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Global ecological impacts of marine exotic species

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Exotic species are a growing global ecological threat; however, their overall effects are insufficiently understood. While some exotic species are implicated in many species extinctions, others can provide benefits to the recipient communities. Here, we performed a meta-analysis to quantify and synthesize the ecological effects of 76 exotic marine species (about 6% of the listed exotics) on ten variables in marine communities. These species caused an overall significant, but modest in magnitude (as indicated by a mean effect size of $g < 0.2$), decrease in ecological variables. Marine primary producers and predators were the most disruptive trophic groups of the exotic species. Approximately 10% (that is, 2 out of 19) of the exotic species assessed in at least three independent studies had significant impacts on native species. Separating the innocuous from the disruptive exotic species provides a basis for triage efforts to control the marine exotic species that have the most impact, thereby helping to meet Aichi Biodiversity Target 9 of the Convention on Biological Diversity.

Exotic species rank among the most serious environmental threats of the new millennium[1–3], as the relocation of species beyond their native range has intensified over the last five decades[4]. The impacts of some of the worst exotic species on biodiversity are well documented, as they are implicated in the local extinction of hundreds of native species[5–7]. While the ecological outcomes of the most damaging exotic species are clearly dramatic, the impact of many appears to be modest, with some even providing ecological benefits[8,9]. These contrasting effects have ignited a contemporary debate about the overall impacts and perceptions of exotic species[10–14], and this debate can only be resolved by distinguishing innocuous from disruptive exotic species[15]. In the case of marine exotic species, there are no documented global extinctions attributed to them[16] (but see also refs. [17–19]), although some can substantially reduce native fauna[20].

Based on previous syntheses and meta-analyses, we made predictions about the expected ecological effects of marine exotic species[21–27] (Supplementary Table 1). Marine ecosystems differ from other environments in a number of characteristics that may mitigate the effects of exotic species on the abundance of native species. The open nature of oceans, with large and continuous marine habitats, and the extensive dispersal potential of many marine species are likely to buffer the effects of exotics through a high capacity to repopulate affected areas. We predict that marine exotic primary producers and predators will exert strong effects on native communities, as reported previously for aquatic and terrestrial systems[21–23,25]. However, marine communities harbour a high proportion of generalist consumers (herbivores and omnivores[28]) that could limit the effects of exotic primary producers. In terrestrial communities[25], exotic herbivores have nonsignificant effects on the richness of native species, but marine exotic herbivores can cause reductions in the abundance and richness of native species[29,30]. We expect, as has been reported for other systems, contrasting effects of marine exotic detritivores and overall innocuous effects of exotic omnivores[25,27]. Exotic seaweeds exert persistent negative effects on native primary producers, but no effects on herbivores and predators[22]. Finally, a previous meta-analysis[24] of marine exotic ecosystem engineers indicated overall nonsignificant effects at the species and community levels and contrasting effects at the ecosystem level.

However, to date, the global effect of exotic species, including higher-order trophic groups, has not been systematically examined in marine ecosystems. Despite this, exotic marine species directly affect 12% of the marine species registered on the Red List of the International Union for Conservation of Nature (IUCN). This value is substantially higher than the percentage of vulnerable species affected by terrestrial and freshwater exotic species (6% and 2%, respectively)[16]. In fact, the signatories of the Convention on Biological Diversity of the United Nations agreed to achieve Aichi Biodiversity Target 9 by 2020, which aims, among other things, to identify and then control or eradicate the worst invasive species[31]. However, this target is not on track, as a systematic assessment of the quantitative ecological effects of exotic species has not yet been produced for the marine environment[15].

Here, we quantified the ecological effects of exotic species on marine communities through an exhaustive meta-analysis of published studies (Supplementary Table 2). We used the effect size Hedges' g as a common metric to determine the change in ecological variables resulting from exotic species. Hedges' g was calculated for 1,111 observations from 159 studies at 151 different sites

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Table 1 | List of the 76 exotic species included in our database by alphabetical order

Exotic species	Taxonomic group	Trophic level	IUCN	Observations	Hedges' *g*	*P* value
Ammophila arenaria (56)[73]	Plant	P. producer	No	1, 4	0.15 ± 0.83	0.714
Arcuatula senhousia[a] (62)[74–77]	Mollusc	Herbivore	No	4, 27	0.21 ± 0.45	0.347
Avicennia marina (38)[74]	Plant	P. producer	No	1, 3	−0.06 ± 0.98	0.893
Avrainvillea amadelpha (68)[78]	Algae	P. producer	No	1, 1	0.32 ± 1.24	0.606
Baccharis halimifolia (42)[79]	Plant	P. producer	No	1, 6	−0.03 ± 0.74	0.926
Balanus glandula (40)[80]	Crustacean	Omnivore	No	1, 4	−0.05 ± 0.84	0.904
Batillaria attramentaria (50)[81]	Mollusc	Detritivore	No	1, 2	0.06 ± 0.96	0.893
Boccardia proboscidea (1)[82]	Annelid	Omnivore	No	1, 12	−1.67 ± 0.91	<0.001
Botrylloides violaceus (51)[83]	Tunicate	Herbivore	No	1, 9	0.08 ± 0.82	0.848
Brachidontes pharaonis (9)[84]	Mollusc	Herbivore	No	1, 6	−0.72 ± 0.73	0.053
Carcinus maenas[a] (10)[85–91]	Crustacean	Predator	Yes	7, 32	−0.71 ± 0.38	<0.001
Carex macrocephala (42)[92,93]	Plant	P. producer	No	2, 11	−0.04 ± 0.5	0.867
Carpobrotus edulis[a] (31)[94–96]	Plant	P. producer	No	3, 12	−0.14 ± 0.49	0.555
Casuarina equisetifolia (45)[97]	Plant	P. producer	No	1, 1	−0.01 ± 0.87	0.981
Caulacanthus ustulatus (63)[98]	Algae	P. producer	No	1, 18	0.23 ± 0.74	0.531
Caulerpa cylindracea[a] (12)[99–108]	Algae	P. producer	No	10, 38	−0.63 ± 0.31	<0.001
Caulerpa taxifolia[a] (23)[109–115]	Algae	P. producer	Yes	7, 40	−0.3 ± 0.34	0.081
Centrostephanus rodgersii (13)[116,117]	Echinoderm	Herbivore	No	2, 23	−0.62 ± 0.63	0.051
Chrysanthemoides monilifera (2)[118]	Plant	P. producer	No	1, 1	−1.3 ± 1.16	0.028
Ciona savignyi (22)[83]	Tunicate	Herbivore	No	1, 8	−0.33 ± 0.84	0.439
Cirolana harfordi (52)[119]	Crustacean	Predator	No	1, 8	0.08 ± 0.81	0.846
Codium fragile[a] (37)[9,120–123]	Algae	P. producer	No	5, 21	−0.07 ± 0.41	0.716
Corbicula fluminea (65)[124,125]	Mollusc	Herbivore	No	2, 17	0.28 ± 0.59	0.347
Corbula gibba (36)[126]	Mollusc	Herbivore	No	1, 4	−0.08 ± 1.07	0.878
Crepidula fornicata (19)[127–129]	Mollusc	Herbivore	No	3, 9	−0.46 ± 0.52	0.082
Didemnum vexillum[a] (57)[83,130,131]	Tunicate	Herbivore	No	3, 16	0.17 ± 0.53	0.52
Diplosoma listerianum (72)[132]	Tunicate	Herbivore	No	1, 4	0.53 ± 0.85	0.221
Elymus athericus (74)[133]	Plant	P. producer	No	1, 4	0.58 ± 0.93	0.216
Ficopomatus enigmaticus[a] (30)[134–140]	Annelid	Omnivore	No	7, 54	−0.15 ± 0.32	0.345
Gracilaria salicornia (53)[141]	Algae	P. producer	No	1, 2	0.1 ± 0.93	0.825
Gracilaria vermiculophylla[a] (60)[142–145]	Algae	P. producer	No	4, 41	0.18 ± 0.41	0.368
Grateloupia turuturu (8)[146]	Algae	P. producer	No	1, 8	−0.75 ± 0.84	0.083
Hemigrapsus sanguineus[a] (4)[90,147,148]	Crustacean	Omnivore	No	3, 9	−0.81 ± 0.65	0.015
Holcus lanatus (39)[149]	Plant	P. producer	No	1, 13	−0.05 ± 0.76	0.887
Juncus acutus (18)[150]	Plant	P. producer	No	1, 8	−0.47 ± 0.82	0.263
Kappaphycus alvarezii (7)[151]	Algae	P. producer	No	1, 4	−0.76 ± 0.78	0.057
Laguncula pulchella (25)[152]	Mollusc	Predator	No	1, 9	−0.22 ± 0.74	0.556
Linepithema humile (27)[153]	Insect	Omnivore	No	1, 3	−0.18 ± 1.01	0.726
Lophocladia lallemandii[a] (54)[103,104,154]	Algae	P. producer	No	3, 16	0.12 ± 0.47	0.591
Loxothylacus panopaei (16)[155,156]	Crustacean	Predator	No	2, 3	−0.48 ± 0.92	0.304
Magallana gigas[a] (59)[59,157–164]	Mollusc	Herbivore	No	9, 143	0.18 ± 0.26	0.175
Maoricolpus roseus (69)[165]	Mollusc	Herbivore	No	1, 4	0.33 ± 0.91	0.467
Marenzelleria arctia (75)[166]	Annelid	Detritivore	No	1, 2	0.77 ± 0.98	0.126
Marenzelleria spp.[a] (70)[167–169]	Annelid	Detritivore	No	3, 10	0.51 ± 0.67	0.136
Megabalanus coccopoma (20)[170]	Crustacean	Omnivore	No	1, 2	−0.36 ± 1.35	0.599
Membranipora membranacea (15)[171]	Bryozoan	Omnivore	No	1, 1	−0.51 ± 1.44	0.482
Mnemiopsis leidyi (33)[172]	Ctenophora	Predator	Yes	1, 3	−0.14 ± 0.75	0.713
Mytella charruana (14)[170]	Mollusc	Herbivore	No	1, 2	−0.55 ± 1.36	0.429
Mytilopsis trautwineana (29)[173]	Mollusc	Herbivore	No	1, 3	−0.16 ± 0.93	0.73
Mytilus galloprovincialis[a] (17)[174–177]	Mollusc	Herbivore	Yes	4, 45	−0.48 ± 0.4	0.02

Continued

Exotic species	Taxonomic group	Trophic level	IUCN	Observations	Hedges' *g*	*P* value
Perna viridis (11)[170]	Mollusc	Herbivore	No	1, 2	−0.69 ± 1.37	0.322
Petrolisthes armatus (73)[178]	Crustacean	Omnivore	No	1, 4	0.53 ± 0.86	0.223
Phragmites australis (26)[179]	Plant	P. producer	No	1, 3	−0.19 ± 0.75	0.602
Poecilia latipinna (48)[180]	Fish	Omnivore	No	1, 1	0.01 ± 1.45	0.981
Potamocorbula amurensis (55)[181]	Mollusc	Herbivore	Yes	1, 2	0.14 ± 1.21	0.815
Potamopyrgus antipodarum (43)[182]	Mollusc	Herbivore	No	1, 8	−0.02 ± 0.83	0.951
Pterois volitans[a] (35)[183–188]	Fish	Predator	No	6, 49	−0.12 ± 0.34	0.488
Rattus norvegicus (66)[43]	Mammal	Omnivore	No	1, 11	0.28 ± 0.75	0.46
Rhizophora mangle (76)[189]	Plant	P. producer	No	1, 12	1.15 ± 0.88	0.01
Ruditapes philippinarum (47)[190]	Mollusc	Herbivore	No	1, 3	0 ± 1.16	0.998
Sabella spallanzanii (64)[191,192]	Annelid	Omnivore	No	2, 8	0.28 ± 0.65	0.395
Sagartia ornata (67)[193]	Cnidarian	Predator	No	1, 2	0.3 ± 0.94	0.532
Sargassum muticum[a] (46)[194–204]	Algae	P. producer	No	11, 108	0 ± 0.25	0.966
Sonneratia apetala (58)[205]	Plant	P. producer	No	1, 2	0.18 ± 1.22	0.773
Spartina alterniflora[a] (34)[206–216]	Plant	P. producer	No	11, 75	−0.13 ± 0.27	0.352
Spartina townsendii var. anglica (6)[217,218]	Plant	P. producer	Yes	2, 11	−0.77 ± 0.59	0.01
Stenotaphrum secundatum (5)[219,220]	Plant	P. producer	No	2, 7	−0.78 ± 0.56	0.006
Styela clava (61)[83]	Tunicate	Herbivore	No	1, 1	0.19 ± 1.43	0.792
Symbiodinium trenchii (28)[221]	Algae	P. producer	No	1, 6	−0.16 ± 0.9	0.713
Tubastraea coccinea (32)[222]	Cnidarian	Predator	No	1, 12	−0.14 ± 0.72	0.69
Undaria pinnatifida[a] (49)[223–225]	Algae	P. producer	Yes	3, 34	0.05 ± 0.46	0.813
Watersipora subtorquata (71)[175]	Bryozoan	Omnivore	No	1, 4	0.51 ± 0.84	0.231
Womersleyella setacea (24)[108,154]	Algae	P. producer	No	2, 5	−0.26 ± 0.78	0.508
Xenostrobus securis (44)[226]	Mollusc	Herbivore	No	1, 7	−0.01 ± 0.79	0.966
Zeacumantus subcarinatus (21)[227]	Mollusc	Herbivore	No	1, 6	−0.33 ± 0.91	0.467
Zostera japonica (3)[68]	Plant	P. producer	No	1, 2	−0.85 ± 1.16	0.149

[a]The 19 sufficiently assessed marine exotic species (with 3 or more studies represented in Fig. 5). The studies used in this meta-analysis for each exotic species are indicated in the first column, and the rank of the exotic species based on their mean Hedges' *g* value is in parentheses. The 'Observations' column includes the number of studies and the number of observations, separated by a comma. Values in the 'Hedges' *g*' column indicate the mean $g \pm$ CI. *P* values were obtained from mixed-effects models that included the study ID number as a random factor and using the rma.mv function from the metafor package for R. P., primary.

(Table 1; Supplementary Figs. 1 and 2; Supplementary Table 2; and https://doi.pangaea.de/10.1594/PANGAEA.895681). This meta-analysis allowed us to achieve the following: (1) determine the ecological effects of marine exotic species across trophic levels, taxonomic groups and ecological complexity; (2) elucidate the role of ecological characteristics such as the environment of the exotic species (for example, freshwater versus marine versus terrestrial), their mobility (mobile versus sessile), the geographical attributes of the native habitat (for example, continent versus island) and latitude on the ecological effects of marine exotics; and (3) create a unique ranking of marine exotic species based on their overall mean quantitative ecological effects.

Invasion ecology is a discipline that has complex terminology[32–34]; therefore, to aid clarity, we provide an explicit definition of the terms used in this study. The term 'exotic' refers to species that have been moved outside their native geographical ranges via human actions. The definition of 'invasive species' varies between and among[33,35] ecologists, stakeholders and policymakers. For many ecologists[34,36], invasive species are established exotic species that are spreading in the new environment (see also ref. [36]), while for most environmental agencies, it refers to exotic species that have a demonstrable ecological or economic impact (for example, American Federal Law). We refer to invasive species or 'pests' as exotic species that exert an overall and statistically significant ecological impact[33,36]. Although this definition relies on human valuations of damage[34], we use it because of the following reasons: (1) we lack quantitative evidence to indicate that the populations of the exotic species in our study are spreading beyond its initial establishment location (or locations); (2) it is followed by many ecologists studying invasive species[33,35]; and (3) it tunes in with the language used by policymakers and environmental managers, providing effective guidance to meet Aichi Biodiversity Target 9. We use the term 'ecological effect' to refer to bidirectional ecological changes (for example, both increases and decreases) attributed to exotic species with regard to a control. The term 'ecological impact' is reserved only for statistically significant ecological changes (that is, mean changes significantly different from 0). Therefore, negative and positive effect size values are decreases and increases in ecological properties, respectively, without implying beneficial or deleterious effects.

Results

Our findings indicate that exotic species overall significantly reduce the ecological properties of native marine communities (mean estimated Hedges' $g = -0.14 \pm 0.1$ ($P = 0.006$); hereafter, mean effect sizes are reported as $g \pm 95\%$ confidence intervals (CI) and *P* values for significance). Ecological changes on marine ecosystems were quantified for 76 exotic species, which constitute 6% of the 1,260 marine and brackish exotic species listed in the Global Register of Introduced and Invasive Species (GRIIS; http://www.griis.org/). The ecological effect of 49 of these 76 exotic species was quantified in only one study each. However, we provide evidence to indicate that our global results are robust against both the number of

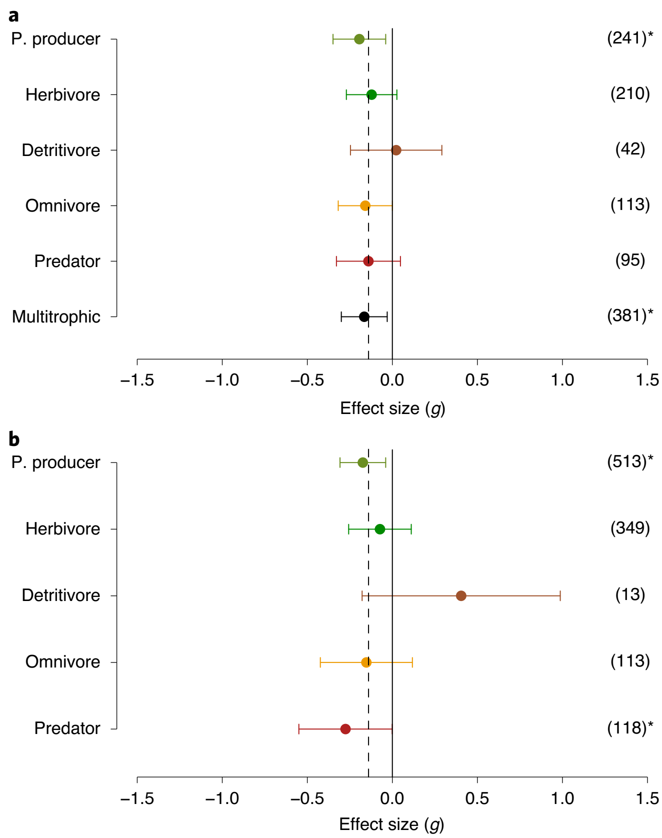

Fig. 1 | Effect of marine exotic species depends on the trophic levels of the native species or community and the exotic species. a,b, The mean effect size (Hedges' $g \pm 95\%$ CI) of the effects of marine exotic species depends on the trophic levels of the native species or community (**a**) and the exotic species (**b**). The unbroken line denotes zero and the broken line indicates the overall mean effect size. The number of observations is specified in parentheses, and $^*P \leq 0.05$. P values were obtained from mixed-effects models that included the study ID and the exotic species name as random factors, using the rma.mv function from the metafor package for R.

exotic species and the number of independent studies based on a comparison of the mean ± 95% CI Hedges' g value for species whose effects were assessed in one or more studies (which included the whole dataset) and for exotic species that included five or more independent studies (nine exotic species in total) (Supplementary Fig. 3). We show that while the effects of individual exotic species not included in this meta-analysis (that is, on our list of 76 species) may vary, the mean ± 95% CI Hedges' g value for marine exotics is robust for the number of species included. There were small differences in the mean $g \pm$ CI for the 19 sufficiently assessed exotic species (which uses a subset of the data) and Table 1 (which uses the full dataset) due to differences in the effects of the random factor. The results for the 19 sufficiently assessed exotic species were more robust and given preference when interpreting the results. We found that the research effort on exotic species in marine ecosystems is not balanced; the GRIIS list of marine exotic species includes <10% of primary producers, which were the subject of almost 50% of our observations (517 out of 1,111).

Effects of trophic level and taxonomic group. Overall, exotic species significantly decreased the ecological properties of native primary producers and multitrophic assemblages ($g = -0.19 \pm 0.15$ ($P = 0.014$) and $g = -0.17 \pm 0.13$ ($P = 0.016$), respectively) but not of native detritivores ($g = 0.02 \pm 0.27$ ($P = 0.870$)), herbivores ($g = -0.12 \pm 0.15$ ($P = 0.108$)), omnivores ($g = -0.15 \pm 0.16$ ($P = 0.051$)) or predators ($g = -0.14 \pm 0.19$ ($P = 0.143$)) (Fig. 1a). Among the exotic species, marine predators and primary producers were the only trophic groups that exerted significant decreases on marine ecological properties ($g = -0.28 \pm 0.27$ ($P = 0.049$) and -0.17 ± 0.13 ($P = 0.011$), respectively), but not herbivores, detritivores or omnivores ($g = -0.07 \pm 0.18$ ($P = 0.438$), $g = 0.40 \pm 0.58$ ($P = 0.173$) and $g = -0.15 \pm 0.27$ ($P = 0.269$), respectively) (Fig. 1b). Finally, the effect of marine exotic filter-feeder species on native communities was not significant ($g = -0.05 \pm 0.16$ ($P = 0.513$)) (Supplementary Fig. 4).

The network analysis of the ecological effects between exotic and native marine species among trophic and taxonomic groups was dominated by decreases in ecological properties (for example, almost 65% and 54% of the total effects, respectively) (Fig. 2). Exotic primary producers and predators caused ecological decreases in almost all trophic levels (Fig. 2). Exotic algae, crustaceans and molluscs were the taxonomic groups that caused overall decreases in the largest number of native taxa (seven, six and five, respectively). Meanwhile, exotic terrestrial mammals, annelids, molluscs and tunicates had the largest number of increasing effects (six, five, five and five, respectively) (Fig. 2).

Changes at species, community and ecosystem levels. Seven out of the ten ecological categories of response variables were not significantly affected by exotic species. Traits related to the behaviour and abundance of native species were significantly reduced by exotic species ($g = -0.53 \pm 0.28$ ($P < 0.001$) and $g = -0.26 \pm 0.10$ ($P < 0.001$), respectively) (Fig. 3). Conversely, ecological traits related to pollution significantly increased ($g = 0.44 \pm 0.41$ ($P = 0.033$)) (Fig. 3). There was no significant effect of exotic species on the following factors: fitness ($g = 0.25 \pm 0.39$ ($P = 0.203$)), growth ($g = -0.11 \pm 0.35$ ($P = 0.544$)), survival ($g = -0.06 \pm 0.23$ ($P = 0.601$)), richness ($g = -0.06 \pm 0.12$ ($P = 0.344$)), biogeochemical elements ($g = 0.20 \pm 0.24$ ($P = 0.108$)), rate processes ($g = 0.08 \pm 0.25$ ($P = 0.511$)) or sediment changes ($g = 0.26 \pm 0.43$ ($P = 0.231$)) (Fig. 3). In general, the ecological effects of exotics at the community level were significant ($g = -0.19 \pm 0.10$ ($P < 0.001$)), while changes at the species and ecological levels were not ($g = -0.15 \pm 0.16$ ($P = 0.084$) and $g = 0.14 \pm 0.19$ ($P = 0.138$), respectively) (Fig. 3).

Context-dependency of ecological effects. Exotics of marine origin caused significant decreases in the ecological variables of marine systems ($g = -0.14 \pm 0.11$ ($P = 0.010$)), while exotic species of freshwater and terrestrial origin did not ($g = -0.05 \pm 0.37$ ($P = 0.795$) and $g = -0.17 \pm 0.31$ ($P = 0.292$), respectively) (Fig. 4a). Sessile exotic species had significant ecological effects on native marine ecosystems ($g = -0.14 \pm 0.11$ ($P = 0.016$)) and mobile species did not ($g = -0.12 \pm 0.22$ ($P = 0.205$)) (Fig. 4b). We found that the ecological effects of exotic species in marine ecosystems were significant in continental margins ($g = -0.17 \pm 0.11$ ($P = 0.003$)) but not on islands ($g = -0.05 \pm 0.18$ ($P = 0.581$)) (Fig. 4c). There was no indication that the ecological effect of marine exotic species varied over latitude ($P = 0.849$ and $P = 0.536$, for the Northern and Southern hemispheres, respectively) (Fig. 4d).

Ranking and significance of exotic species based on their ecological effects. We identified eight exotic species (*B. proboscidea*, *C. maenas*, *C. cylindracea*, *C. monilifera*, *H. sanguineus*, *M. galloprovincialis*, *S. anglica* and *S. secundatum*) that caused overall significant decreases (mean $g < 0$ and 95% CI did not overlap 0; Table 1). Meanwhile, one species caused significant increases (*R. mangle*), and 67 species did not cause significant ecological changes (Table 1). A subset of 19 exotic species, whose effects were

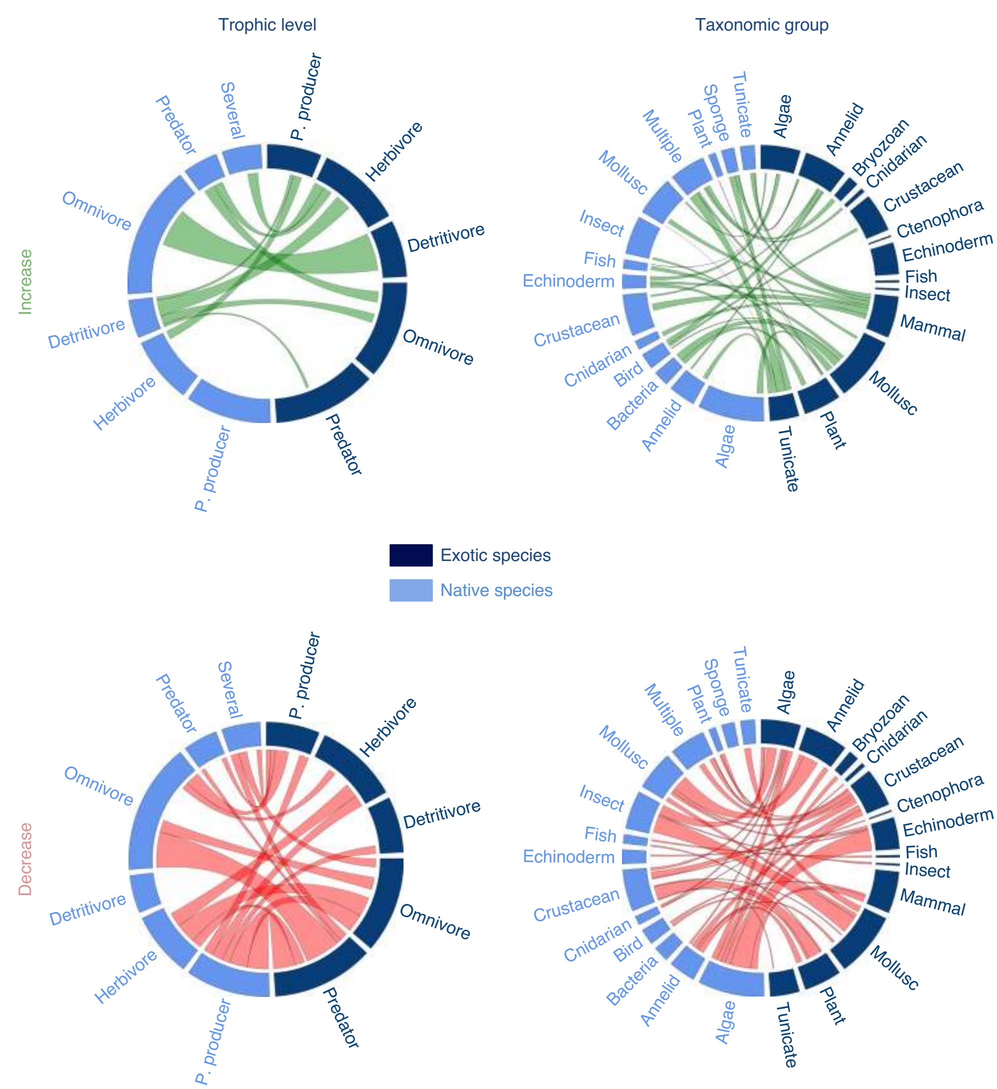

Fig. 2 | Network diagram of the ecological effects of marine exotics on native species classified by trophic level and taxonomic group. The width of the band represents the mean effect size Hedges' *g*, where effect sizes that increase or decrease ecological properties are presented in the upper and lower panels, respectively. The insect group includes arachnids. Interactive diagrams are available at https://kaust-vislab.github.io/Biological-Network/.

assessed in three or more independent studies, was chosen to produce a robust ranking of marine exotic species based on their ecological effects. In this ranking of sufficiently assessed exotic species, only the European green crab *C. maenas* and the green macroalgae *C. cylindracea* had overall significant impacts (Fig. 5).

Discussion

Our findings indicate that globally, exotic species induce significant changes on many ecological attributes of marine systems ($g = -0.14 \pm 0.1$). This global effect is modest in magnitude compared to other quantified human stressors, such as the overall impact of dual environmental stressors in freshwater ecosystems ($g = -0.64 \pm 0.46$, as calculated from data in ref. [37] after removing the effects of invasive species) or the worldwide effects of fishing pressure on reef fish behaviour ($g = 1.3 \pm 0.13$; values obtained from figure 3 in ref. [38]). The global impact of marine exotic species is comparable to the overall effect reported for freshwater exotic species worldwide ($g = -0.27 \pm 0.25$; values calculated from raw data available in ref. [23]). However, it is larger than the nonsignificant ecological effects reported for exotic ecosystem engineers on the abundance or richness of marine native species ($g = 0.04 \pm 0.19$ and 0.06 ± 0.26, respectively)[24].

We provide a quantitative synthesis of ecological effects across both trophic levels and taxonomic groups, while previous meta-analyses evaluated the effects of exotic species on certain native trophic levels[22,23,25] or taxonomic groups[21,24–26]. Overall, exotic species had significant effects on primary producers and multitrophic assemblages, while the other native trophic levels experienced overall contrasting effects. Native primary producers were affected by all trophic levels of exotics, which surpassed our expectations drawn from freshwater systems[23] in that they were also affected by exotic predators and detritivores. Exotic predators and primary producers were the only trophic groups that exerted substantial impacts on marine ecological properties; these trophic groups were therefore identified as the most disruptive of all marine exotics. Exotic predators, arguably the most detrimental group for terrestrial and freshwater native communities[6,7], caused overall decreases in the ecological properties of all marine trophic groups except detritivores. Similarly, exotic primary producers caused ecological decreases at most trophic levels and taxonomic groups, which is

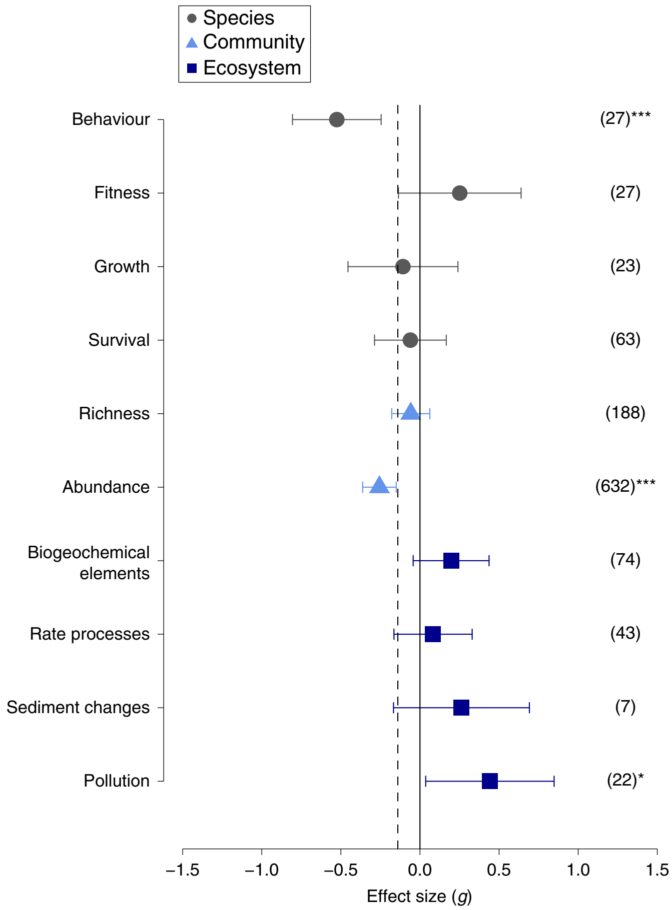

Fig. 3 | Mean effect size (Hedges' $g \pm 95\%$ CI) of marine exotic species on response variables classified by the levels of ecological complexity. The unbroken line denotes zero, and the broken line indicates the overall mean effect size. The number of observations is specified in parentheses, and $^*P \leq 0.05$, $^{***}P \leq 0.001$. P values were obtained from mixed-effects models that included the study ID and exotic species name as random factors, using the rma.mv function from the metafor package for R.

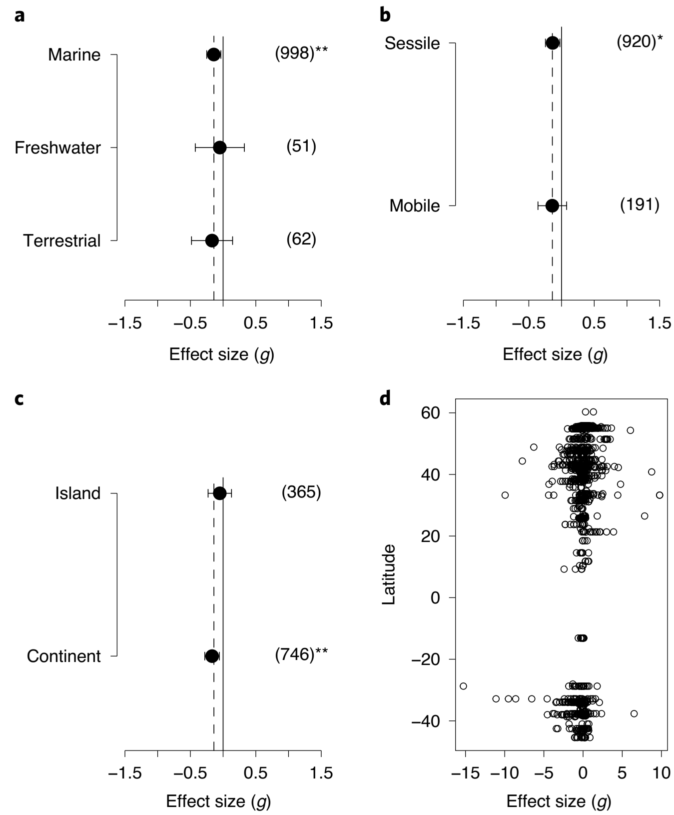

Fig. 4 | Mean effect size (Hedges' $g \pm 95\%$ CI) of marine exotic species based on different variables. a–d, Effects were based on the environment of exotic species (**a**), mobility of exotic species (**b**), if the study location was a continent or an island (**c**) and the latitude of location (**d**). The unbroken line denotes zero and the broken line indicates overall mean effect size. The number of observations is specified in parentheses, and $^*P \leq 0.05$, $^{**}P \leq 0.01$. P values were obtained from mixed-effects models that included the study ID and exotic species name as random factors, using the rma.mv function from the metafor package for R.

in contrast to previous studies that reported contrasting effects of exotic primary producers in freshwater[23] and marine systems[22]. Conversely, exotic marine herbivores, detritivores and omnivores, of which previous information is scarce[23], had contrasting effects on other trophic levels of the food web. These contrasting effects were probably context-dependent, with changes compensating for each other by going in different directions.

Exotic molluscs and crustaceans, for which no information from previous meta-analyses was available to make predictions, were the other two taxonomic groups that induced overall ecological decreases in many native marine taxa. The findings for exotic mammals, the taxon that caused increases in the largest number of native taxa, were surprising since they are a very disruptive group in terrestrial ecosystems[5,6,39,40] as well as in some marine coastal communities[41,42]. This result is derived from one publication[43], where the exotic brown rat (*R. norvegicus*) triggered a trophic cascade by directly predating on birds but indirectly enhancing the abundance of many benthic taxa. Further investigation is required to test the generality of this finding.

Exotic species significantly decreased the abundance of native species but not diversity, as reported in freshwater systems[23]. Marine exotics might prompt rapid declines in species abundance, but they may take a long time to generate local extinctions (an 'extinction debt'[44]).Our decoupled results between decreases in abundance but not overall changes on ecosystem functioning are comparable to those reported for exotics in freshwater[23] and terrestrial systems[21], and by other anthropogenic factors elsewhere[45]. This indicates that changes in community composition are often decoupled from those at the ecosystem level. Possible buffering mechanisms conferring ecosystem resistance against exotic species in the marine realm include functional redundancy between exotic and native species or between affected and non-affected native species[46]. Our results differ from those reported for marine exotic ecosystem engineers, which exert contrasting strong effects on native ecosystem functioning but not on native community abundance[24]. The contrasting results among studies might be due to targeting different suites of marine exotic species and clustering ecological response variables differently. Interestingly, we found a lack of ecological effects on survival, growth and fitness of native species, but profound changes in animal behaviour. Changes in behaviour of native species could affect native species populations in the short term and, where adaptation of behavioural traits is possible, buffer the effects in the long term[47]. We found significant increases in ecological traits related to pollution, mainly through the increased concentration of heavy metals in the tissues of the exotic species compared with native species.

Relating features of exotic species with their ecological effects is of utmost importance if we aim to control thousands of exotic species[48]. Sessile exotics or those with a marine origin exerted significant

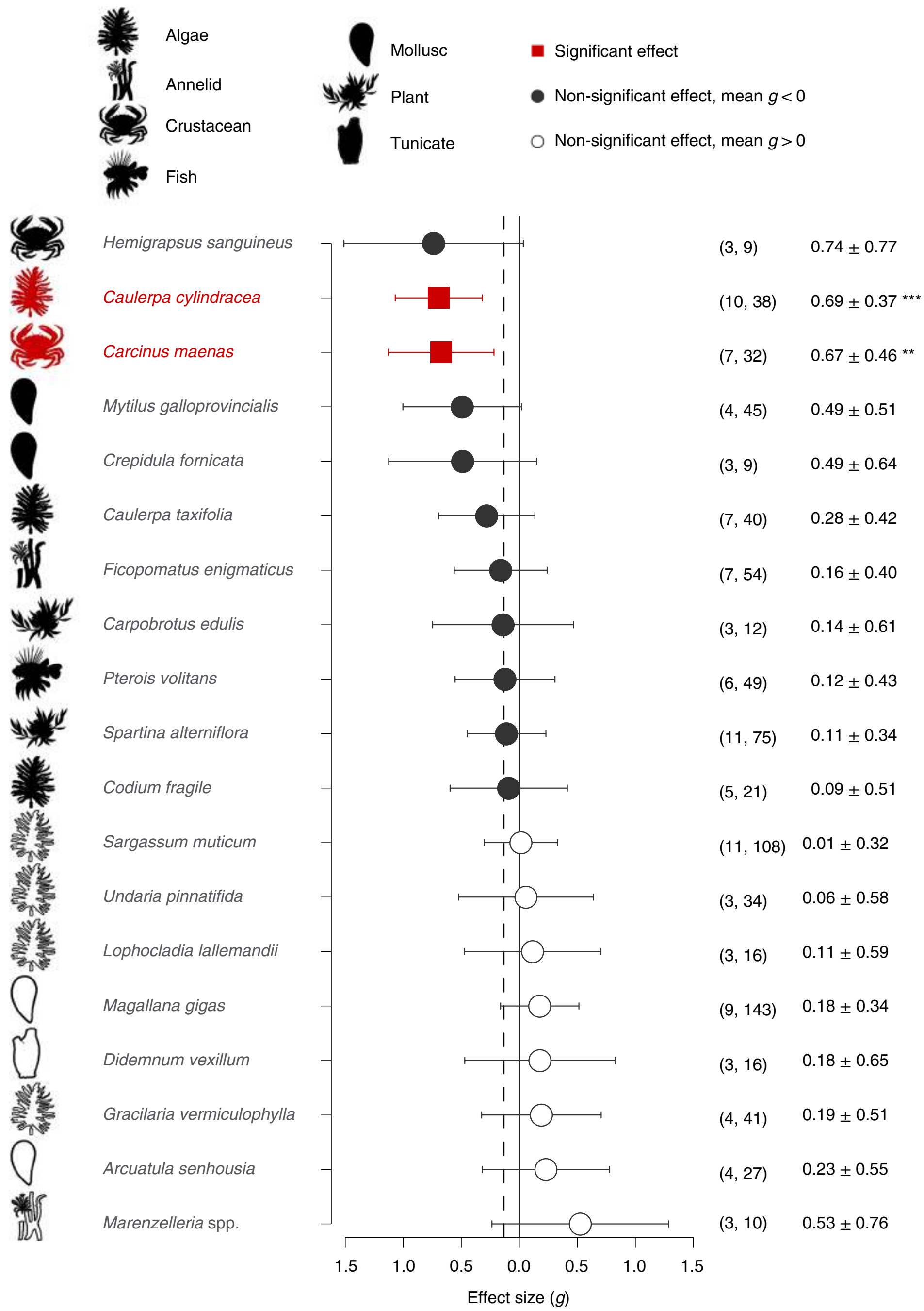

Fig. 5 | Ranking of the 19 sufficiently assessed marine exotic species based on the species mean effect size. Effect size indicates an increase ($g > 0$) or decrease ($g < 0$) with respect to a reference control. Bars represent 95% CI, which denote significant effects when they do not overlap zero. The unbroken line represents zero, and the broken line indicates the overall mean effect size. The number of studies (left) and the number of observations (right) are specified in parentheses, and $^{**}P \leq 0.01$, $^{***}P \leq 0.001$. *P* values were obtained from mixed-effects models that included the study ID as a random factor, using the rma.mv function from the metafor package for R. Red squares indicate significant ecological effects of exotic species, which would be categorized as invasive species[33] or pests[36]. Circles indicate nonsignificant effects of exotic species, with black and white filled circles indicating mean $g < 0$ or $g > 0$, respectively. Credit: Allende Bodega Martinez (silhouettes).

changes on marine native communities, while mobile exotics or those with a freshwater or terrestrial origin did not. This result therefore identifies important characteristics of potentially detrimental exotic species. Environmental and geographical attributes of the invaded communities can also influence the establishment and success of exotic species. We found that the ecological effects of exotic species on marine ecosystems were substantial in continental margins but not on islands, which was unexpected based on reports for exotic avian species[40] or terrestrial plants[21]. There was no clear indication that the ecological effects of marine exotic species varied over latitude, although we anticipated low effects at low latitudes due to their high biodiversity, low space availability and strong biotic interactions[49,50]. This finding has two possible explanations. First, although benthic biodiversity is highest at tropical latitudes for many marine habitats (for example, coral reefs, seagrass meadows or mangrove forests), this does not apply to all marine ecosystems (for example, macroalgae beds and saltmarshes)[51,52]. Second, there were a few tropical and polar study locations (ten and one, respectively), which might have influenced the results.

About 10% of marine exotic species were qualified as invasive species (as defined in ref. [33]) or pests (as defined in ref. [36]) by causing overall significant decreases in ecological variables. This percentage is similar to the proportion of exotic species that had been previously estimated to have sizeable impacts on native communities[36,48,53,54]. However, these former estimates were based on semiquantitative data, unlike our estimate, which was based on a common metric, thus enabling a rigorous evaluation across species and types of impacts[55]. Four species (*C. maenas*, *C. taxifolia*, *M. galloprovincialis* and *U. pinnatifida*) were included in the world's 100 most invasive species by the IUCN[56]. While the overall ecological impact of *C. maenas* was obvious, those of *C. taxifolia*, *M. galloprovincialis* and *U. pinnatifida* are of concern since the wide error bars around the mean indicate that they can exert large impacts. The IUCN list[56], the most reputable compilation of the worst exotic species worldwide, was based on expert judgment, and our list is an upgrade for marine exotics[57]. By separating the disruptive from the innocuous species, we provide a basis for prioritizing and triaging eradication and management efforts, thereby offering a solid foundation to help meet Aichi Biodiversity Target 9 of the international Convention on Biological Diversity.

Our ranking of exotic species is based on the magnitude of the mean global effect for each exotic species. However, it is important to consider not only the mean but also the variability of the effects. For instance, exotic species that inflict strong disparate impacts depending on geographical locations or habitat types[58,59] will have large error bars around the mean, which was the case for some exotic species on our list. Therefore, many of the exotic species on our list could qualify as invasive in some locations but not others, although their global effect might not be significant. The lowest confidence interval (that is, the largest ecological decrease) could therefore be used to rank the species under a precautionary approach. The resulting ranking would, however, be very similar to that resulting when using the mean *g*.

The effects summarized here may be biased towards the most damaging of exotic species because studies with negligible ecological effects are usually underreported in the literature[60]. This is probably because exotic species present at low abundances might go unnoticed or are difficult to study. In addition, quantitative analyses of the effects of exotic species are often funded and initiated when detrimental impacts are suspected, thereby probably targeting the most aggressive exotics. Therefore, our quantified ecological effects of marine exotic species may reflect a 'worst case' scenario, but one that is relevant to inform management actions under a precautionary principle.

Recent assessments indicating that marine exotic species, based on ecosystem engineer species, have overall nonsignificant effects[24] are challenged when a broader suite of species is assessed, revealing significant ecological changes of exotic species at a global scale. Hence, concerns about the effects of marine exotics are warranted[10], especially since they will probably intensify as the vectors of introduction of marine exotics are expanding and diversifing[61,62]. However, our analysis also partially supports tempered views on the effects of marine exotics[63] through the finding that the overall changes in magnitude are moderately significant ($g < 0.2$)[64] and that there is a prevalence of overall nonsignificant effects for the majority of exotic species (~90%).

In conclusion, the results provided here offer an integrated, quantitative assessment of the effects of exotic species, enabling the reconciliation of the two polarized sides of the current debate. We also provide a ranked assessment of marine exotic species based on their quantitative ecological effects on native communities. Together, these results contribute to efforts to meet Aichi Biodiversity Target 9 of the Convention on Biological Diversity of the United Nations, and reveal previously unknown ecological patterns, such as the trend of exotic marine predators and primary producers to cause the largest ecological impacts.

Methods

Literature search. Quantitative data from the literature were gathered to assess the ecological effects of marine exotic species. We performed an exhaustive and systematic review on 4 May 2016 following the guidelines of TOP[65] (transparency and openness promotion) and PRISMA[66] (preferred reporting items for meta-analyses) (Supplementary Table 3; Supplementary Fig. 1). We used the Web of Science (Thomson Reuters) search engine to find studies using the following terms: (invader OR exotic OR invasive OR non-native OR alien) NEAR/5 (impact OR effect OR influence OR consequence*) AND (marine OR coastal OR sea OR estuar* OR ocean) NOT (lake OR stream OR freshwater OR terrestrial). The search resulted in 1,012 publications. Each reference was randomly assigned to authors, who each extracted information from a set of papers.

Study selection criteria and data entering. The following criteria were used to select studies to include in the analysis. First, we only included studies within marine systems, up to and including environments getting sea spray. These comprised exotic species that inhabit brackish-water estuaries (such as the snail *P. antipodarum*) or that cover the coastal zones (such as the succulent terrestrial plant *C. edulis*). We included freshwater and terrestrial exotic species reported to interact with native marine species. Indeed, some of these species have been described as potential threats to coastal marine communities, such as the exotic terrestrial American mink (*Mustela vison*), which can deplete many species of European native fish and crabs in the rocky intertidal[42]. Second, we included species (for example, exotic species or species from the native community) that spend any stage of their life cycle in the marine environment. Third, we only included studies that quantitatively compared control and experimental treatments (for example, exotic species removals versus additions, or exotic species versus native species treatments). Articles lacking appropriate controls were excluded. Fourth, we only included studies reporting the mean values of variables, number of replicates and a measure of variability around the mean. If these data could not be obtained from a paper but did appear to have been recorded, the authors of the original study were contacted to request the relevant information. Fifth, when multiple and distinct habitat types or exotic species were examined separately within the same article, they were entered in the database as separate observations (for example, each observation was a row in our database). Sixth, if an article reported data on studies conducted at several locations, they were included as independent studies. Seventh, if more than two densities of exotic species were compared in a study (for example, low, medium and high abundance of the exotic species), they were entered in the database as separate observations. Eighth, if response variables were measured at multiple time points, we recorded the first and last sampling events except if there was a clear pattern in the data that was missed by recording only the first and last sampling events. In those cases, an additional point in the middle was recorded. Ninth, if multiple sampling techniques were used to estimate impacts within one area, only results from the most efficient sampling method were included. Tenth, for studies reporting multiple native community measures (for example, abundance, biomass, richness and diversity) and data on individual native species, we extracted information on community abundance and richness and collected data for a maximum of two individual native species either from the most abundant species or from the native species that was the focus of the study. Eleventh, for studies that reported results for the same species at several life stages or sizes, they were entered in the database as separate observations.

From an initial selection of 1,012 published studies, 159 studies were found to contain suitable quantitative data from 151 study locations (Supplementary Table 2; Supplementary Figs. 1 and 2). We assessed the effects of exotic species on the following ten types of metrics (Supplementary Table 4): abundance, richness, biogeochemical elements (stocks or fluxes of carbon, nitrogen, phosphorus and silicate), rate processes (production, photosynthesis, respiration and decomposition), survival (including mortality), growth (including percentage growth), fitness, behaviour, pollution (including heavy metal concentration and water clarity), and sediment changes. We then grouped these response variables at the species, community and ecosystem levels (Supplementary Table 4). A dropdown list was provided to co-authors to standardize data entry and to exclude redundant measurements. The trophic level of the species was determined after performing data searches on the diet of each exotic species in the Web of Science database and in the Invasive Species Compendium in the Center for Agriculture and Biosciences International. Filter-feeders were categorized as follows: (1) bivalve molluscs, tunicates and suspension-feeding gastropods were categorized as herbivores because they consume primarily phytoplankton; and (2) barnacles, bryozoans and suspension-feeding annelids and crabs were categorized as omnivores because they are not restricted to microscopic algae for food. The same criteria were followed to categorize the trophic level of the native species, for which, in addition, sponges were classified as omnivores. For exotic species names, we used the ones most recently listed in the World Register of Marine Species. Data were obtained from tables or extracted from plots using Graph Click (available at http://www.arizona-software.ch/graphclick/download.html).

Data analysis. Hedges' *g* effect size and variance were calculated for each observation (1,111 observations in total; see also https://doi.pangaea.de/10.1594/PANGAEA.895681) to estimate the differences in the response variable between control and experimental treatment. Hedges' *g* weighs cases by their sample size and the inverse of their variance[67]. Hedges' *g* ranges from $-\infty$ to $+\infty$ and can be interpreted as follows[64]: $|g| \leq 0.2$ considered a small effect; $0.2 \leq |g| \geq 0.5$ a medium effect; $0.5 \leq |g| \geq 0.8$ a large effect; and $|g| \geq 1.0$ a very large effect. The effect size Hedges' *g* was calculated as follows[67]:

$$g = (X_E - X_C) \times J / \text{s.d.}_{\text{pooled}}$$

where X_E and X_C are the mean of the experimental (for example, presence of exotic species) and control groups (for example, absence of exotic species), respectively. *J* corrects for bias attributed to different sample sizes by differentially weighting studies as follows:

$$J = 1 - (3 / (4 \times (N_E + N_C - 2) - 1))$$

The pooled standard deviation (s.d.$_{\text{pooled}}$) was calculated as follows[64,67]:

$$\text{s.d.}_{\text{pooled}} = \sqrt{((N_E - 1) \times (\text{s.d.}_E)^2 + (N_C - 1) \times (\text{s.d.}_C)^2) / (N_E + N_C - 2)}$$

where s.d. is the standard deviation of the experimental or control group and *N* is the sample size. We weighted the effect sizes to account for inequality in study variance by using the inverse of the sampling variance, in which the variance for each effect size (V_g) was calculated as follows[64]:

$$V_g = ((N_E + N_C) / (N_E \times N_C)) + (g^2 / (2 \times (N_E + N_C)))$$

Meta-analyses were completed using the metafor package for R[69]. We ran mixed-effects models that included the study identification (ID) number and exotic species name as random factors to account for the effect of the exotic species within a study and across studies (for example, when several observations for a species were obtained from the same publication or from several publications). For models with categorical fixed factors (for example, trophic level of native species, trophic level of exotic species, level of ecological complexity, type of ecological response variable, origin and mobility of exotic species, continentality and exotic species name), effect sizes were significant if the following criteria were met: (1) their 95% CI did not overlap with zero; and (2) *P* values were ≤ 0.05. For the model with a continuous fixed factor (latitude), the predictor was considered to have significant effects at $P \leq 0.05$. In all statistical models, we used the rma.mv function, which determines statistical significance based on a Wald-type test.

Filter-feeders are a special guild that comprises several trophic levels and can have important ecological effects. We therefore performed an additional analysis on the effects of the trophic level of exotic species on native species including filter-feeders as a trophic level (27 exotic species were filter-feeders) to quantify their effects.

Publication bias. Publication bias, which is the selective publication of articles finding significant effects over those that find nonsignificant effects, might distort the results in a meta-analysis[64]. In our case, publication bias could lead to an overestimate of the effects of exotic species in marine ecosystems. The functions regtest and trimfill are not implemented in the metafor package for mixed-effects models[69]. Therefore, potential publication bias was evaluated using Egger's regression test[70] by running models that included the standard error (s.e.) of the effect sizes (included as the square root of the variance) as a moderator[71]. Potential publication bias was determined when the intercept of the model was different from zero at $P \leq 0.05$. If potential bias was detected, we examined the data for potential outliers by looking at the effect sizes with standardized residual values exceeding the absolute value of three[72] using the rstandard function in R. Potential outliers were removed to adjust for publication bias. Adjusting for publication bias did not changed the outcome of the analyses (by comparing fitted random-effects models with and without the influence of the potential outliers), except for both the effects of exotic species on native omnivores and the biogeochemical elements (Supplementary Table 5). We removed the potential outliers detected in the sensitivity analysis and re-ran the mixed-effects models for the effects of exotic species on the effects of trophic level (represented in Fig. 1) and the ecological categories of the response variables (represented in Fig. 3). Otherwise, our sensitivity analyses showed that our findings are robust against publication bias (Supplementary Table 5).

Standardization of variables. We performed the following calculations to standardize our dataset.

Variation around the mean. The s.d. was used as the measure of variation. When another statistic was reported (for example, s.e. or CI), it was converted to the s.d. using the following calculations (where *n* is the number of replicates, d.f. the degress of freedom and α the probability of rejecting the null hypothesis):

$$\text{s.d.} = \text{s.e.} \times \sqrt{n}$$

$$\text{CI} = \text{s.e.} \times t_{\alpha,\text{d.f.}}$$

Growth data. If data were reported as biomass increase, we used the initial (B_o) and final (B_t) reported in the paper, and calculated the fractional growth (F_g):

$$F_g = [B_t / B_o]$$

The s.d. of F_g (s.d.$_{Fg}$) is then $\text{s.d.}_{Fg} = F_g \times (\text{s.d.}_{Bt} / B_t)$. When data were reported as the percentage growth (%G) with its s.d. (s.d.$_{\%G}$), we converted %G into F_g.

Mortality and survivorship data. If data were reported as initial and final number of individuals in the populations (N_o and N_t, respectively), we calculated the fraction of survivors (F_s) as follows:

$$F_s = [N_t / N_o]$$

where N_t is the number of the survivors at time *t* and N_o is the number of individuals at the beginning of the experiment.

The s.d. of F_s (s.d.$_{Fs}$) was calculated as follows:

$$\text{s.d.}_{Fs} = F_s \times (\text{s.d.}_{Nt} / N_t)$$

When data were reported as percentage survivorship (%S) with its s.d. (s.d.$_{\%S}$), we converted %S to F_s.

When the data were reported as number of dead and when the results were reported as percentage mortality, the calculations were performed as above, but converted from number of percentage dead into number of percentage surviving.

Reporting Summary. Further information on research design is available in the Nature Research Reporting Summary linked to this article.

Data availability

All data underlying the study have been deposited in PANGAEA at https://doi.pangaea.de/10.1594/PANGAEA.895681.

Code availability

The R script used in this manuscript will be deposited in the Github community repository upon publication (https://github.com/ngeraldi/marine-exotics-global-analysis).

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Author contributions

C.M.D., A.A., C.E.L. and N.R.G. conceived and designed the study. A.A., N.R.G., C.E.L., E.T.A., S.B., J.C., D.K.-J., N.M., P.M., J.M.P. and J.S.-G. constructed the dataset. A.A. and N.R.G. performed the data analyses with contributions from all co-authors. All authors contributed to writing and improving the manuscript and approved the submission.

Competing interests

The authors declare no competing interests.

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Research sample	An exhaustive literature search was performed in ISI Web of Knowledge using the following terms: (invader OR exotic OR invasive OR non-native OR alien) NEAR/5 (impact OR effect OR influence OR consequence*) AND (marine OR coastal OR sea OR estuar* OR ocean) NOT (lake OR stream OR freshwater OR terrestrial). A search performed on May 4 2016 resulted in 1012 publications.
Sampling strategy	In order to extract data from the published literature, we created a set of study selection criteria and a protocol for data extraction from the literature
Data collection	All authors (11 in total), except CMD, extracted data and information from published literature. Each of the 1012 references was randomly ordered and given an original reference number, and authors extracted information from a set of papers (all authors extracted information from 60 papers except AA and NRG that extracted information from 200+ papers). Agreement between authors on the application of criteria was achieved after discussion and clarification of study selection criteria against particular studies. An exhaustive protocol was then created to extract data from publications. Agreement on data extraction between authors was attained by extracting information using a common subset of references (n=2), followed by an amendment of the protocol for data extraction.
Timing and spatial scale	Data from publications was extracted from November 2016 to April 2017.
Data exclusions	Only studies that met our study criteria (see methods) were included in the analysis
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