A meta-analysis reveals global patterns of sediment effects on marine biodiversity

Rafael A. Magris^{1,2}, Natalie C. Ban²

¹ Chico Mendes Institute for Biodiversity Conservation, Brazilian Ministry of Environment, Brasilia, Brazil

² School of Environmental Studies, University of Victoria, Victoria, Canada

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ABSTRACT

Aim

Sediment disturbances are important threats affecting marine biodiversity, but the variety of biological responses have not yet been synthesized. Here, we collate all available information to compare the extent of impacts across different taxonomic groups, habitat types, and pathways of impact (light attenuation, suspended sediment, and sedimentation).

Location

Global

Time period

Data collected from 1979 to 2017

Major taxa studied

Coral, fish, seagrass, sponge, macroalgae, ascidian, bryozoan, crustacean, echinoderm, mollusc, polychaeta

Methods

We used meta-analyses to evaluate the effects of sediments across 842 observations found in 110 publications. We also evaluated some of the biological and methodological factors that could explain the variable effects observed in different studies.

Results

We found a significant negative effect of sediments on behavioural responses of species, reproduction and recruitment processes, organism's morphology, physiology, community abundance and diversity, and species interactions. In contrast, the overall effect on abundance of individual species was statistically non-significant and there was a strong positive effect on abundance for sponge and polychaete species. Many individual studies described physiological effects on coral reefs, but effects on diversity of soft-bottom and coral reef communities were particularly detrimental. Phototrophic species were generally more negatively impacted by sediments than heterotrophs, driven by strong physiological responses in crustose coralline algae and seagrass. Additionally, species with limited mobility were more vulnerable to sediment disturbances than highly mobile species. Sedimentation alone triggered more consistently negative effects on most biological responses than light depletion and suspended sediments. We found evidence for increased impacts on community diversity when more than one pathway of impact was present, indicating that these disturbances can disrupt whole ecosystems.

Main conclusions

Our meta-analysis for the first time provided strong quantitative support of negative effects of sediments on marine biodiversity. Taxonomic groups, habitat types, and life history characteristics were most influential in determining biological responses to sediment disturbances, highlighting the importance of an ecosystem-based approach when fully accounting for the impacts of sediments.

INTRODUCTION

Increased sediment discharge to the ocean and resuspension events in nearshore and coastal waters represent major threats to marine biodiversity worldwide (Thrush *et al.*, 2004; Syvitski *et al.*, 2005; Crain *et al.*, 2009; Doney, 2010). Due to the ever-increasing pressure on land from activities such as logging and agriculture (Venter *et al.*, 2016), sediment runoff and rate of sedimentation have increased by one to two orders of magnitude in many parts of the world (Thrush *et al.*, 2004). Anthropogenically enhanced soil erosion is predicted to be increasing by 2.3 billion metric tons annually (Syvitski *et al.*, 2005), which intensifies the amount and rate of sediment delivery entering coastal zones in the aftermath of rainfall events (McCulloch *et al.*, 2003; Fabricius, 2005; Kroon *et al.*, 2012). Although the damming of rivers constrains the delivery of sediments to the sea (Walling, 2006), extensive human land use significantly alters sediment-loading regimes (Thrush *et al.*, 2004). Moreover, point sources of pollutants (e.g. mining) have affected the quality and the quantity of the downstream flow of suspended sediment locally in many places (Galván *et al.*, 2016; Magris *et al.*, 2019), further compounding the problem. Anthropogenic activities along the coastal fringe (e.g. urbanization) have also led to an increase in coastal erosion (Mentaschi *et al.*, 2018), hastening the flow of sediments to coastal waters. Additionally, expansion of shipping and port activities require an increase in dredging services (e.g. Barletta *et al.*, 2016; Jones *et al.*, 2016; Fraser *et al.*, 2017), which also cause episodic events of elevated turbidity associated with dumping of dredged sediments over coastal waters. Given the extended degradation of marine ecosystems as a consequence of increased inputs of sediments (Wilber & Clarke, 2001; Eyre & Ferguson, 2006; De'Ath & Fabricius, 2010; Bessell-Browne *et al.*, 2017b; Humanes *et al.*, 2017a), the number of studies exploring the impacts of sediment pollution has proliferated considerably in recent years (Fig. 1).

Figure 1. Chronological trend in the number of publications assessing the impact of sediment-related stressors on marine biodiversity. The cumulative number of publications represents the total of publications selected for full text reading and potential use in the meta-analysis ($n = 820$); see Material and Methods section for details on how they were selected.

Several pathways or mechanisms that underlie sediment impacts have been proposed to understand the biological effects on marine species, including reduction in light availability (Bessell-Browne *et al.*, 2017b), elevated suspended sediment concentrations (Jones *et al.*, 2016), and increased rates of sedimentation (Jones *et al.*, 2015). A decrease in light penetration has been frequently perceived as the most influential proximate stressor on autotrophs (Jones *et al.*, 2016). Sediments reduce or alter irradiance levels and restrict photosynthesis, which negatively affect species physiology (Bach *et al.*, 1998; Anthony, 2006) and subsequently reduce energy for growth and reproduction (Fabricius, 2005; Collier *et al.*, 2012; Jones *et al.*, 2016). However, reduction in light availability can also disrupt foraging activities or decrease foraging efficacy of heterotrophic organisms that rely on visual cues to detect prey (Wenger *et al.*, 2012; Kjelland *et al.*, 2015). The detrimental impacts of constrained light availability have been mostly measured in corals (Bessell-Browne *et al.*, 2017b), seagrass (Erftemeijer & Robin

Lewis, 2006), macroalgae (Eriksson & Johansson, 2005), and fish assemblages (Kjelland *et al.*, 2015). Light attenuation may also exacerbate abiotic conditions with negative effects on marine biota (Ban *et al.*, 2014; Bessell-Browne *et al.*, 2017b).

Despite ample emphasis on light attenuation, much of the literature has focused on quantifying biotic responses to increased suspended sediment concentrations and sedimentation with only little attention paid to combined effects (e.g. Pineda *et al.*, 2017). Suspended sediment in the pelagic domain can lead to serious physical damage associated with sediment abrasion, clogging of feeding mechanisms, tissue injuries and necrosis (Rogers, 1990; Fabricius, 2005; Erftemeijer *et al.*, 2012b). Deposition of increased amounts of sediment on the seafloor causes smothering following burial by sediments (Fabricius & Wolanski, 2000; Liu *et al.*, 2015; Humanes *et al.*, 2017a). With an increase in suspended sediment concentration and deposition, alterations of the physical and chemical environment can reduce suitability of habitats, resulting in physical displacement of organisms or forcing them to migrate to other areas (Waycott *et al.*, 2009; Pulfrich & Branch, 2014; Barletta *et al.*, 2016). The grain size and geochemical properties of sediments also inhibit fertilization success and larval development of some marine fishes and invertebrates exhibiting a biphasic life cycle, suggesting that sediment loads can directly affect recruitment (Erftemeijer *et al.*, 2012a; Ricardo *et al.*, 2015, 2016; Humanes *et al.*, 2017b). Lastly, sediment deposition increases the energy expended for the removal of particles and other activities to cope with stress, meaning that less energy is available for growth and reproduction (Bell *et al.*, 2015; Bessell-Browne *et al.*, 2017a).

Several qualitative reviews of ecological impacts of light attenuation, suspended sediment and sedimentation on specific biological communities have been published (Rogers, 1990; Airolidi 2003; Fabricius, 2005; Erftemeijer & Robin Lewis, 2006; Erftemeijer *et al.*, 2012b; Bell *et al.*, 2015; Jones *et al.*, 2015, 2016). The main variation in biological responses are hypothesised to be explained by the following: (i) phototrophic corals will be more sensitive

to light attenuation than heterotrophic corals (e.g. Erftemeijer *et al.*, 2012b); (ii) early life-history stages will be more sensitive to elevated suspended sediment levels than later life-history stages in fish (e.g. Wenger *et al.*, 2017); and (iii) highly mobile species will be more capable of avoiding increased sedimentation than sessile species in soft-sediment communities (e.g. Fraser *et al.*, 2017; Gomes *et al.*, 2017), making sessile species particularly susceptible to increased rates of sedimentation. However, the current evidence base for marine ecosystem-scale impacts of sediments is scattered and incomplete (Brodie *et al.*, 2012; Fraser *et al.*, 2017; Wenger *et al.*, 2017), requiring synthesis, and a better understanding of the variability or generality of biological responses to support more rigorous assessment of the environmental impact of sediment disturbances.

Here we apply formal meta-analysis to provide the most comprehensive impact assessment of sediments on marine biodiversity to date (1979-2017). Our goal was to evaluate the strength of evidence for the hypotheses mentioned above across a range of coastal marine ecosystems around the world based on all available evidence. Our study also complements and expands previous meta-analyses by Wenger *et al.* (2017) by accounting for a wider range of taxonomic groups (e.g. corals, seagrasses, sponges) and multiple sources of sediments (e.g. land-based activities, natural disturbances) instead of only considering impacts of dredging on fish species. Specifically, we tested whether effects on early developmental stages of species that prevent their successful recruitment are the foremost negative consequences of sediment disturbances on marine biota in comparison to other responses (e.g. physiological processes). To examine the variability associated with life history characteristics, we tested for differences between broad taxonomic groups and habitat types, and explored whether sediments have a larger effect on autotrophs vs. heterotrophs and on sessile species vs. mobile species. Because the effect of sediments can be context-dependent, we also evaluated whether effects of sediments depended on the methodological approaches used in the reviewed studies. Finally,

when assessing the strength of the sediment-response relationship, we investigated whether effects are larger when two or more pathways of impact (i.e. light attenuation, elevated suspended sediment, and sedimentation) acted in combination.

MATERIALS AND METHODS

We investigated the magnitude of effects of sediments, including all categories of responses, ranging from individual effects at a species level (e.g. physiological and behavioural alterations that occur within a lifetime of an organism) to community-level indicators for the structure and functioning of marine ecosystems (e.g. community abundance and diversity) (Table 1). For each category of response, we tested whether specific factors were possible drivers of variation in responses across studies, including biological and methodological factors. We then assessed the possibility of publication bias within each category of response.

Publication search and selection

Publications included in this meta-analysis (1979-2017) were collected through searches in the Web of Science (All Databases; Thomson Reuters 2017) database for all peer-reviewed articles published before 2017 using the following combination of key words: (“sediment*” OR “turbid*”) AND [“coral reef” OR “seagrass” OR “coralline algae” OR “rhodolith” OR “algae bed” OR “seaweed” OR “macroalgae” OR “fish” AND (“marine” OR “coast*”) OR “invertebrate” AND (“marine” OR “coast*”) OR “phytoplankton” AND (“marine” OR “coast*”) OR “zooplankton” AND (“marine” OR “coast*”)]. The combinations of search terms covered publications studying effects of sediments in biotic components of marine ecosystems, resulting in 3,235 publications that were imported into Endnote (Thomson Reuters, New York, NY, USA, 1988-2012). From this whole universe of publications, we first scanned primary titles to remove the ones considered outside the scope of our analysis (e.g. assessing sediment in a geological or geochemical context). We then manually assessed all

abstracts of the remaining publications to further select those that examined the effect of the stressor of interest on any response variable. This was done by searching for the following key words at each abstract: “effect”, “response”, “impact”, and “stress”. A pool of 820 publications were finally selected for full-text screening. Eligible publications for final analysis were included only if they (i) met all the criteria for inclusion in a meta-analysis (i.e. reporting sample sizes, means, and measures of variation around the means); (ii) explicitly controlled the effects of confounding variables (e.g. examining individual effects of sediments without the interaction of other environmental parameters or chemical contaminants); and (iii) provided a relevant comparison (e.g. design involved measurements of both an affected treatment and a control sample – i.e. without sediment or with sediment at background levels).

We further supplemented the relevant articles with a manual search in key review publications, and in the reference lists of the publications selected as above. Review publications were excluded. We considered publications conducting experiments and performing field observations. This resulted in a total number of 110 publications for data extraction.

Data extraction

For each selected publication, we considered an observation as every single and independent measurement of a biological response obtained at a treatment and a control level (hereafter, a ‘study’). All publications except one reported data on multiple observations. For example, many publications performed separate experiments as different categories of response; we considered each one of them as independent studies because the data for each category of response was analysed in separate meta-analyses. Many publications also tested multiple species in each experiment, even within the same category of response. We also handled species-specific measurements as independent studies because it allowed us to explore responses across a broader range of species. However, some publications performed multiple

observations (potentially correlated) for the same category of response as matched (paired) groups and for the same species, or had multiple treatment levels sharing a single control group. We took account of this in the meta-analysis (see section ‘Data analysis’ below). If species-specific responses were provided as well as multi-species measurements (e.g. community abundance), we then excluded the combined response and included only the more specific ones, preventing double-counting.

Field-based publications typically had multiple sampling sites, which we considered independent studies as long as the distance between them exceeded 1 km, in order to avoid spatial autocorrelation and pseudo replication. Reported lengths of experiments or observations ranged from two minutes to sixteen years (mean of 20.25 months). Following previous meta-analytical approaches (e.g. Ban *et al.*, 2014), if the experiment reported a time series data on the response, we used the last time point in the analyses. Sediment impacts generally accumulate over time, giving us an estimate of sediments’ long-term effects, and also allowing us to avoid using many non-independent estimates. However, in a few studies (n=9), the experiment reported full mortality before the last time point, and we then used the last nonzero values. If the experiment included a recovery phase, we disregarded this part of the experiment and reported only the last point of exposure to the sediment. Finally, if publications had before – after and impact – control approaches, we included only the after situation. We extracted 1,553 observations or studies across the 110 publications.

To explore the whole variety of biological effects of sediments, we assigned all studies into one of the eight categories of response as defined in Table 1: behaviour, reproduction and recruitment, morphology, physiology, single-species abundance, community-level abundance, community diversity, and species interaction. We assigned each observation into one of these categories according to the primary author's interpretation of the assessed study and our definition (Table 1). Reproduction and recruitment grouped specific responses reported within

the early developmental stages of marine species (sperm, egg, embryo, larvae, and juveniles) regardless of whether studies examined behavioural, physiological, mortality, or any other direct and indirect effect of sediments. However, to examine whether early life history stages had larger negative effects than juveniles, we also recalculated the effect sizes for this category of response omitting the effects measured on juveniles. When possible, we extracted means, standard errors or standard deviations and sample sizes directly from the articles (as tables or in the text). However, almost all publications reported results in graphical form (n=106). In those cases, we used WebPlotDigitizer (Rohatgi, 2011) to extract the underlying data and populate our database.

We also recorded the following study characteristics to examine the role played by potential moderators in modifying the effect of sediments: (i) taxonomic group; (ii) type of habitat assessed or from where species used in the experiment were collected; (iii) primary nutritional mode of the species (i.e. phototrophic or heterotrophic); (iv) mobility mode of the species (i.e. sessile, weakly mobile or mobile); (v) type of study (i.e. laboratory experiments or field-based studies); (vi) the physical proximate stressor identified as causal pathways of impact (Jones *et al.*, 2016); (vii) duration of exposure to sediments or length of sediment stress events; and (viii) intensity of the stressor (expressed as a difference between treatment and control conditions). With respect to pathways of impact, studies were categorized according to the way exposure was measured. Studies focusing on increased suspended sediments measured/simulated concentrations of particle matter in the water column to characterise the impact, usually expressed as reduced feeding activity or as a change in the energy balance of species when processing or transporting intercepted sediments (e.g. cleaning processes). Studies that focused on impacts associated with light attenuation documented changes in quality or quantity of light, with effects such as reduced autotrophy and hypoxia. Studies that estimated sediment deposition on the seafloor were classified as sedimentation, with damage

arising from smothering or impacts derived from the physical removal of organisms. Some studies (n=251) used a combination of the three pathways of stress response to quantify the biological effects. Understanding the sole and combined effect of these pathways is crucial to evaluate whether there are interactive effects and increased impacts when more than one is present. Lastly, we also recorded the geographical location of studies and the source of sediments mentioned as the cause of impact for field-based studies or whether the experiment was intended to mimic any specific source of sediments.

Meta-analysis

The effect of sediment on marine biodiversity was measured for each study using Hedges' d as an estimate of the unbiased standardised mean difference (i.e. the effect size) (Equations 1-3). The primary advantage of using it is that d has only a slight bias due to small sample sizes (Gurevitch *et al.*, 2001). Negative Hedges' d effect sizes imply a reduction in the individual measurement of the treatment group (i.e. exposed to sediments) as compared to control conditions, and vice versa.

$$d = \frac{\bar{X}^t - \bar{X}^c}{S} J, \quad (1)$$

where $\bar{X}^t$ equals the mean of sediment treatment, $\bar{X}^c$ is the mean for the control, S is the pooled standard deviation, and J is a weighting factor that corrects for bias due to small sample size. S and J are calculated as the following:

$$S = \sqrt{\frac{(N^t-1)(s^t)^2 + (N^c-1)(s^c)^2}{N^t + N^c - 2}}, \quad (2)$$

$$J = 1 - \frac{3}{4(d_f)-1}, \quad (3)$$

where N^t is the sample size for the sediment treatment, N^c is the sample size for the control, s^t and s^c are the standard deviations of the treatment and control groups, respectively, and d_f is the degrees of freedom used to calculate S .

We also calculated the bias-corrected 95% bootstrapped confidence interval (CI) with 9999 iterations. We regarded a mean effect size to be significant when its 95% confidence interval (CI) did not overlap zero. For the cases in which effect sizes could not be considered independent (i.e. studies sharing the same control), we calculated a synthetic effect size as the average of individual effect sizes, and a variance that took into account the correlation among different treatments (Borenstein *et al.*, 2009). To correct for the type of duplication related to observations within the same category of response and for the same species (e.g. studies with paired groups), we calculated a combined effect and pooled variation for each set of pseudoreplicated values (Borenstein *et al.*, 2009). The corrections required for potential non-independence of these observations reduced our initial dataset of 1,553 studies to 842 studies across 110 publications. To be able to compare the effect sizes correctly, we changed the sign of the effect size estimates derived from biological measures where a higher value in a treatment signified greater impact, e.g. percentage of abnormal development or percentage of mortality (see Table 1 for all metrics that were standardised to obtain a common direction). All analyses were conducted in R with the *metafor* package (Viechtbauer, 2010) and DerSimonian–Laird estimator (DerSimonian & Laird, 1986). Supporting Information S1 provides an account of how we estimated the effect size and variance for studies with different designs.

To estimate the overall mean effect of sediment disturbances on each category of response, we performed random effects meta-analysis. We chose to use random effect models to account for differences across the wide range of species included in the analysis within each category of response, in addition to the variety of methodological approaches used. Random effect models account for this true variation among studies and weight the effect size estimates by their inverse variances, such that studies with larger sample sizes were given more weight (Borenstein *et al.*, 2009), increasing the precision of summary effects. We used *Q*-test to assess

heterogeneity in effect sizes for each category of response. A significant Q -test statistic indicates there is heterogeneity within the mean effect size.

Within each category of response, we also carried out three analyses to evaluate evidence of publication bias. Publication bias appears whenever the strength or direction of the results of published studies differ from those of unpublished studies (Møller & Jennions, 2001). First, we examined potential publication bias by assessing funnel plots' asymmetry around the mean effect size followed by fill and trim procedures. This technique provides an estimate of how the overall effect size would change if we were able to integrate all missing studies (Jennions & Møller, 2002). A visual inspection of a funnel plot reveals if there is asymmetry around the mean effect size. Second, we evaluated the number of studies that would need to be added to change the results of the initial model for each category of response from significant to non-significant, i.e. the Rosenthal's fail-safe number (Rosenthal, 1991). Finally, we used Kendall's rank correlation test to compare the standardized effect size of the raw data and the sample size. Significant p -values might indicate publication bias whereby studies with small sample size are only published if they show large effect sizes.

Moderator analyses

We carried out subgroup mixed effects meta-analyses, allowing the establishment of nesting groups, to understand the role played by moderators in the effects estimated in different studies. For each category of response, the following moderators were tested: taxonomic group, habitat type, nutritional mode, mobility mode or movement type of species, pathway of impact, study type, exposure duration, and intensity of exposure. Because exposure duration and intensity of stressor had a large variation across observations, we log₁₀-transformed them to increase linearity. Mixed effect models were used with fixed (i.e. all studies within a group share a common effect size due to an identical moderator) and random effects to account for differences across studies, assuming they do not share a common mean effect but that there is

random variation among studies, in addition to within-study sampling variation (Borenstein *et al.*, 2009). The models also considered the hierarchical dependence in our data due to cases where multiple observations were gathered from the same study.

The importance of each moderator was assessed using a Q -test. To examine the variation in effects of sediments within each category of response, we compare mean effect sizes between *a priori* defined group of studies (e.g. phototrophic organisms and heterotrophic organisms). Effect sizes were considered significantly different from zero if their 95% CIs did not include zero (Borenstein *et al.*, 2009). To quantify the heterogeneity of effect sizes, we examined the p -value of Q between groups to find out if there was a significant difference, i.e. the mean effect size observed was related to the moderator tested. We reported results for subgroup analyses for all categories of response, as long sufficient data were available (i.e. subgroups with more than $n=5$ studies).

RESULTS

Description of publications

The 110 publications (published between 1979 and 2017) covered marine ecosystems of all continents containing tropical, subtropical and temperate regions (there were no publications conducted in the Arctic, sub-Arctic, Antarctic, and sub-Antarctic waters; Fig. 2), with some geographical bias towards the Great Barrier Reef, on the north-east coast of Australia (30 publications; 30 publications; for list of data sources, see Supporting Information Appendix S1 and for details on publications, see Table S1). 54.9% of the 1,553 observations in the dataset were made in coral reef habitats. The remaining observations were conducted in other habitats, including rocky reefs (23.4%), seagrasses (10.7%), pelagic habitats (4.8%), soft-bottom substrata (3.7%), and crustose coralline algae forming rhodolith beds (2.5%). When examining observations across different taxonomic groups, Cnidaria

species were overrepresented, accounting for about 28.9% of the observations, whereas studies focusing on macroalgae made up about 16.8% of all observations. Studies related to sponge and fish species were relatively more represented (about 17.6% and 14.9% of all observations) compared to seagrasses (10.8%) and other invertebrates such as Mollusc (3.5%) and Polychaete (1.7%). Observations on Ascidian, Bryozoan, Crustacea, and Echinodermata were very scarce and summed up 5.8% of all observations. No studies on effects of sediments on plankton assemblages met our criteria for inclusion in the meta-analysis.

Figure 2 Locations of the sampling points from publications investigating the effects of sediments on marine biodiversity. Each colour represents a different publication (n=110).

Sediment disturbances have been substantially documented via experiments with laboratory-based publications (n=66; 60% of articles). Most publications considered terrestrial run-off associated with land-based activities (such as deforestation, agriculture and urbanisation) and dredging as the main source of disturbances (32 and 19 publications, respectively, which correspond to 29 and 17% of articles; Fig. 3). Disturbances derived from natural processes (not considered to be influenced by anthropogenic activities) such as

364 resuspension and discharges related to natural erosion and flooding were considered as the
 365 main source of stress for 11 publications (10% of articles; also mostly supported by
 366 experiments). Field-based research was mostly conducted to address impacts of aquaculture,
 367 land-based mining and coastal development, but they represented only 10 publications (9% of
 368 articles). The remaining publications addressed a combination of disturbances (n=13; 11.8%
 369 of articles), ocean-based mining (n=2; 1.8% of articles), or did not specify any driver of
 370 disturbance (n=13; 11.8% of articles).

371

372 **Figure 3** Number of publications evaluating different drivers acting as sources of
 373 sediment disturbances. Dark grey represents studies conducted in a laboratory and black
 374 indicates studies performed in the field. Mix refers to combinations of any of the other drivers.
 375

376 Overall effects of sediments on different categories of response

377 As hypothesized, a meta-analysis across all studies together showed that sediment
 378 stressors had a significant negative effect on marine biodiversity (weighted overall mean effect
 379 of -0.667, 95% CI $\pm$ 0.069). The number of studies for each category of response ranged from
 380 21 (behaviour) to 357 (physiology). All categories of response except for single-species

abundance were significantly negatively affected by sediment disturbances (Fig. 4). The negative effect of sediment disturbances was most pronounced for community diversity, such as decline in species richness, decrease in diversity, or changes in community evenness. The effects on species physiology and on reproduction and recruitment were also clear and stronger than the overall mean effect; their mean effects were less than the lower bound of the 95% CI for the overall mean effect. When effects on juveniles were excluded from the meta-analysis on reproduction and recruitment, effects on early life history stages had similar magnitudes (1.12 ± 0.19) to effects on community diversity (1.16 ± 0.49). The estimates on the most sensitive responses were followed by a slightly less negative effect on species interactions. Negative mean effect for species morphology and community abundance were detected to have similar magnitudes to the overall mean effect (i.e. estimated mean within the confidence intervals derived from the complete data set). We identified a smaller negative effect for behavioural responses to sediments. There was significant heterogeneity in all categories of response (behaviour: $Q = 138.05$, d.f. = 20; $p < 0.05$; reproduction and recruitment: $Q = 1681.73$, d.f. = 140; $p < 0.05$; morphology: $Q = 422.88$, d.f. = 33; $p < 0.05$; physiology: $Q = 3151.14$, d.f. = 356; $p < 0.05$; single-species abundance: $Q = 221.82$, d.f. = 30; $p < 0.05$; community abundance: $Q = 1557.31$, d.f. = 183; $p < 0.05$; community diversity: $Q = 277.46$, d.f. = 35; $p < 0.05$; species interaction: $Q = 444.82$, d.f. = 36; $p < 0.05$).

Figure 4 The effects of sediment disturbances on different categories of response of marine biodiversity (see Table 1 for definitions) from random-effects meta-analyses. The mean effect sizes $\pm$ 95% confidence intervals (CI) are shown for separate analyses on each response. Solid black line indicates no effect and numbers the sample size. *The mean effect size is significant when the 95% CI does not overlap zero.

Funnel plots for the relationship between effect size of response categories and standard error were slightly asymmetrical only for single-species abundance and morphology (Supporting Information Figure S1). However, the adjusted effect sizes, calculated using trim and fill procedures, would not qualitatively change the results from the original estimates (Table S2). Rosenthal's fail safe numbers were high for all categories of response, except for abundance at species level, which were smaller than expected without publication bias. Kendall's rank correlation tests did not show significant relationships between effect sizes and sample sizes, indicating absence of publication bias (Table S3; see Supporting Information S3 for more details on the publication bias assessment for all categories of response).

Moderator analyses: examining variation in responses to sediment disturbances

Biological factors (taxonomic group, habitat types, nutritional mode, and movement

type) and pathways of impact were significant moderators for most categories of response (Table 2). Conversely, methodological factors (e.g. duration of exposure to sediments) did not have consistent effects on mean effect size. For example, we found significant differences between the effects observed in laboratorial and field-based studies for only one category of response (morphology).

Effects of sediments on different taxonomic groups

Taxonomic group was a significant moderator for most categories of response; only effects on community diversity and morphology did not depend on the taxonomic identity of biota (Table 2). Molluscs were the only taxonomic group with a significant negative effect size for behavioural effects (Fig. 5a). All taxonomic groups had significant negative effect sizes for reproduction and recruitment (Fig. 5b). The effect sizes on non-coral invertebrates (e.g. echinoderms and sponges) were the most negative. Physiological effects were nonsignificant for fish and molluscs, with macroalgae and seagrass showing significantly large negative effects (Fig. 5c). For abundance, we detected the only significant positive effects found in our study: sediments had positive effects on abundance at both species and community level in studies with polychaeta, and positive effects on abundance at the community level in studies with sponge (Fig. 5d-g). In contrast, we found the most pronounced negative effects for community abundance of cnidarians, seagrasses, and mixed invertebrates. For species interaction, sediments had a significant negative effect on fish and mollusc species, with the most negative effects on the latter (Fig. 5h).

Figure 5 Effect sizes (Hedges' d) comparing impacts on each taxonomic group (y-axis) in relation to undisturbed controls. Values are mean and bias-corrected bootstrapped 95% confidence intervals (CI) for separate analyses on each category of response (a-h panels) that had a significant influence of different taxonomic groups. The number of studies in each analysis is shown in parentheses. No mean effect size indicates there were too few studies for a comparison ($n < 5$). The vertical solid line indicates no effect. Values > 0 indicate a positive effect of sediments on the respective response, and values < 0 indicate a negative effect of sediments on the respective response. *The mean effect size is significant when the 95% CI does not overlap zero.

Effects of sediments on different habitats

Habitat type was a significant moderator of all categories of response except for behaviour (Table 2). For reproduction and recruitment, all habitat types (i.e. crustose coralline algae, pelagic, coral reef, and rocky reefs) had significant negative effects (Fig. 6a), with studies conducted in crustose coralline algae beds, pelagic habitats, and rocky reefs being particularly sensitive to sediments. For morphology, negative effect sizes on coral reefs were significant, whereas strong positive effects were identified for seagrass, but nonsignificant (Fig. 6b). While we could not detect significant negative effects for physiological responses in pelagic, rocky reef, and soft-bottom habitats, strong negative significant effects were observed for seagrasses and crustose coralline algae beds (Fig. 6c). For community abundance, the

clearest difference was between the strong negative significant effects observed in coral reefs, seagrasses, and soft-bottom habitats and the nonsignificant effects observed in rocky reefs (Fig. 6d). For community diversity, we detected significant negative effects for coral reefs and soft-bottom habitats, with effects on the later being the most negative (Fig. 6e). For species interaction, we found that sediments had a significant negative effect on coral reefs (Fig. 6f).

Figure 6 Effect sizes (Hedges' d) comparing impacts on each habitat type (y-axis) in relation to undisturbed controls. Values are mean and bias-corrected bootstrapped 95% confidence intervals (CI) for separate analyses on each category of response (panels a-f) that had a significant influence of different habitat types (i.e. crustose coralline algae - CCA, coral reef, pelagic habitat, rocky reef, seagrass, and soft-bottom). The number of studies in each analysis is shown in parentheses. No mean effect size indicates there were too few studies for a comparison ($n < 5$). Single-species abundance panel was omitted because only rocky reef habitats had enough number of studies. The vertical solid line indicates no effect. Values > 0 indicate a positive effect of sediments on the respective response, and values < 0 indicate a negative effect of sediments on the respective response. *The mean effect size is significant when the 95% CI does not overlap zero.

Effect of sediments on different nutritional mode of species

Nutritional mode was a significant moderator for five categories of response: behaviour, reproduction and recruitment, physiology, single-species and community abundance (Table 2). These analyses revealed a noteworthy result: phototrophic organisms

were more strongly affected by sediments than heterotrophic organisms across the majority of responses (Fig. 7a-d). Effects on heterotrophic organisms were both statistically significant and larger than phototrophic ones only for reproduction and recruitment, despite a large variability in effect sizes (Fig. 7a).

Figure 7 Effect sizes (Hedges' d) comparing impacts on each nutritional mode of species (y-axis) in relation to undisturbed controls. Values are mean and bias-corrected bootstrapped 95% confidence intervals (CI) for separate analyses on each category of response (panels a-d) that had a significant influence of different nutritional modes. The number of studies in each analysis is shown in parentheses. No mean effect size indicates there were too few studies for a comparison ($n < 5$). Behaviour panel was omitted because only heterotroph had enough number of studies. The vertical solid line indicates no effect. Values > 0 indicate a positive effect of sediments on the respective response, and values < 0 indicate a negative effect of sediments on the respective response. *The mean effect size is significant when the 95% CI does not overlap zero.

Effect of sediments on different types of movement of species

Movement type moderated the magnitude of effect sizes in our observations in five categories of response: behaviour, reproduction and recruitment, physiology, community abundance, and community diversity (Table 2). Agreeing with previous findings, sediment effects were particularly evident for sessile and weakly mobile species across all these

categories of response (Fig. 8a-e). These two types of movement of species had significant negative effects in all categories. There was a significant negative effect on mobile species for physiology (Fig. 8c).

Figure 8 Effect sizes (Hedges' d) comparing impacts on each movement type of species (y-axis) in relation to undisturbed controls. Values are mean and bias-corrected bootstrapped 95% confidence interval (CI) for separate analyses on each category of response (panels a-e) that had a significant influence of different movement types. The number of studies in each analysis is shown in parentheses. No mean effect size indicates there were too few studies for a comparison ($n < 5$). The vertical solid line indicates no effect. Values > 0 indicate a positive effect of sediments on the respective response, and values < 0 indicate a negative effect of sediments on the respective response. *The mean effect size is significant when the 95% CI does not overlap zero.

Effect of sediments depending on the pathway of impact

The effect of sediments differed significantly between the pathways of impact for all categories of response except for abundance at species and community level (Table 2). Sedimentation had significant and strong negative mean effects on several responses (e.g. morphology, physiology, and species interaction, see Fig. 9b, c and e). All pathways of impact had significant negative mean effects on reproduction and recruitment, and physiology (Fig. 9a and c). We detected stronger negative mean effects when there was a combination of

pathways of impact than those experiencing individual pathways only for community diversity (labelled as “mix” in Fig. 9d).

Figure 9 The influence of different pathways of impact (y-axis) on the effects (Hedges' d) of sediments in relation to undisturbed controls. Values are mean and bias-corrected bootstrapped 95% confidence intervals (CI) for separate analyses on each category of response (panels a-e) that had a significant influence of different pathways of impact. The number of studies in each analysis is shown in parentheses. No mean effect size indicates there were too few studies for a comparison ($n < 5$). Behaviour panel was omitted because only suspended sediment had enough number of studies. The vertical solid line indicates no effect. Values > 0 indicate a positive effect of sediments on the respective response, and values < 0 indicate a negative effect of sediments on the respective response. *The mean effect size is significant when the 95% CI does not overlap zero.

Effect of methodological variation in responses to sediments

We did not detect significant differences between field and laboratory studies for all categories of response except for morphology (Table 2). For morphology, studies conducted in the laboratory had a significant negative effect (Supporting Information S4 and Fig. S2). We detected a significant linear relationship between both intensity and duration of exposure and the mean effect size on community abundance with larger negative effects when studies had higher concentrations of the stressor, or when studies were conducted over longer periods

(Supporting Information S4 and Fig. S3). We also found a significant relationship between the duration of exposure and the mean effect size on species physiology (Supporting Information S4 and Fig. S4).

DISCUSSION

Our meta-analyses offer the first quantitative synthesis of the effects of sediments on marine biodiversity worldwide, and allowed us to identify important research gaps. Although our results indicated that the effects on some responses were diverse (e.g. sponge and polychaete species responded positively to sediment increases in terms of abundance), they confirmed that sediments often have a detrimental impact on many marine organisms, with stronger negative consequences for community diversity, reproduction and recruitment processes, and physiological functions. Our results revealed considerable ecological effects on both soft-bottom and coral reef community structures. As expected, early developmental stages of species were vulnerable to sediment disturbances, thus effects on reproduction and recruitment were consistently strong and significant across all taxonomic group and habitat type combinations. Physiological responses were mostly driven by strong negative effects on autotrophs such as crustose coralline algae beds and seagrasses. This pattern was also highlighted in the differences in taxonomic groups, where photosynthesizing species (e.g. seagrasses, macroalgae) were particularly susceptible to sediments across other categories of response. Our analyses also supported the hypothesis that sessile and weakly mobile species are the most susceptible to sediments across a range of response variables. Lastly, we found a large variation in response to sediments that was mostly driven by differences between taxonomic groups, habitat types, life history characteristics and pathways of impact, with interactions between light, suspended sediment, and sedimentation likely to be more severe when triggering community-wide responses.

The impacts that sediments exert on coral reef communities has long been debated (e.g. Dodge & Vaisnys, 1977; Rogers, 1979; Cortés & Risk, 1985). Although our study encompasses a large variety of coral reef areas around the globe, most studies were focused on the Great Barrier Reef (GBR). This geographic bias may arise because the GBR is a World Heritage Area threatened by drivers that include sediments, the focus of continued research on pollution assessment for sediments (Brodie *et al.*, 2012), and where sediment enrichment has prevented the recovery of reefs from cumulative and multiple impacts (Fabricius *et al.*, 2014, 2016). While these biogeographic and taxonomic biases are therefore expected, this review also reveals that the scientific interest in sediment-induced responses on a large variety of marine species and habitats has greatly increased in the past two decades.

Our search for literature suggested that research on the effects of sediments has focused largely on physiological, individual-level responses of corals to sediment disturbances, in line with the general view of the literature that sediments severely interfere in the energy balance of corals (Rogers, 1990; Riegl & Branch, 1995; Fabricius, 2005; Erftemeijer *et al.*, 2012b). In contrast, some studies have now shown that variation in morphological and structural characteristics prove some coral species more resilient than others (Anthony, 2000; Sofonia & Anthony, 2008; Loiola *et al.*, 2013), reducing the extent of photophysiological stress in more resilient species. Our meta-analysis is consistent with the current literature, indicating that any potential ability of some species to benefit from sediments (e.g. obtaining alternative sources of energy) was swamped by more pronounced negative effects of sediments, such as tissue injuries associated with the increased energy expenditure of the species and a decrease in the photosynthesis activity. While understanding these species-level effects is important, we found that few studies investigated the ecological impacts of sediments at the community level (e.g. coral reef diversity), which appeared to be more negatively affected by sediments. These results

suggest the need to re-orientate research efforts on quantitative links between sediment impacts and community level measurements of diversity.

Primary producers were particularly sensitive to increased sediments. The negative effects on seagrass abundance were, in all cases, caused by reduction of light availability. High-turbidity events capable of attenuating light were suggested to impact community abundance through a decline in several seagrass species even over the short-term (e.g. Longstaff & Dennison, 1999). The stronger physiological responses on macroalgae were due to either reductions in light levels (e.g. Liu *et al.*, 2015) or enhanced sedimentation (e.g. Harrington *et al.*, 2005). Furthermore, the impacts from sediments on algae ranged from strong positive, such as studies observing species-specific proliferation of opportunistic foliose fleshy algae (Fabricius *et al.*, 2005), to strong negative, such as observations and experiments on coralline or fine filamentous forms (Reynier *et al.*, 2015), which were less tolerant to sediment-stressed conditions.

Across taxonomic groups, sediments were found to have consistent directional positive impact on sponge and polychaete species' abundance. This might be seen as an expected finding because it agrees with some studies indicating the adaptive capacity of sponge species to tolerate or resist physical impacts of sediments (Bell *et al.*, 2015; Pineda *et al.*, 2016) and demonstrating that particulate matter may also include important sources of food for suspension and detritus feeding benthic animals (Airoldi, 2003), such as polychaete communities (e.g. Cardoso *et al.*, 2007). Similarly, our results support the hypothesis that highly mobile species are more resilient to sediment disturbances than those with limited mobility. For instance, at least for a few categories of response (e.g. behaviour and community abundance), fish and crustaceans were not negatively affected by sediments. The negative effects of sediments can probably be compensated for by indirect advantages such as reduced competition and/or predation for certain species and size groups of fish (Kjelland *et al.*, 2015).

Because studies with crustaceans were few and some responses on fish were strongly negative (e.g. reproduction and recruitment), the contrasting effects of sediments make it difficult to rule out ecological impacts on these groups, and hence the generalization of these findings requires caution. Overall, the results of the meta-analyses suggested that mobility alone does not indicate that highly-mobile groups are not at risk from the effects of sediments.

Our results are in accordance with a previous meta-analysis, which concluded that early life stages like eggs and larvae of fish were most vulnerable to elevated suspended sediment concentrations associated with dredging activities (Wenger *et al.*, 2017). However, our conclusions expand knowledge about sediment effects on marine species in several ways. First, there was no consistent evidence that early life stages were the most affected by sediment across all taxonomic groups. For instance, meta-analyses from our dataset indicated that physiological responses in macroalgae and impacts on community diversity in corals had significantly higher effects than on their respective reproduction and recruitment processes. Second, Wenger *et al.* (2017) assessed suspended sediment concentration effects as a pathway of impact and found that the risk of detrimental impacts depended on the intensity and duration of exposure to sediments. Conversely, our analyses highlighted that, overall, methodological aspects could not explain the variation in responses to sediment across all taxonomic groups. Third, there was little overlap in the studies included in both analyses. This was because Wenger *et al.* (2017) focused on including all dredging-related impacts on fish species such as contamination with harmful compounds and noise pollution. Thus, the results from our meta-analyses represented a different dataset.

A gap in our meta-analysis was that we did not consider chemical contaminants and nutrients that might be associated with sediments. Chemical contamination is likely important because it has generally increased sediment impacts on marine species (Weber *et al.*, 2012; Restrepo *et al.*, 2016), and biological responses will be determined by the relative toxicity of

the different pollutants, such as heavy metals and pesticides. Organic matter will also mediate the ecological interactions between stressors by moderating the relative scaling of their responses to sediment loading (Humanes *et al.*, 2017b). Cumulative and interacting effects across all contaminants should be emphasised by future research to evaluate the overall vulnerability of marine biodiversity to sediment disturbances and to specify under which circumstances sediments would lead to more extensive degradation.

The present review provided some opportunities to outline important research gaps in studies of sediment disturbances on marine biodiversity. It was clear that heterotrophic species had a strong and significant negative effect when sediments change the benthic community whereby sensitive species can be particularly suppressed. Although several key mechanisms can explain these strong effects on benthic communities (e.g. reduced food supply, reduction in habitat available, changes in biotic interactions), few studies meeting the criteria set out by this meta-analysis focused on the ecological effects at the community level in soft-bottom habitats. Therefore, there is a need for more studies quantifying community effects on how specific traits of the benthic species (e.g. mobile burrowers, sedentary surface dwellers) respond to sediments between impacted and non-impacted sites. We also found that coral reef habitats are one of the primary targets for research on sediment impacts, whereas other, less-studied habitat-forming species were severely impacted by sediments, including coralline algae and seagrass. Additionally, we lacked observations on phyto- and zooplankton assemblages. It is thus important that these species inhabiting pelagic habitats become the focus of future assessments to increase our understanding of sediment-induced disturbances on other marine ecosystems, including measurements on a broad range of processes such as early life history stages. We call for more empirical studies and syntheses focusing on the habitats particularly susceptible identified here.

Driven by terrestrial runoff, dredging operations, and natural accumulation of sediments, sediment disturbances have become a concern in many coastal areas. Our study complements previous qualitative reviews on the impacts of sediments on specific ecosystems or taxonomic groups by providing quantitative estimates of their net effects across several marine taxonomic groups and standardised methods to rank the effects between studies and species affected. This approach will enable directing attention towards integrated marine ecosystem-based management, which typically involves assessing the relative vulnerability of a range of target ecosystems and species to one or more stressors, while accounting for the likely adaptive capacity of the targets to the stressors (Glick *et al.*, 2011). Meeting this requirement is a severe challenge due to the lack of robust and comprehensive estimates of sediment impacts across the whole range of ecosystems. Our meta-analysis provides estimates of mechanism, habitat-, and taxon-specific impacts as a result of sediment-induced disturbances after a review of the available evidence base. It also provides insights into the interaction between sediment-related stressors, such as light depletion, suspended sediment, and sedimentation. Coupled with large-scale maps of exposure to sediments and high-resolution maps of habitats (e.g. Magris *et al.*, 2019), along with estimates of disturbance recovery, our findings will enable further analysis of sediment impacts and risk assessments to advise policymakers and conservation planners on best-practices in the environmental management of this threat.

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DATA ACCESSIBILITY STATEMENT

All relevant data for the paper are provided in the supplementary material.

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TABLES

898 **Table 1.** Definition of categories of response for sediment disturbances, and metrics used by
 899 publications to evaluate the impacts of sediments. The sign of the effect sizes was
 900 reversed for metrics in bold italic to make them comparable with other performance
 901 metrics (e.g. survival, relative growth rate, size, fecundity).

Categories of response	Definition	Metrics
Behaviour	Behavioural changes at the organism level such as modified movement, restriction of sensory capabilities, and changes in the motivation state	<i>Clearance rate; changes in the pre-stimulus baseline behaviours; changes in organism movement or activity patterns</i>
Reproduction and recruitment	Effects that impair the main pre- and post-settlement processes and reproductive success, such as gamete production, egg fertilization, embryo development, larval survival, larval settlement and metamorphosis, and juvenile post-settlement survival	Percentage of larvae survivorship; percentage of fertilization; sperm counts or mean number of spermatocytes; <i>mortality rate</i> or size of embryos; gametophyte density; <i>percentage of dead eggs</i> ; percentage, number, or size of germlings; metamorphosis rate; percentage or number of larvae settled; <i>percentage of abnormal embryo development</i> ; hatching success; mean number, percentage, biomass, or density of recruits; survival or size of juveniles; maximum potential quantum yields, respiration or growth of juveniles
Morphology	Anatomical modifications or abnormalities (phenotypic)	Number of leaves in a seagrass; <i>partial mortality of a coral colony</i> ; body dimensions; <i>percentage of necrosis</i> ; leaf cluster density; plant dimension measurements
Physiology	Physiological or biochemical modifications that affect growth rate or individual performance required for basic maintenance of the organism	Growth rate; calcification rate; weight gain or <i>weight change</i> ; lipid or protein contents; chlorophyll concentrations or ratios; respiration rate measurements; maximum potential quantum yields; photochemical efficiency; colour or condition indexes; <i>mucous production</i> ; tissue content or mass; symbiosis or zooxanthellae density; RNA-DNA ratios; enzyme activities; blood content analysis; leaf contents; leaf biomass; leaf elongation rate; <i>leaf loss rates</i>
Single-species abundance	Increase or decrease in the number, density, biomass, or cover of individuals of a single species	Biomass; percent cover; density or number of individuals; shoot density
Community-level abundance	Increase or decrease in the pooled biomass, density, total number of individuals, or percent cover of multiple species	Biomass; percentage cover; density of individuals; number of individuals or colonies; shoot density
Community diversity	Change in species composition, species richness, diversity, or	Number of species; number of taxa; species richness; species evenness; Shannon-Wiener diversity index

	any other community-wide measure of diversity	
Species interaction	Social disruption, food web dynamic alterations, changes in competition, predator-prey or any other type of association between species	Attack rate or success on prey; foraging, grazing or ingestion rate; survival of preys; <i>changes in movement patterns across habitats; increase in antipredator behaviour as response to chemical cues</i>

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Table 2. Summary table showing tests of moderators and heterogeneities from each meta-analysis applied to separate response categories. Significant influence of moderators is indicated in bold (when 95% CI does not include zero) at $p < 0.05$.

Category of response	Moderators	d.f.	Q	p
Behaviour	Taxonomic group	3	16.55	<0.05
	Residual	17	92.71	<0.05
	Habitat type	2	2.61	0.27
	Residual	18	133.45	<0.05
	Nutritional mode	1	26.98	<0.05
	Residual	19	83.58	<0.05
	Movement type	2	11.93	<0.05
	Residual	18	101.86	<0.05
	Pathway of impact	1	8.26	<0.05
	Residual	19	126.28	<0.05
	Study type	1	0.38	0.53
	Residual	19	136.76	<0.05
	Stressor intensity	1	0.088	0.76
	Residual	19	138.05	<0.05
	Duration (log scale)	1	1.64	0.19
	Residual	19	130.81	<0.05
Reproduction and recruitment	Taxonomic group	5	89.37	<0.05
	Residual	136	1540.30	<0.05
	Habitat type	3	72.27	<0.05
	Residual	138	1622.58	<0.05
	Nutritional mode	1	23.8	<0.05
	Residual	140	1650.66	<0.05
	Movement type	2	58.06	<0.05
	Residual	139	1576.95	<0.05
	Pathway of impact	1	53.14	<0.05
	Residual	140	1598.34	<0.05
	Study type	1	0.90	0.34
	Residual	140	1671.35	<0.05
	Stressor intensity	1	1.16	0.28
	Residual	140	1621.55	<0.05
	Duration (log scale)	1	4.71	0.063
	Residual	140	1583.78	<0.05
Morphology	Taxonomic group	5	9.81	0.08
	Residual	28	405.15	<0.05
	Habitat type	2	9.577	<0.05
	Residual	31	423.44	<0.05
	Nutritional mode	1	0.54	0.46
	Residual	32	420.97	<0.05
	Movement type	1	0.001	0.89
	Residual	32	421.64	<0.05
	Pathway of impact	1	7.87	<0.05
	Residual	32	417.33	<0.05
	Study type	1	16.28	<0.05

	Residual	32	402.32	<0.05
	Stressor intensity	1	0.34	0.55
	Residual	32	387.92	<0.05
	Duration (log scale)	1	1.36	0.24
	Residual	32	415.7	<0.05
Physiology	Taxonomic group	5	70.15	<0.05
	Residual	351	3064.56	<0.05
	Habitat type	5	76.77	<0.05
	Residual	351	3059.27	<0.05
	Nutritional mode	1	12.73	<0.05
	Residual	355	3135.15	<0.05
	Movement type	1	4.80	<0.05
	Residual	355	3136.93	<0.05
	Pathway of impact	1	72.34	<0.05
	Residual	355	3052.13	<0.05
	Study type	1	1.99	0.15
	Residual	355	3150.72	<0.05
	Stressor intensity	1	2.55	0.11
	Residual	351	3115.84	0.05
	Duration (log scale)	1	8.22	<0.05
	Residual	339	3008.90	<0.05
Single-species abundance	Taxonomic group	4	23.27	<0.05
	Residual	26	175.82	<0.05
	Habitat type	2	21.57	<0.05
	Residual	28	191.17	<0.05
	Nutritional mode	1	24.59	<0.05
	Residual	29	209.32	<0.05
	Movement type	1	3.68	0.055
	Residual	29	208.39	<0.05
	Pathway of impact	1	2.99	0.35
	Residual	29	211.28	<0.05
	Study type	1	0.67	0.41
	Residual	29	218.68	<0.05
	Stressor intensity	1	2.07	0.15
	Residual	29	157.03	<0.05
	Duration (log scale)	1	0.76	0.38
	Residual	29	221.8	<0.05
Community abundance	Taxonomic group	11	114.6	<0.05
	Residual	172	1192.8	<0.05
	Habitat type	3	14.87	<0.05
	Residual	180	1511.75	<0.05
	Nutritional mode	1	9.35	<0.05
	Residual	182	1505.29	<0.05
	Movement type	3	16.50	<0.05
	Residual	180	1506.91	<0.05
	Pathway of impact	1	0.88	0.84
	Residual	182	1544.2	<0.05
	Study type	1	0.29	0.58

	Residual	182	1553.04	<0.05
	Stressor intensity	1	14.51	<0.05
	Residual		1433.67	<0.05
	Duration (log scale)	1	51.81	<0.05
	Residual	171	1345.29	<0.05
Community diversity	Taxonomic group	3	4.01	0.259
	Residual	32	256.09	<0.05
	Habitat type	2	7.45	<0.05
	Residual	33	273.26	<0.05
	Nutritional mode	1	0.48	0.78
	Residual	34	277.37	<0.05
	Movement type	2	15.3	<0.05
	Residual	33	260.82	<0.05
	Pathway of impact	1	8.78	<0.05
	Residual	34	272.39	<0.05
	Study type	1	1.93	0.16
	Residual	34	275.47	<0.05
	Stressor intensity	1	3.67	0.17
	Residual	29	299.22	<0.05
	Duration (log scale)	1	2.12	0.14
	Residual	27	211.46	<0.05
Species interaction	Taxonomic group	2	9.31	<0.05
	Residual	34	428.13	<0.05
	Habitat type	2	6.35	<0.05
	Residual	34	440.79	<0.05
	Nutritional mode	1	0.69	0.40
	Residual	35	442.47	<0.05
	Movement type	2	5.25	0.072
	Residual	34	432.54	<0.05
	Pathway of impact	1	8.91	<0.05
	Residual	35	425.38	<0.05
	Study type	1	0.71	0.39
	Residual	35	438.81	<0.05
	Stressor intensity	1	0.51	0.47
	Residual	35	444.38	<0.05
	Duration (log scale)	1	0.0045	0.94
	Residual	35	443.96	<0.05

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