

Indiscriminate data aggregation in ecological meta-analysis underestimates impacts of invasive species

Mads Solgaard Thomsen ^{1,2}

ARISING FROM A. Anton et al. *Nature Ecology & Evolution* <https://doi.org/10.1038/s41559-019-0851-0> (2019)

A global meta-analysis recently reported that marine invasive species generally have small and non-significant effects on ecological responses¹. For example, 80% of the impacts reported in the results were ‘weak’ (that is, 28 out of 35 Hedges’ g values were $\leq |0.2|$, see figs. 1, 3 and 4 and the main text in ref. ¹) and only 11% of the best-studied invasive species had significant effects (fig. 5 in ref. ¹). These impacts were evaluated from an impressive literature compilation and included novel network analyses. Here I demonstrate that many of the reported weak impacts occurred because effect sizes were aggregated and averaged across opposing ecological processes and methodological approaches (Fig. 1). Unfortunately, based on the many reported aggregated weak impacts, readers may conclude that marine ecosystems have been little affected by invasive species, and in turn (and against the evidence from the primary literature) down-prioritize future research and management of invasive species. I therefore recommend that ecologists aim to avoid aggregating impacts across important opposing processes and methodologies to avoid reporting unnecessarily small and unrepresentative values in future meta-analyses.

One of the main objectives of ecological meta-analysis is to aggregate and average effect sizes (Hedges’ g in ref. ¹) across different case studies in search of generality^{2,3}. However, identifying the optimal aggregation level is complicated; averaging effect sizes across increasingly detailed data aggregations reduces replication levels, test power and scientific generality, and eventually reverts the analysis back to idiosyncratic case studies. By contrast, coarse and indiscriminate data aggregations can cancel out opposing effect sizes and may underestimate impacts and fail to identify the underpinning processes. I exemplify below how indiscriminate data aggregation in ref. ¹ could affect conclusions about invasion impacts. Specifically, I illustrate how the reported small effect sizes arose, in part, because data were aggregated across invader characteristics and ecological responses (Fig. 1a), across community responses where the invader’s own data were either included or excluded (Fig. 1b) and across different types of uninvaded control (Fig. 1c).

First, I suggest that the analysis in ref. ¹ should have tested key characteristics of the invader (the independent variable; the trophic position of the invader, for example, which could be a plant) against well-defined ecological responses (the dependent variable; the trophic position of the native species, for example, which could be a herbivore), because this ‘pairing’ approach has previously been shown to change non-significant to significant

results in meta-analyses (Fig. 1a, see also refs. ^{4–7}). However, all types of invader characteristic and ecological response were aggregated before analysis in ref. ¹, thereby cancelling out important negative and positive effect sizes. For brevity, I reanalyse just two examples from ref. ¹: impacts from invasive primary producers (see fig. 1 in ref. ¹) and, on a species-specific basis, impacts from the red seaweed *Gracilaria vermiculophylla* (see fig. 5 in ref. ¹). In these two examples, effect sizes were calculated as being relatively small on all the aggregated ecological responses ($g \leq |0.22|$, black circles in Fig. 1a). These results imply that the invasive organisms have minor impacts on ‘everything’ in the invaded systems. However, the magnitude and direction of the effect sizes changed considerably when I reanalysed how these invaders affected specific ecological responses. The invasive primary producers now had stronger negative impacts on native primary producers ($g = -0.32$, red squares in Fig. 1a, see Supplementary Data 1–2 for details of this meta-analysis, including forest plots and associated P values that quantify heterogeneity between studies) but also had a positive impact on native herbivores ($g = 0.25$, blue squares in Fig. 1a). Similarly, the reanalysis of the *Gracilaria* data demonstrated that this invasive seaweed now had stronger negative impact on native plants ($g = -0.31$, red squares in Fig. 1a, see Supplementary Data 3 for the meta-analysis) but also a large positive impact on native animals ($g = 0.73$, blue squares in Fig. 1a). These new results thereby support the many case studies and reviews that have concluded that this seaweed has altered estuarine ecosystems around the world^{4–11}. Furthermore, the recalculated effect sizes also align with previous meta-analyses by demonstrating that invasive primary producers can have positive and negative effects on different trophic levels, probably through underpinning mechanisms such as habitat formation and grazing (here with positive effects on higher trophic levels) and competition (here with negative effects on the same trophic level)^{4–7}. More generally, these examples highlight that non-significant meta-analytical results should be interpreted carefully and preferably in a context of ecological hypotheses. Or, in other words, researchers should cross-examine whether small effect sizes calculated from coarsely aggregated responses reflect true small effect sizes or instead mask important underpinning opposing ecological processes (see refs. ^{5,12–14} for additional examples and discussions).

Second, I argue that meta-analysis on community responses should distinguish between whether data for the invasive species (for example, its abundance or its oxygen production) are included or

¹Centre for Integrative Ecology and Marine Ecology Research Group, School of Biological Sciences, University of Canterbury, Christchurch, New Zealand. ²UWA Oceans Institute and School of Plant Biology, University of Western Australia, Crawley, Western Australia, Australia. e-mail: mads.thomsen@canterbury.ac.nz

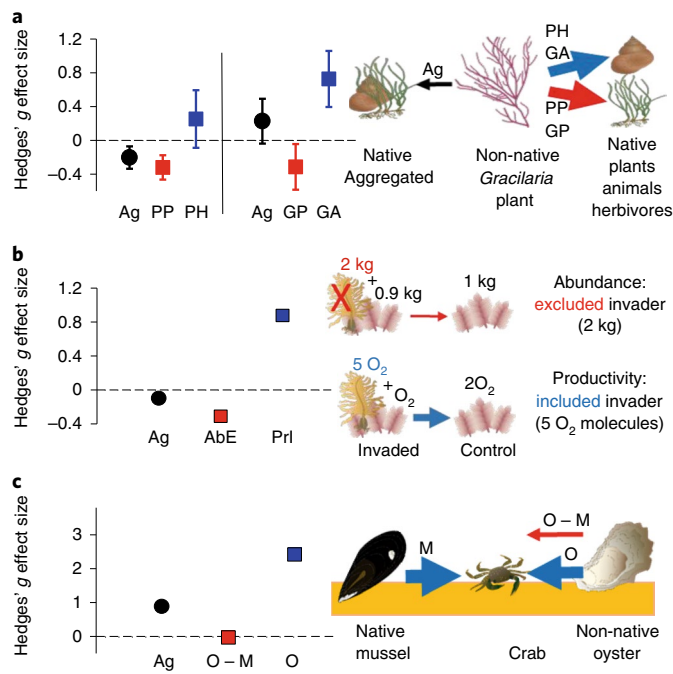


Fig. 1 | Illustration of how the impacts of invasion change depending on data aggregation of invader characteristics and native responses, different analytical approaches and different controls. **a**, Invader characteristics (the independent variable) should be relevant to specific responses of the native species (the dependent variable) to produce ecologically meaningful effect sizes. The two examples illustrate that aggregated smaller effect sizes from invasive plants and invasive *Gracilaria* on 'everything', change to larger positive and negative effect sizes for ecologically relevant responses, such as the abundance of native plants, animals and herbivores. **b**, Exclusion or inclusion of data for the invasive species changes effect sizes. Exclusion versus inclusion tests how invasive species affect the native communities alone, or change the entire invaded system, respectively. For example, impact of the invasive kelp *Undaria pinnatifida* was negative on the abundances of native communities, in part because *Undaria*'s own biomass was excluded from the response. By contrast, the impact on the productivity of the entire invaded system was large and positive, in part because *Undaria*'s own oxygen production was included in the response¹⁷. **c**, Characteristics of different controls change effect sizes. The example shows that the impact of the invasive oyster *Magallana gigas* on native crabs is large compared with bare mudflats, but small compared with the effect of mudflats inhabited by native mussels. Error bars in **a** are 95% confidence intervals calculated from a meta-analysis in OpenMEE³¹ reusing the data from ref. ¹⁹ (see Supplementary Data 1–5 for more details). Panels **b** and **c** shown mean effect sizes without confidence intervals as they could only be exemplified with individual case studies (used in ref. ¹⁹). Black circles are aggregated effect sizes as reported in ref. ¹ (Ag). Blue and red squares are positive and negative effect sizes recalculated from aggregated data (**a,b**) or from raw data extracted from ref. ²² (**c**), a primary study included in ref. ¹. P, plant; H, herbivore; G, *Gracilaria vermiculophylla*; A, animal (the first and second letters in the labels show the pairing of the invasive species characteristics to the native response). AbE, abundances where the invader's data is excluded from the response; Prl, productivity where the invader's data is included in the response; M, effects from mussels; O, effect from oysters; O – M, difference in effects between oysters and mussels. Images of organisms courtesy of the Integration and Application Network, University of Maryland Center for Environmental Science (<https://ian.umces.edu/symbols/>).

excluded in the estimation of effect sizes (Fig. 1b and Supplementary Data 4). Exclusion versus inclusion tests how invasive species affect the native communities on their own, or the entire invaded system

in which the invasive species is now a component, respectively. Failure to differentiate between these approaches can change effect sizes significantly, as demonstrated in both case studies and meta-analysis^{15,16}. Inclusion and exclusion approaches were aggregated in ref. ¹ with unknown implications for effect sizes and the wider ecological consequences. To demonstrate this methodological conundrum, I recalculated effect sizes from a case study analysed in ref. ¹, which quantified impacts from the invasive kelp *Undaria pinnatifida* on seaweed abundances and primary productivity¹⁷. It was not possible to demonstrate the meta-analytical implications of this aggregation in ref. ¹ because the required background information denoting whether the invader was included or excluded was not presented in ref. ¹⁸. The effect size of *Undaria* was small on the aggregated response ($g = -0.10$, black circle in Fig. 1b). However, hidden in this small effect size were large negative and positive values that were contingent on the contrasting inclusion–exclusion methods. More specifically, the impact on abundances of native species (that is, in this analysis the abundance of *Undaria* itself was excluded from the response) was now larger and more negative ($g = -0.31$, red square in Fig. 1b) whereas impact on community-wide primary productivity (an analysis in which the oxygen production of *Undaria* was included in the response) was also much larger but now positive ($g = 0.88$, blue square in Fig. 1b). This inclusion–exclusion conundrum could, in part, explain why the effect sizes reported in fig. 3 of ref. ¹ were negative for abundances and richness (where the invader's own data is typically excluded) but positive for rate processes and biogeochemical cycling (where the invader's own data is often included)^{15,16}. To better understand the impacts of invasive species, future meta-analysis of community responses should differentiate between inclusion and exclusion approaches, and this information should be used as a covarying moderator if both approaches are included in the analysis. More generally, the inclusion–exclusion conundrum could affect any effect size reported from meta-analyses in which the independent variable could be part of the response, for example when analysing community-wide impacts of foundation species, drift seaweeds or pulse–press removal experiments (see refs. ^{15,16} for more detailed discussions).

Finally, impact studies should also differentiate between different types of control data (Fig. 1c and Supplementary Data 5). Observational (before–after or control–invaded comparisons) and manipulative (addition–removal comparisons) experiments often target different spatiotemporal scales and taxonomic groups, and often have different types of control^{19–21}. For example, in a typical impact experiment analysed in ref. ¹, invasive oysters and native mussels were both added to bare intertidal mudflats²². Irrespective of which results were analysed in ref. ¹, two valid but ecologically different comparisons are possible: how invasive oysters affect organisms inhabiting bare mudflats (addition experiment) and how effects on the mudflat biota differ between invasive oysters and native mussels (a trait comparison). In this example, the aggregated impact of the invasive oysters on the native crab (*Carcinus maenas*) would be reported to be positive ($g = 0.87$, black circle in Fig. 1c). However, ecologically important small negative ($g = -0.03$, red square in Fig. 1b) and much larger positive ($g = 2.42$, blue square in Fig. 1b) effects are masked in this aggregated response. These opposing effect sizes reflect that invasive oysters are inferior habitat for crabs compared with native mussels, but superior habitat compared with bare mudflats^{23,24}. I could not evaluate the meta-analytical implications of aggregating different types of control in ref. ¹ because the required background information was not available in ref. ¹⁸. However, as highlighted here, aggregating data across different types of control can change effect sizes and therefore conclusions about invasion impacts. This differentiation may be especially important in marine systems, where many studies have quantified impacts from invasive habitat-forming foundation species. For example, *Gracilaria vermiculophylla*, *Magallana gigas*, *Spartina*

alterniflora and *Ficopomatus enigmaticus* (all analysed in ref. ¹) often build biogenic three-dimensional structures when they invade bare mudflats and therefore facilitate many native animals, but in doing so may also compete with and inhibit native foundation species that have relatively similar traits and ecological functions^{9,24–26}.

The many small effect sizes reported in ref. ¹ accurately reflect averaged impacts but do so in the specific context of the aggregated ecological responses. Here I illustrated how the reported effect sizes varied dramatically depending on data aggregation choices (Fig. 1). Readers unfamiliar with aggregation pitfalls and caveats, including many ecologists, managers, conservationists, journalists and students, could be left with a false impression that even the best-studied and most successful high-profile invasive species have little impact on invaded marine ecosystems. I also suggest that the issues discussed here could extend beyond the meta-analysis of invasion impacts. That is, they are relevant to many types of ecological meta-analysis, such as the analysis of impacts from seaweeds, ecosystem engineers or foundation species^{12,27–30}. I therefore hope future meta-analyses will quantify the implications of aggregation procedures and ask hypothesis-driven questions in a search for generality about why effect sizes have different magnitudes and directions.

Received: 3 May 2019; Accepted: 15 January 2020;

Published online: 17 February 2020

References

- Anton, A. et al. Global ecological impacts of marine exotic species. *Nat. Ecol. Evol.* **3**, 787–800 (2019).
- Gurevitch, J., Koricheva, J., Nakagawa, S. & Stewart, G. Meta-analysis and the science of research synthesis. *Nature* **555**, 175–182 (2018).
- Borenstein, M., Hedges, L. V., Higgins, J. P. & Rothstein, H. R. *Introduction to Meta-Analysis* (John Wiley & Sons, 2011).
- Thomsen, M. S., Wernberg, T., Tuya, F. & Silliman, B. R. Evidence for impacts of nonindigenous macroalgae: a meta-analysis of experimental field studies. *J. Phycol.* **45**, 812–819 (2009).
- Thomsen, M. S. et al. Impacts of marine invaders on biodiversity depend on trophic position and functional similarity. *Mar. Ecol. Prog. Ser.* **495**, 39–47 (2014).
- Maggi, E. et al. Ecological impacts of invading seaweeds: a meta-analysis of their effects at different trophic levels. *Diversity Distrib.* **21**, 1–12 (2015).
- Gallardo, B., Clavero, M., Sánchez, M. I. & Vilà, M. Global ecological impacts of invasive species in aquatic ecosystems. *Glob. Change Biol.* **22**, 151–163 (2016).
- Hu, Z.-M. & Juan, L.-B. Adaptation mechanisms and ecological consequences of seaweed invasions: a review case of agarophyte *Gracilaria vermiculophylla*. *Biol. Invasions* **16**, 967–976 (2014).
- Thomsen, M. S., Ramus, A. P., Long, Z. T. & Silliman, B. R. A seaweed increases ecosystem multifunctionality when invading bare mudflats. *Biol. Invasions* **21**, 27–36 (2019).
- Martínez-Lüscher, J. & Holmer, M. Potential effects of the invasive species *Gracilaria vermiculophylla* on *Zostera marina* metabolism and survival. *Mar. Environ. Res.* **69**, 345–349 (2010).
- Ramus, A. P., Silliman, B. R., Thomsen, M. S. & Long, Z. T. An invasive foundation species enhances multifunctionality in a coastal ecosystem. *Proc. Natl Acad. Sci. USA* **114**, 8580–8585 (2017).
- Lyons, D. A. et al. Macroalgal blooms alter community structure and primary productivity in marine ecosystems. *Glob. Change Biol.* **20**, 2712–2724 (2014).
- Thomsen, M. S. & Wernberg, T. The devil in the detail: harmful seaweeds are not harmful to everyone. *Glob. Change Biol.* **21**, 1381–1382 (2015).
- Lyons, D. et al. There are no whole truths in meta-analyses: all their truths are half-truths. *Glob. Change Biol.* **22**, 968–971 (2016).
- Thomsen, M. S., Wernberg, T., South, P. M. & Schiel, D. R. To include or not to include (the invader in community analyses)? That is the question. *Biol. Invasions* **18**, 1515–1521 (2016).
- Thomsen, M. S., Wernberg, T., South, P. M. & Schiel, D. R. in *Seaweed Phylogeography* (eds Hu, Z. M. & Fraser, C.) 147–185 (Springer, 2016).
- South, P. M. et al. Transient effects of an invasive kelp on the community structure and primary productivity of an intertidal assemblage. *Mar. Freshw. Res.* **67**, 103–112 (2016).
- Anton, A. et al. Global ecological impacts of marine exotic species. PANGAEA <https://doi.org/10.1594/PANGAEA.895681> (2019).
- Hurlbert, S. H. Pseudoreplication and the design of ecological field experiments. *Ecol. Monogr.* **54**, 187–211 (1984).
- Sol, D., Vila, M. & Kühn, I. The comparative analysis of historical alien introductions. *Biol. Invasions* **10**, 1119–1129 (2008).
- Kumschick, S. et al. Ecological impacts of alien species: quantification, scope, caveats, and recommendations. *Bioscience* **65**, 55–63 (2014).
- Kochmann, J., Buschbaum, C., Volkenborn, N. & Reise, K. Shift from native mussels to alien oysters: differential effects of ecosystem engineers. *J. Exp. Mar. Biol. Ecol.* **364**, 1–10 (2008).
- Ruesink, J. L. et al. Introduction of non-native oysters: ecosystem effects and restoration implications. *Annu. Rev. Ecol. Syst.* **36**, 643–689 (2005).
- Bateman, D. C. & Bishop, M. J. The environmental context and traits of habitat-forming bivalves influence the magnitude of their ecosystem engineering. *Mar. Ecol. Prog. Ser.* **563**, 95–110 (2017).
- Schwindt, E., Bortolus, A. & Iribarne, O. O. Invasion of a reef-builder polychaete: direct and indirect impacts on the native benthic community structure. *Biol. Invasions* **3**, 137–149 (2001).
- Wang, Q. et al. Invasive *Spartina alterniflora*: biology, ecology and management. *Acta Phytotaxon. Sin.* **44**, 559–588 (2006).
- Thomsen, M. S. et al. A meta-analysis of seaweed impacts on seagrasses: generalities and knowledge gaps. *PLoS ONE* **7**, e28595 (2012).
- Romero, G. Q., Gonçalves-Souza, T., Vieira, C. & Koricheva, J. Ecosystem engineering effects on species diversity across ecosystems: a meta-analysis. *Biol. Rev.* **90**, 877–890 (2015).
- Guy-Haim, T. et al. Diverse effects of invasive ecosystem engineers on marine biodiversity and ecosystem functions: A global review and meta-analysis. *Glob. Change Biol.* **24**, 906–924 (2018).
- Thomsen, M. S. et al. Secondary foundation species enhance biodiversity. *Nat. Ecol. Evol.* **2**, 634–639 (2018).
- Wallace, B. C. et al. Open MEE: Intuitive, open-source software for meta-analysis in ecology and evolutionary biology. *Methods Ecol. Evol.* **8**, 941–947 (2017).

Competing interests

The author declares no competing interests.

Additional information

Supplementary information is available for this paper at <https://doi.org/10.1038/s41559-020-1117-6>.

Correspondence and requests for materials should be addressed to M.S.T.

Reprints and permissions information is available at www.nature.com/reprints.

Publisher's note Springer Nature remains neutral with regard to jurisdictional claims in published maps and institutional affiliations.

© The Author(s), under exclusive licence to Springer Nature Limited 2020