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The complex threats of marine exotic species - A reply to Thomsen

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Exotic species are a growing ecological threat although their factual ecological effects are currently debated. Our global meta-analysis¹ recently reported that marine exotic species have an overall significant but modest effect on native communities. Thomsen² argues

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the data in this meta-analysis was aggregated in a manner that might underestimate the ecological impacts of marine exotic species. Here we discuss the data aggregation methodologies proposed by Thomsen² and evaluate, whenever possible, if the findings meet the expectations.

Meta-analysis is a powerful statistical tool for synthesizing evidence across independent studies and is commonly used in ecology³–⁵. Meta-analysis involves the aggregation of extensive data sets to perform analyses that aim to answer specific questions. Thomsen² argues that the weak significant impacts of marine exotic species on native communities reported in our recent meta-analysis¹ were potentially due to an indiscriminate aggregation of data. Thomsen² stated that he “demonstrates that many of the reported weak impacts occurred because effects were aggregated and averaged across opposing ecological processes and methodological approaches”. However, his analyses selected single examples for each of the three instances where, in his view, the way we aggregated (analyzed) data underestimated the impact of marine exotic species. We evaluate these three instances, but rather than focusing on single examples, we re-ran the analyses with the entire data base, where possible, to statistically confirm or refute Thomsen’s hypotheses².

First, Thomsen² argues that our “analysis should have tested key characteristics of the invader against well-defined ecological responses, because this approach has previously been shown to change non-significant to significant results in meta-analysis”. Thomsen², however, overlooked that in our meta-analysis we did pair the attributes of the non-native
and exotic species using network diagrams (Figure 2 in Anton et al.\textsuperscript{1}) and calculated mean effect sizes among trophic levels and taxonomic groups. We went one step further and ran a meta-analysis among trophic levels to test the statistical effects among all trophic levels (e.g., pairing the attributes of exotic to native species as proposed by Thomsen\textsuperscript{2}; Fig. 1). We found that, as illustrated in the updated network diagram (Fig. 1) and also predicted by Thomsen\textsuperscript{2}, exotic primary producers caused significant decreases (g=-0.34±0.26; p=0.01; Fig. 1) on the ecological properties of native primary producers. However, we did not find evidence supporting the prediction by Thomsen\textsuperscript{2} that native herbivores were facilitated by exotic primary producers (g=0.04±0.28; p=0.793; Fig. 1), perhaps because our re-analyses of the data included random factors to account for the lack of independence among replicates obtained from the same study (unlike Thomsen\textsuperscript{2}). We also conducted a full quantification of the effects of exotic species on native communities pairing the attributes of the exotic and native trophic levels, as suggested by Thomsen\textsuperscript{2}. Our results concur with our original finding\textsuperscript{1} that overall the effects of marine exotic species are mainly non-significant (77\% of the pairing interactions), sometimes significantly negative (18\%) and rarely significantly positive (5\%, Fig. 1). With regard to \textit{Gracilaria vermiculophylla}, Thomsen\textsuperscript{2} argues that, after pairing the attributes of the non-native and exotic species, the red seaweed “had stronger negative impact on native plants (g=-0.31) but large positive impacts on native animals (g=0.73)”\textsuperscript{2}. We tested this statement by re-running the analysis of \textit{Gracilaria vermiculophylla} after pairing the trophic attributes and found that results partially support the claims by Thomsen\textsuperscript{2}: \textit{G. vermiculophylla} did not cause significant effects on native primary producers (g=-0.19±0.22; p=0.096), but increased the ecological properties of native herbivores.
(g=0.60±0.49; p=0.017). To further test the generality of Thomsen’s predictions, we looked at the effects of the other eight species of exotic primary producers with sufficiently representation (species with ≥3 studies; Carpobrotus edulis, Caulerpa cylindracea, Caulerpa taxifolia, Codium fragile, Lophocladia lallemandi, Sargassum muticum, Spartina alterniflora, and Undaria pinnatifida) on native primary producers and herbivores. The results did not match Thomsen’s expectations, as only 43% (3 out of 7 observations; Supplementary Table 1) and 25% (2 out of 8 observations; Supplementary Table 1) of the species of exotic primary producers significantly decreased and increased the ecological properties of native primary producers and herbivores, respectively. Hence, Thomsen’s arguments were only partially supported by the examples he chose but were generally unsupported by a consistent analysis across the entire data set.

The second argument by Thomsen was that “meta-analysis on community responses should distinguish between whether data for the invasive species (e.g., its abundance or oxygen production) are included or excluded in the estimation of effect sizes”. This argument, however, needs to consider the fundamental difference between the questions of whether exotic species affect (a) ecosystem processes, and (b) populations of native species. Question (a) requires that the effects of exotic species be included in the evaluation of ecosystems processes (e.g., biogeochemical cycling and community metabolic processes) as they are indeed contributors to these processes, and hence, the vast majority of studies evaluating the effects of exotic species on ecosystem processes do include the exotic species in the measurements of ecosystem processes. In contrast,
the response variable in question (b) excludes exotic species, consistent with the
exclusion of exotic species in the majority of reports evaluating changes of exotic species
on native species at the species and community level (e.g., abundance or richness). In
addition, we were explicit when providing a definition of the terms in our study\textsuperscript{1}. For
instance, we avoided the use of negative or positive impacts attributed to exotic species
but instead refer to “increases and decreases of the ecological properties attributed to
exotic species with regard to a control”, in order to accommodate changes at different
levels of ecological complexity (e.g., species, community or ecosystem). The inclusion of
exotic species when evaluating ecosystem processes is, logically, the standard practice in
general invasion ecology studies, as reflected in a range of previous meta-analyses
evaluating the effects of exotic species at multiple levels of ecological complexity\textsuperscript{6-9}, and
a common practice beyond invasive ecology on the analysis of environmental
impacts\textsuperscript{11,12}.

Finally, Thomsen\textsuperscript{2} argues that “impact studies should also differentiate between different
types of control data”. For example, when exotic oysters invade intertidal mudflats,
studies can use two valid comparisons: exotic oyster vs mudflat and exotic oyster vs a
comparable native bivalve that also grows on mudflats (mussel). In our meta-analysis we
aggregated data across different types of controls in order to capture the general changes
produced by exotic species\textsuperscript{1}. We agree with Thomsen\textsuperscript{2} that choosing one type of control
“aggregating data across different types of controls can change effect sizes and
conclusions about invasion impacts”. Given that the primary goal of our study was to
quantify and describe global trends, these specific questions were beyond the scope of
our analyses. However, our data set is publicly available\(^\text{13}\), so researchers can build on
our efforts to explore other questions, such as the effect of the type of control included in
the study.

In summary, a reanalysis of the data set\(^\text{1}\), focusing on the entire data set rather than on
single cases, does not support Thomsen’s conclusion that the reported weak impacts of
marine exotics occurred because effects were aggregated and averaged\(^\text{2}\). The
comprehensive data set we compiled and made available\(^\text{13}\) represents a valuable resource
to explore additional questions, but with the caveat that this should done consistently (and
tested statistically) to achieve robust inference.

Author contribution statement
A.A., C.M.D., and N.R.G. conceived the reply; A.A. analyzed and interpreted the data;
A.A. wrote the first draft and N.R.G., C.E.L., E.T.A, S.B., J.C., D.K-J., N.M., P.M.,
J.M.P., J.S-G., and C.M.D contributed to improving it and approved the submission.

Competing interests
The authors declare no competing interests

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2. Thomsen, M. S. Indiscriminate data aggregation in ecological meta-analysis
3. *Handbook of Meta-analysis in Ecology and Evolution.* (Princeton University Press,
   2013).


Figure Legend

Figure 1. Network diagram of the ecological effects of marine exotic species on native species. Green, red and grey bands indicate significant increases, significant decreases and non-significant changes in ecosystem properties across trophic levels. Yellow bands indicate insufficient data with less than 3 observations. The width of the band represents the mean effects size while the variance is represented by border intensity. Data from\textsuperscript{13}.