^2 (df = 2) = 5.47, $P = 0.065$.

Type	Effects	Observed, N	Observed, %
All studies	Negative	51	46
	None	28	26
	Positive	19	19
	Multidirectional	10	9
Correlative studies	Negative	28	41
	None	19	28
	Positive	13	19
	Multidirectional	9	13
Experimental studies (all)	Negative	23	59
	None	9	23
	Positive	6	15
	Multidirectional	1	3
Experimental studies (field based)	Negative	11	58
	None	5	26
	Positive	3	16

reduce the abundance of fish recruits and the survival of small transplanted kelps, but only when these were already stressed by epiphytic cover, and no effects were observed for growth of transplanted kelp or invertebrate abundance (Levin et al. 2002). Similarly, the studies by Scheibling and Gagnon (2006) and Schmidt and Scheibling (2007) also documented that *C. fragile* reduces kelp abundance, but in the latter study, only after a reanalysis that focused on sampling times of highest NIMS abundance (Table S1). Again, these studies also had many nonsignificant effects. *U. pinnatifida* is considered one of the world's most invasive species (Lowe et al. 2000), and various eradication efforts have been undertaken (reviewed in Schaffelke and Hewitt 2007). Still, only two experimental field-based impact studies exist; one did not detect any impacts (Valentine and Johnson 2005), whereas the other documented relatively strong reductions in species richness and diversity of the native assemblages (Casas et al. 2004). Impacts of two *Caulerpa* species have been measured in field experiments, with three studies each. *C. racemosa* has been shown to have a positive effect on *Zostera noltii* shoot density and *Cymodocea nodosa* flower density (Ceccherelli and Campo 2002), although the latter result may reflect increased seagrass stress. *C. racemosa* can also reduce algal richness and cover of various algal form groups (NIMS additions, Piazzini et al. 2005), although these effects were less clear in a follow-up study (NIMS removals, Piazzini and Ceccherelli 2006). Finally, the invasion by *C. taxifolia* is probably the best-known NIMS introduction anywhere. Of the three manipulative impact studies, only one documented negative effects (on seagrass shoot density, Ceccherelli and Cinelli 1997). This short-term study was continued for another year, and the follow-up publication reported a single significant, but positive, effect on seagrass leaf length (Ceccherelli and Sechi 2002).

Weak-to-large effect sizes of NIMS. It is possible that the relatively small $ES_{\text{cumulative}}$ are methodological artifacts due to the limited set of existing experiments, low levels of replication, choice of response variables, methods of manipulations, and so forth. If so, more intensive and diverse field studies are called for. However, if the studies truly reflect that NIMS typically have weak to moderate effects on native species, the reasons need to be discussed. First, it could simply be that invasions are more often a consequence than a cause of stress and disturbance (i.e., that NIMS are generally passengers, not drivers, of change; Didham et al. 2005). This model has been suggested to explain the apparent lack of documented negative impacts of *C. taxifolia* (Jaubert et al. 1999, 2003). Second, small effect sizes may be related to the life-history of many NIMS. The tested NIMS are pseudoperennials (although *U. pinnatifida* may occasionally have a biannual thallus) with a large conspicuous

thallus in summer, but a significantly reduced thallus in winter (Wernberg et al. 2001). Strong interference effects based on competition or facilitation can therefore be limited in time, so experiments that include a full annual cycle may demonstrate smaller effects compared to studies that focus on the "blooming period" (see Ceccherelli and Cinelli 1997 vs. Ceccherelli and Sechi 2002, and analysis by Schmidt and Scheibling 2007 on entire vs. selected data for tests that focus on the blooming vs. average conditions, respectively). Third, NIMS often substitute biomass in systems already dominated by macrophytes. For example, *C. fragile* may partially replace native kelps: *C. taxifolia*, native seagrasses; *S. muticum*, various large native brown algae; and *U. pinnatifida*, other native algae. In these cases, some system-level ecological functions, such as provision of food and habitat and amelioration of environmental conditions, may remain relatively intact. In contrast, stronger effects will be expected when invaders add or remove, rather than substitute, ecosystem function or structure, similar to when nonnative angiosperms convert homogenous soft-bottom systems to seagrass beds, mangrove forests, and salt marshes (e.g., *Zostera japonica*, *Avicennia marina*, or *Spartina alterniflora*, Wallentinus and Nyberg 2007). Two of the NIMS studies included tests of "barren-to-green" habitat conversions (Bulleri et al. 2006, Gribben and Wright 2006), and both documented, as expected, positive effects on the native species abundance (see Bulleri et al. 2008 for in-depth discussion). Other possible, but not yet tested, NIMS examples are where *S. muticum* or *Gracilaria vermiculophylla* invade unvegetated sand and mudflats (Buschmann et al. 2005, Thomsen et al. 2006, 2007). Here we expect strong, but positive, effects on epiphytes, sessile animals, and algal-associated invertebrates, but negative effects on sediment fauna. Fourth, several studies did not report the actual abundance of the NIMS. Thus, standardized $ES_{\text{cumulative}}$ (per biomass, percent cover, or density of NIMS) could not be calculated, making it more difficult to compare values among studies, NIMS, habitats, or with regard to other marine competitors. It also leaves open the possibility that several of the smaller ES_{average} may have been caused by low NIMS abundance. Clearly, quantifying NIMS abundance is vital to enable researchers to compare effect sizes and calculate common "invader-stress metrics." Presenting NIMS abundance will also make it possible to conduct impact analysis as a two-staged test, first on the native component (without the abundance of the NIMS) and, secondly, on the entire community (including the abundance of the NIMS). So far, only the first approach has been applied, but the latter may reveal if the invaded system has changed its total structural complexity, amount of habitat for associated flora

and fauna, or ability to transfer energy and matter or ameliorate abiotic conditions. Such two-part impact analysis may also add insight into the debate on whether assemblages are saturated or open, but from a different perspective than the typical richness-invasibility paradox (Fridley et al. 2007). Finally, it is possible that field experiments are simply not adequate for detecting strong impacts, because they are time consuming to conduct and therefore generally characterized by few replicates measured over small spatial and short timescales, or because they generally measure impacts in areas that may be irreversibly altered by the NIMS prior to experimental manipulations (Eastwood et al. 2007). Larger-scale correlative studies that include preinvasion data, therefore, provide important complimentary information on impacts. Extracting and summarizing this impact information through formal meta-analyses (work in progress) is, however, much more complicated and associated with its own biases and limitations.

Regardless of the causes associated with the relatively low $ES_{\text{cumulative}}$, it is important to reemphasize that only the most conspicuous and widely distributed and abundant NIMS (Nyberg and Wallentinus 2005, Schaffelke and Hewitt 2007, Williams and Smith 2007) have been tested experimentally. It therefore seems unlikely that future experiments on the hundreds of more inconspicuous NIMS will show strong negative effects on existing macroalgal communities or seagrass beds. Consequently, future experiments will most likely support the paradigm that only a fraction of NIS cause large effects (Williamson 1996). Clearly, the experiments represent a very limited subset of taxa, and our analysis, therefore, has low extrapolation power. Including a more random sample of NIMS would, as discussed, likely decrease effect sizes. Publication bias may further reduce generality if studies that find nonsignificant effects are either not submitted or rejected by reviewers and editors as uninteresting, or if nonsignificant response variables are excluded from the publication. If these zero/near-zero effect sizes were going to be quantified, and included, in future meta-analyses, the numerical value of the “true” $ES_{\text{cumulative}}$ for all NIMS would likely decrease. It also emphasizes that it is important that researchers aim to, and are allowed to, publish nonsignificant results (Browman 1999).

Finally, it is important to note that most studies did not include experimental procedural treatments (Table S1); that is, most studies did not provide experimental tests to document if the physical disturbances associated with removing or adding NIMS alone affected the native species assemblages. To provide unambiguous experimental data on NIMS impacts, both NIMS abundance and effects associated with experimental manipulations need to be quantified and clearly presented.

Conclusions and recommendations. We found NIMS to have significant small-to-medium negative effects on “macrophyte abundance” and medium-to-large negative effects on “macrophyte assemblages.” In contrast, $ES_{\text{cumulative}}$ values were not significantly different from zero for “macrophyte processes,” “animal abundance,” or “animal assemblages,” but these response variables were characterized by few studies and should therefore be reevaluated when more field experiments accumulate. The results are likely biased toward larger effect sizes because only the most conspicuous NIMS have been tested and because nonsignificant effects are less likely to be published.

Despite relatively low $ES_{\text{cumulative}}$, we argue that NIMS affect the ecology of native assemblages, are important to study, and should be managed and potentially controlled. First, it is possible that effects may increase in the future, for example, in combination with other human stressors, such as global warming or eutrophication. Second, some ES_{average} were indeed < -0.8 suggesting that, in some cases, NIMS can have large negative effects in marine communities. From a conservation perspective, a precautionary principle could be adopted, focusing on these worst-case scenarios, rather than cumulative effect sizes. Third, also from a conservation perspective, any significant NIMS-induced change may be considered unwanted, regardless of the magnitude or direction of the effect. Fourth, in contrast to several other types of anthropogenic activities that can be directly managed, the establishment, spread, and impacts of many NIMS are potentially irreversible. Fifth, NIMS are likely to cause biotic homogenization (i.e., loss of biodiversity in the broadest sense) at large spatiotemporal scales (Olden and Rooney 2006), a topic generally not addressed in site-specific manipulative experiments. Sixth, even weak effects may potentially have large implications when accumulating over evolutionary timescales. Hence, our key finding, that macrophyte competitors are negatively affected by NIMS, is of concern. We reiterate that to better understand and rank NIMS impacts, more manipulative experiments are needed, testing more species, under contrasting environmental conditions, in combination with other manipulated stressors, and including procedural control treatments as well as reporting the abundance of the NIMS. We conclude that the NIMS that have been tested in manipulative impact studies represent a few well-known conspicuous invaders, and these NIMS have an overall negative effect on their native macrophyte competitors.

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Supplementary Material

The following supplementary material is available for this article:

Table S1. Manipulative field experiments testing for impacts of nonindigenous macroalgal species on native species and assemblage structures. NIS, nonindigenous species; NIS–, absence of NIS; NIS+, presence of NIS.

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