



The impact of cumulative stressor effects on uncertainty and ecological risk

Vera Rullens^{a,*}, Fabrice Stephenson^{a,b}, Judi E. Hewitt^{b,c}, Dana E. Clark^d, Conrad A. Pilditch^a, Simon F. Thrush^e, Joanne I. Ellis^f

^a School of Science, University of Waikato, Hamilton, New Zealand

^b National Institute for Water and Atmospheric research, Hamilton, New Zealand

^c Department of Statistics, University of Auckland, Auckland, New Zealand

^d Cawthron Institute, Nelson, New Zealand

^e Institute of Marine Science, University of Auckland, Auckland, New Zealand

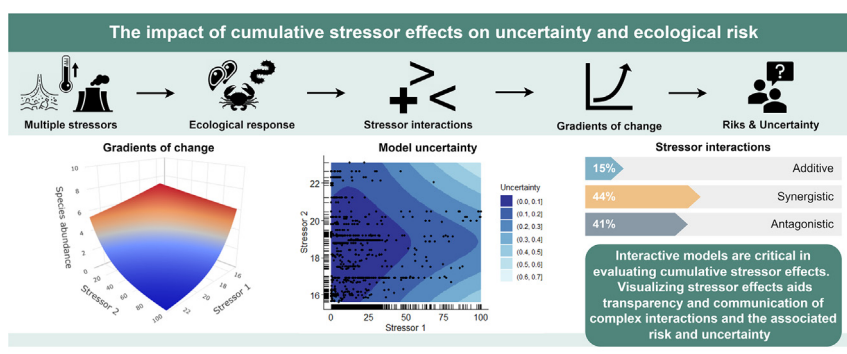
^f School of Science, University of Waikato, Tauranga, New Zealand



HIGHLIGHTS

- Marine environments experience multiple stressors that have cumulative effects.
- Transparency on the risks and uncertainties from cumulative effects are essential.
- In models for estuarine invertebrates, non-additive stressor effects dominated.
- 3D-plots provide insights on complex stressor interactions and gradients of change.
- Steep gradients of change and high uncertainty invoke precautionary management.

GRAPHICAL ABSTRACT



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ABSTRACT

To enable environmental management actions to be more effectively prioritized, cumulative effects between multiple stressors need to be accounted for in risk-assessment frameworks. Ecological risk and uncertainty are generally high when multiple stressors occur. In the face of high uncertainty, transparent communication is essential to inform decision-making. The impact of stressor interactions on risk and uncertainty was assessed using generalized linear models for additive and multiplicative effect of six anthropogenic stressors on the abundance of estuarine macrofauna across New Zealand. Models that accounted for multiplicative stressor interactions demonstrated that non-additive effects dominated, had increased explanatory power (6 to 73 % relative increase between models), and thereby reduced the risk of unexpected ecological responses to stress. Secondly, 3D-plots provide important insights in the direction, magnitude and gradients of change, and aid transparency and communication of complex stressor effects. Notably, small changes in a stressor can cause a disproportionately steep gradient of change for a synergistic effect where the tolerance to stressors are lost, and would invoke precautionary management. 3D-plots were able to clearly identify directional shifts where the nature of the interaction changed from antagonistic to synergistic along increasing stressor gradients. For example, increased nitrogen load and exposure caused a shift from positive to negative effect on the abundance of a deposit-feeding polychaete (*Magelona*). Assessments relying on model coefficient estimates, which provide one effect term, could not capture the complexities observed in 3D-plots and are at risk of mis-identifying interaction types. Finally, visualising model uncertainty demonstrated that although error terms were higher for multiplicative models, they better captured the uncertainty caused by data availability. Together, the steep gradients

* Corresponding author at: Private Bag 3105, Hamilton 3240, New Zealand.
E-mail address: vera.rullens@waikato.ac.nz (V. Rullens).

of change identified in 3D-plots and the higher uncertainty in model predictions in multiplicative models urges more conservative limits to be set for management that account for risk and uncertainty in multiple stressor effects.

1. Introduction

Although marine and coastal ecosystems are recognised as ecologically and culturally significant, they are also among those most heavily impacted, diminishing their health, functioning, and the services they provide to people (MEA, 2005; Halpern et al., 2007; He and Silliman, 2019; Gissi et al., 2021). Estuarine and coastal environments are situated at the interface between land and sea and experience unprecedented anthropogenic pressures originating from land (e.g. eutrophication, sedimentation, or pollution), activities at sea (e.g. fishing, dredging) and global climate change (Halpern et al., 2008; Robins et al., 2016; Cabral et al., 2019). When ecosystems experience multiple stressors, the response may not be characterised as a simple additive effect. Rather, interactions between stressors are regularly observed and can have devastating consequences. The cumulative effects of multiple stressors remains a key research area in marine ecosystem ecology (Breitburg et al., 1998; Borja et al., 2020) and can alter the way marine and coastal environments are managed (Stelzenmüller et al., 2018). Much of the concern over multiple stressors stems from the potential for synergistic or antagonistic effects, where their combined effect is either greater or smaller (respectively) than what is expected additively (Folt et al., 1999; Crain et al., 2008). This implies that synergistic effects are of highest priority in ecological risk assessments, where effective management actions reducing one stressor may provide additional benefits by simultaneously reducing the synergistic effect (Falkenberg et al., 2013; Brown et al., 2014; Mach et al., 2017). For antagonisms on the other hand, management actions that reduce one stressor may be ineffective.

Cumulative effect assessments have been conducted using a variety of methods to gain insights into the nature of interactive effects between multiple stressors across different ecological scales (individual to ecosystem) (Hodgson and Halpern, 2019). Empirical findings on cumulative stressor impacts are predominantly derived from laboratory studies focussing on single species responses and a narrow range of few (two or three) easily amenable stressors for which synergistic effects dominate (Crain et al., 2008). Although these studies provide valuable insights and can identify cause-effect relationships, their small-scale application can render results to be context specific. The dynamics in real ecosystems, which experience multiple stressors of different duration, timing, magnitude, and spatial extent, are much more complex (Gunderson et al., 2016; Gladstone-Gallagher et al., 2019b; Jackson et al., 2021). These dynamics are key in deciphering the real-world response of a system to stress. To this end, a variety of modelling approaches exist to determine the potential impact of multiple stressors by analysing responses across wide spatial and temporal gradients of environmental stressors (Hodgson and Halpern, 2019). Modelling studies that explicitly consider non-additive effects and determine the nature of stressor interactions remain limited but are critically important to progress our understanding and reduce the risk of unanticipated ecological responses.

Regression models offer a way of quantifying stressor interactions and have been used in estuarine environments to determine cumulative stressor impacts on benthic communities as indicators of ecosystem health (O'Brien et al., 2016). Notably, changes in dominant species and community composition provide insights into the systems response to stress and identify priority stressor interactions (e.g. Thrush et al., 2008b; Jennerjahn and Mitchell, 2013; Ellis et al., 2017a; Clark et al., 2021). Regression models, including (linear) regression, quantile regression or regression trees, determine cumulative effects through correlation between stressors and the response of interest (e.g. species abundance) and can encompass real-world variability and complexity in stressor gradients. Although regression trees (e.g. Random Forest and Boosted Regression Trees) are increasingly used in ecological studies (Elith et al., 2008), including those on multiple stressors effects (e.g. Hewitt et al., 2016; Kotta et al., 2017; Ceccarelli et al., 2020),

they rarely distinguish among interaction types (Teichert et al., 2016). Multiple linear regression on the other hand can identify stressor interaction types from the direction and magnitude of estimated model coefficients (e.g. Thrush et al., 2008b; Feld et al., 2016; Ellis et al., 2017a; Ellis et al., 2019; Birk et al., 2020). Although this provides a way to identify additive, antagonistic, or synergistic effects, the form of stressor interactions along increasing gradients of stress has only recently been explored. Visualising these effects across gradients of stress may aid better interpretation and communication of multiplicative effects (Feld et al., 2016).

One area that receives little attention in any of the aforementioned methods, is the risk and uncertainty associated with cumulative stressor impacts on species or ecosystems. Stressors that threaten the environment (i.e. negatively impact the state of the environment) need to be managed to mitigate their effects. Environmental management and decision making often rely on risk assessments to identify the probability and potential consequences of an event and decide if this risk is acceptable or needs to be mitigated (ISO, 2009). Risk can arise when there is uncertainty about the consequences of a threat. In environmental stressor research, the effects of two stressors can greatly deviate from the expected outcome derived for single stressors or their additive effects. Uncertainty in the response of a system to stress, and potentially unknown synergistic or antagonistic effects, therefore increases risk. In marine environments there are a large number of stressors and new stressor interactions are still being uncovered (Gissi et al., 2021). Until more stressor combinations and the mechanisms behind them are understood, there is a risk of unanticipated consequences of stressors on the environment, which needs to be communicated from scientists to decision makers and other stakeholders. Ecologists can contribute to a reduction of risk by researching the mechanisms behind cumulative stressor effects, creating models that more accurately predict a systems response to multiple stressors, and by transparently communicating about the uncertainty from the model assessment (Marcot, 2020).

Although transparency about model uncertainty is critically important for management and decision making, few studies provide an assessment of the uncertainty associated with model outputs in cumulative effect analyses (Stelzenmüller et al., 2018). Model uncertainty is multi-dimensional, with factors pertaining to the nature, level, and location of uncertainty (Walker et al., 2003). The nature of uncertainty can be epistemic (i.e. incomplete knowledge) or ontological (i.e. natural variability) and the level can range from complete certainty to deeply uncertain (Walker et al., 2003; Marcot, 2020). The location of model uncertainty refers to uncertainty originating from, among others, technical aspects, model inputs, data, and parameter calibration (Walker et al., 2003). Three aspects of risk and uncertainty are important when considering cumulative effects. First, studies focussed on stressor interactions, as opposed to single stressors or additive effects, reduce the risk of missing important interactions that alter expected ecological responses, and thereby address a deeper level of epistemic uncertainty in the conceptual structure of the model. Second, the uncertainty associated with model outcomes often accumulates from different aspects and can be expressed as an overall prediction error or other measures of inaccuracy. For example, Stock and Micheli (2016) studied uncertainty from model assumptions and data quality in cumulative impact mapping and found aggregated uncertainty from different origins. Third, data availability and quality (e.g. accuracy and consistency in data collection, sampling biases, spatial and temporal resolution; Walker et al., 2003) are important drivers of uncertainty in ecological models (Halpern and Fujita, 2013; Rueda-Cediel et al., 2015; Jenkins and Quintana-Ascencio, 2020).

In this study, we aim to determine how the cumulative effects of multiple stressors affect uncertainty and ecological risks by studying the effect of multiple stressors on species abundance in models with and without stressor interactions. We show how (model) uncertainty changes when

interactive effects between stressors are included compared to additive effects alone, and link this back to data availability. Linear regression models were developed to assess the impact of local and climate stressors on the abundance of estuarine macroinvertebrates as indicators of estuarine health (O'Brien et al., 2016), using datasets from surveys and monitoring programs conducted across New Zealand. We hypothesise that the inclusion of multiplicative interactive effects will increase model predictive ability, compared to models with only additive effects. Data availability covering the combined stressor space was expected to be a key limitation for the inclusion of interactive effects and was therefore analysed as a driver of uncertainty. Finally, we visualised interactive effects based on 3-dimensional plots of important stressor pairs. The need to better incorporate and transparently communicate risk and uncertainty from multiple stressor effects is universal for risk assessments of any ecosystem, and the approach described in this study is applicable beyond the stressors, species, and estuarine environment considered in this example.

2. Methods

2.1. Study area

Data were compiled from the macrofauna database from the National Institute of Water and Atmospheric research (NIWA) that included environmental surveys and large-scale experiments conducted in New Zealand estuaries (Thrush et al., 2003; Thrush et al., 2008a; Hewitt et al., 2010; Lohrer et al., 2012; de Juan et al., 2013; Hailes et al., 2015; Ellis et al., 2017b; Kraan et al., 2020; Drylie, 2021; Thrush et al., 2021) and the National Estuary Dataset (NED) that compiled additional datasets from regional government authorities (Berthelsen et al., 2020a; Berthelsen et al., 2020b). Combined, the datasets covered 770 independent sites across 45 estuaries sampled between 2000 and 2019, in austral spring to autumn (October to May). Sites spanned a total of 12° latitude across New Zealand, although datasets were skewed to the northern North-Island (Fig. S1). For sites sampled over multiple events, data from the most recent event were selected to ensure temporal independence; to ensure spatial independence sites within estuaries had to be >25 m apart (Douglas et al., in review).

2.2. Macrofauna data

At each site, infauna samples were collected to assess the macrofauna community composition. Samples were taken using a 13 cm diameter core to 15 cm depth, sieved to 500 µm, and all individuals were identified by taxonomic experts to the lowest practicable taxonomic level. Over 500 species or taxa were identified in the datasets, and for further analysis a subset of 8 species was selected (Table 1). Species were selected because they were identified to a consistent taxonomic resolution across datasets with different prevalence and abundances and covered a variety of taxonomic and functional groups commonly occurring in New Zealand's estuarine benthic communities (Table 1) (Rodil et al., 2013; Greenfield et al., 2016). The data were checked for consistency and a few sites were omitted

if unclear (e.g. for *Magelona dakini* 72 sites were dropped from the analyses due to taxonomic discrepancies). At each site, a variable number of replicate cores were used to sample the macrofaunal community (ranging from n = 3–12) depending on the study/monitoring dataset. To ensure macrofaunal community data were comparable between sites (and datasets), three replicate cores were averaged (for sites where n was >3 these were randomly selected) resulting in a single estimate of macrofauna community data for each site (which was paired to a single measure of environmental data). Species prevalence in the datasets showed lowest prevalence for the crab *Austrohelice crassa* (11 %), and highest prevalence for both bivalves *Austrovenus stutchburyi* and *Macomona liliana* (73 and 72 % respectively) (Table 1) across sites. Some of the most abundant taxa were polychaetes and oligochaetes with over 200 individuals per core (Table 1).

2.3. Environmental stressor data

The effect of six environmental variables were assessed as drivers of macrofauna abundance. These variables can act as stressors when human activities cause them to exceed their natural range of variability (Sanderson et al., 2002; Halpern et al., 2007). Three local, land-derived stressors, including sediment mud content (Mud), organic matter content in sediments (OM), Nitrogen load (N-load), and three climate stressors, namely maximum sea surface temperature (maxSST), a climate index (Southern Oscillation Index - SOI), and wind-wave exposure (Exposure) were included in this study. Whilst other stressors impact estuaries around the world (notably pollutants), the choice of stressors in this study was driven by relevance to the case study area and data availability from monitoring programs. Mud content was used as a proxy for sediment run-off into estuaries, which can cause smothering of benthic communities (Thrush et al., 2004). For most species, high mud content acts as a stressor (e.g. Thrush et al., 2004; Anderson, 2008; Robertson et al., 2015), with only few species preferring muddy conditions (e.g. the 'mud crab' *Austrohelice crassa*). Similarly, OM and N-load are indicators of eutrophication in estuaries (Pinckney et al., 2001), with high OM and N-load were considered to be stressors (Savage et al., 2002). The three climate stressors reflected the impact of climate change related variables. MaxSST, the highest temperature experienced during the month of sampling, reflects stress from global warming. The wind-wave exposure of sampling sites was used as a proxy for vulnerability from increased severe weather events, like hurricanes, that occur with climate change. SOI reflects a wider shift in climatic patterns in the southern Pacific (El-Nino Southern Oscillation) and has a bi-directional effect as a stressor under both high (La-Nina) and low (El-Nino) conditions.

For the local stressors, Mud and OM content were determined concurrently with macrofauna sampling during the environmental surveys, by collecting samples from the top 2 cm of the sediment. Mud, as the fraction of sediment with a grain size <63 µm, was determined using either wet sieving or laser diffraction analysis. For the sampled sites, Mud covered a wide spectrum of conditions, varying between 0 and 99 % mud, skewed towards low mud content (Table 2). OM was analysed by drying a subsample

Table 1

Taxonomic information on the selected species for modelling, including taxonomic and functional groups. Functional groups provide information on body hardness, feeding behaviour, living position, movement ability, living structure created, and/or body size (Greenfield et al., 2016). The species prevalence (Prev, %) and abundance range (ind core⁻¹) averaged over three replicate cores are given.

| Species | Taxa | Functional group | Prevalence (%) | Abundance (ind core ⁻¹) |
|--------------------------------|--------------|--|----------------|-------------------------------------|
| <i>Austrovenus stutchburyi</i> | Bivalvia | Calcified, suspension-feeding, top 2 cm, freely mobile, large | 73 | 0–129 |
| <i>Macomona liliana</i> | Bivalvia | Calcified, deposit-feeding, deep, limited mobility, large | 72 | 0–35 |
| <i>Heteromastus filiformis</i> | Polychaeta | Soft-bodied, deposit-feeding, below surface, limited mobility, small | 69 | 0–202 |
| <i>Scoloplos cylindrifera</i> | Polychaeta | Soft-bodied, deposit-feeding, below surface, freely mobile, medium | 31 | 0–56 |
| <i>Aonides</i> sp. | Polychaeta | Soft-bodied, deposit-feeding, below surface, limited mobility, small | 46 | 0–439 |
| <i>Magelona dakini</i> | Polychaeta | Soft-bodied, deposit-feeding, below surface, limited mobility, small | 25 | 0–30 |
| Oligochaeta | Clitella | Soft-bodied, predator/scavenger, top 2 cm, limited mobility, small | 41 | 0–241 |
| <i>Austrohelice crassa</i> | Malacostraca | Rigid, predator/scavenger, below and on surface, freely mobile, burrow former, large | 11 | 0–14 |

Table 2

Overview of environmental stressors used in modelling species abundance responses, including the spatial resolution and temporal correspondence with the macrofauna sampling and data type. OM: organic matter, N-load: nitrogen load, SOI: Southern Oscillation Index, maxSST: maximum sea surface temperature (SST).

| | Mud | OM | N-load | SOI | maxSST | Exposure |
|-----------|------------|------------|-----------|-------------|----------|--------------|
| | (%) | (%) | (TN/year) | | (°C) | |
| Minimum | 0.0 | 0.43 | 0.0 | -1.60 | 15.6 | 0.0 |
| Mean | 17.6 | 2.30 | 3.0 | 0.48 | 18.6 | 30.2 |
| Median | 11.5 | 1.95 | 1.0 | 0.77 | 18.7 | 18.7 |
| Maximum | 99.9 | 10.0 | 151.6 | 2.17 | 23.1 | 112.5 |
| Spatial | Site | Site | Site | National | Estuary | Site |
| Temporal | Concurrent | Concurrent | Year | 3-month lag | Month | Steady state |
| Data type | Measured | Measured | Modelled | Modelled | Modelled | Modelled |

of sediment to constant weight and measured as the loss of mass on ignition (LOI), ranging from 0.4 to 10.0 % (Table 2). Whilst Mud and OM were collected in situ, proxies were obtained for the other stressors from models, which were integrative over space/time (Table 2). N-load was calculated for each site based on modelled mean annual in-stream total nitrogen loads derived from the Catchment Land Use for Environmental Sustainability (CLUES) model (version 10.3; Semadeni-Davies et al., 2016, Semadeni-Davies et al., 2020). The in-stream loads are the sum of the upstream total nitrogen loadings (t/year) for the terminal reach of a stream. For each site, the mean annual in-stream total nitrogen loads for terminal reaches discharging into the estuary within 1 km of the sampling site were summed to calculate a cumulative nitrogen load for the site. N-load values were square root transformed to account for few sites with high N-load that exerted undue influence on the analysis (Zuur et al., 2010).

Modelled daily SST data were obtained from the JPL MUR MEaSUREs Project (Nasa/Jpl, 2015; Chin et al., 2017). MaxSST for the month and year of sampling were obtained from a location near the seaward entrance of each estuary, resulting in one value for all sites within an estuary at a given sampling event. SST data were not available from this source prior to 2002, therefore the median monthly value of maxSST from 2003 to 2020 were used for sites sampled prior to 2002 ($n = 240$). In the study area, the range of SST during the month of sampling was between 15.6 and 23.1 °C, capturing both seasonal and latitudinal variability in maxSST. SOI provides a measure of the strength of the El-Niño Southern Oscillation (ENSO), which drives climatic conditions in the southern pacific in a 2 to 7-year cycle. Prolonged periods (>3 months) of SOI below -1 or above 1 characterise El-Niño and La-Niña events respectively. Therefore, SOI was calculated as the 3-month running average prior to the month and year of sampling at each site. Wind-wave exposure was calculated for each site following a similar approach to that used by Burrows et al. (2008) and Clark et al. (2021). Fetch (distance to land, m) was calculated for each site in 20° intervals, with a maximum distance of 20 km if not intersecting with land. Three years of wind direction and speed data (2010–2013) were acquired from the nearest weather station from NIWA Cliflo database (cliflo.niwa.co.nz) and binned into 20° intervals to determine predominant wind direction and speed at sites. Each fetch measurement was then multiplied by the total number of days that the predominant wind was from that direction and the average wind speed (surface wind at 9 am, $m s^{-1}$) for those days. Wind-wave exposure values per bin were summed and divided by 100,000 to create an exposure index ranging from 0 to 112.5 (Table 2), with high values reflecting exposed sites experiencing high wind/wave energy.

2.4. Modelling species responses to environmental stressors

Generalized linear models (GLM) were used to study the response of species abundance to environmental stressors. For each species, GLMs were created with additive effects between stressors only (see Eq. (1)), hereafter referred to as ‘additive models’ and those with multiplicative

interaction effects between stressors (see Eq. (2)), hereafter referred to as ‘multiplicative models’.

$$y = a + b_1x_1 + b_2x_2 \quad (1)$$

$$y = a + b_1x_1 + b_2x_2 + b_3x_1x_2 \quad (2)$$

where y represents the response variable (here species abundance), a the intercept, and b_i the slope coefficient for independent variables x_i (here stressors or their interaction). All stressors were rescaled from 0 to 1 to enable comparison between stressor effects on log-transformed abundance, following:

$$x_{\text{scaled}} = \frac{x - \min(x)}{\max(x) - \min(x)} \quad (3)$$

Stressors and interaction effects were determined through a stepwise backwards selection for the multiplicative model (Murtaugh, 2009). From the full model including the six stressors and all first order interaction effects, variables were dropped out and added back in to obtain the most parsimonious model with the lowest Bayesian Information Criteria (BIC) score (Schwarz, 1978). Additive models were then built using the same variables, but without multiplicative terms. Model performance was compared among and between species and additive/multiplicative models, using the amount of variance explained by the model and the adjusted R^2 . Adjusted R^2 is a measure of model performance that reflects the variance explained by the model and accounts for the addition of more terms in the model, thereby enabling a comparison between additive and multiplicative models per species. The absolute and relative change in adjusted R^2 value ($\Delta \text{adj. } R^2$) between additive and multiplicative models was used to assess improvement in model performance per species. All analyses were conducted in R statistical software using the ‘stats’ package (R Core Team, 2020).

2.5. Interactive effects and uncertainty estimates

The model outputs were used to identify the presence of additive and multiplicative effects between stressor pairs and study the prevalence and nature of interactive effects. First, an assessment of additive, synergistic, or antagonistic effects was conducted using the estimates and direction of model coefficients, as per Thrush et al. (2008b). Additive effects were identified when the effect of a stressor was independent from other stressors and was not part of any multiplicative term in the model. Additive models by default only include additive effects, whereas the multiplicative models could include both additive and multiplicative effects depending on the stressor. For multiplicative effects a distinction was made between synergistic and antagonistic effects based on the directions and estimates of coefficients for the main effects and the multiplicative terms of stressor pairs. Synergistic effects represent situations where the combined stressor effect causes a stronger increase or decrease in abundance compared to the additive effect of the two stressors, whereas antagonistic effects represent situations where the combined effect is dampened. Main effects can either act in the same or in opposing directions. If both main effects act in the same direction, synergistic effects were considered when the multiplicative term acted in the same direction as both main effects (see Eq. (2)) whereas antagonistic effects are considered when the multiplicative term acted in the opposite direction:

$$y = a + b_1x_1 + b_2x_2 - b_3x_1x_2 \quad (4)$$

When main effects acted in opposing directions, synergistic and antagonistic effects were identified from the magnitude of the estimated coefficients for main and multiplicative terms. In this case, synergistic effects were considered if the coefficient for the multiplicative term was larger than the sum

Table 3

Model performance overview per species for models with additive effects between stressors (Additive) and those with additive or multiplicative effects between stressors (Multiplicative). Two metrics for model performance were used: the amount of variance explained by the model, and adjusted R² that accounts for the number of terms in the model. The difference in adjusted R² value for additive and interactive models (Δ adj.R²) reflects the improvement of model performance by adding multiplicative interactive terms to the model. The number of interactive terms (N. interactions) retained in the multiplicative models are given, with detailed model summaries available in Supplementary Materials, Table S1.

| Species | Model | Variance explained (%) | Adjusted R ² | Absolute Δ adj.R ² | Relative Δ adj.R ² (%) | N interactions |
|--------------|----------------|------------------------|-------------------------|-------------------------------|-----------------------------------|----------------|
| Austrovenus | Additive | 13.0 | 0.12 | | | |
| | Multiplicative | 15.5 | 0.15 | 0.03 | 25.0 | 2 |
| Macomona | Additive | 15.1 | 0.15 | | | |
| | Multiplicative | 17.7 | 0.17 | 0.02 | 13.3 | 1 |
| Heteromastus | Additive | 16.9 | 0.16 | | | |
| | Multiplicative | 21.9 | 0.21 | 0.05 | 31.3 | 3 |
| Scoloplos | Additive | 10.3 | 0.10 | | | |
| | Multiplicative | 15.6 | 0.14 | 0.04 | 40.0 | 5 |
| Magelona | Additive | 32.0 | 0.32 | | | |
| | Multiplicative | 34.8 | 0.34 | 0.02 | 6.3 | 3 |
| Aonides | Additive | 11.0 | 0.11 | | | |
| | Multiplicative | 20.1 | 0.19 | 0.08 | 72.7 | 4 |
| Oligochaeta | Additive | 26.1 | 0.26 | | | |
| | Multiplicative | 31.6 | 0.31 | 0.05 | 19.2 | 5 |
| Austrohelice | Additive | 13.6 | 0.13 | | | |
| | Multiplicative | 18.5 | 0.17 | 0.04 | 30.1 | 6 |

of the main effects (Eq. (5)) (e.g. in $y = a + b_1x_1 - b_2x_2 - b_3x_1x_2$, if $b_3 > b_1 + b_2$), and antagonistic effects when the coefficient estimate was smaller than the main effects (Eq. (6)).

$$y = a + b_1x_1 - b_2x_2 - b_3x_1x_2, \text{ if } b_3 > b_1 + b_2 \tag{5}$$

$$y = a + b_1x_1 - b_2x_2 - b_3x_1x_2, \text{ if } b_3 < b_1 + b_2 \tag{6}$$

Multiple stressor effects were visualised to gain a better understanding of the shape and effect of multiplicative effects compared to additive effects of the same stressor pair. To this end, 3-Dimensional Partial Dependence Plots (3D-PDP) were created by predicting the abundance of a species from both the additive and multiplicative model for the combined stressor space whilst keeping all other stressors in the model at their mean. For 2500 combinations of a significant stressor pair, predictions were made from the minimum to maximum stressor values in the dataset on the normalised scale and back transformed to the original stressor values (see Table 2). Shapes and gradients from the 3D-PDP for the additive model were then compared to the multiplicative model to determine how our understanding of the stressor effect changes by adding multiplicative terms to the model. The standard errors (SE), a measure of precision in mean estimates, were displayed as an upper confidence band in the 3D-PDP (overlaid in grey). Finally, these SE were used to reflect uncertainty from model predictions in contour plots as the difference between the mean and upper bound for combinations of two stressors in the 3D-PDP. A narrow or wide confidence band in the 3D-PDP match low and high SE in the error contours, respectively. Contour plots display data availability along the single stressor gradients and in the combined stressor space to determine how data availability impacts model uncertainty for different stressor pairs. All 3D figures were created in R statistical software (R Core Team, 2020), using the ‘plotly’ (Sievert et al., 2021) package.

3. Results

3.1. Model overview

Model performance was expressed as variance explained (between 10.3 and 34.8 %) and adjusted R² (ranged from 0.10 to 0.34) for additive and multiplicative models (Table 3). For all species, the adjusted R² increased with the addition of first-order multiplicative interactive effects between stressors to the models, compared to those with additive effects of the same stressors alone (paired t-test, $t = 5.9545$, $p < 0.001$). Adjusted R² increased by 0.02 to 0.08 (Absolute Δ adj.R²) which was a 6 to 73 % relative increase in model performance (Relative Δ adj.R², Table 3). Models for

Magelona had the highest amount of variance explained in the additive and multiplicative models but had the smallest increase in model performance. On the other hand, model performance was most improved for *Aonides* sp., where 4 multiplicative effects between stressors increased relative performance by 73 % compared to the additive model (Tables 3, S1). The number of first order multiplicative interactions included in the multiplicative models ranged from 1 (e.g. *Macomona liliana*), to 6 (*Austrohelice crassa*) (Table 3). For detailed model summaries, see Supplementary Materials, Table S1.

3.2. Interactive effects

In the multiplicative models, a total of 34 significant stressors effects were observed across the eight species, of which 15 were synergistic, 14 antagonistic, and 5 additive based on coefficient estimates from the models (Table 4, Table S1). For multiplicative interactive effects (synergistic or antagonistic), at least one climate stressor (maxSST, SOI, and Exposure) was involved in 57 % of multiplicative interactions, whereas local stressors (Mud, OM, N-load) were included in 43 %. MaxSST was found to be the

Table. 4

Overview of terms retained in the multiplicative model and the interpretation of the interaction as either additive, synergistic or antagonistic from the model coefficient estimates.

| | Additive | Synergistic | Antagonistic | Total |
|----------|----------|-------------|--------------|-------|
| maxSST | | | | |
| Exposure | 2 | | | 2 |
| SOI | 1 | | | 1 |
| Mud | 1 | | | 1 |
| OM | | | | |
| N-load | 1 | | | 1 |
| maxSST | | 4 | | 4 |
| maxSST | | | 3 | 3 |
| maxSST | | 1 | 1 | 2 |
| maxSST | | 1 | 1 | 2 |
| maxSST | | 1 | | 1 |
| Exposure | | 2 | | 2 |
| Exposure | | 1 | 2 | 3 |
| Exposure | | | 2 | 2 |
| Exposure | | 1 | 1 | 2 |
| SOI | | 1 | | 1 |
| SOI | | 1 | 1 | 2 |
| SOI | | | 1 | 1 |
| Mud | | 1 | 1 | 2 |
| Mud | | 1 | | 1 |
| OM | | | 1 | 1 |
| Total | 5 | 15 | 14 | 34 |

most common interactive stressor for this dataset and was included in 12 multiplicative terms of which 7 were found to be synergistic. MaxSST noticeably interacted with Mud as the most frequent stressor pair (4 times), with synergistic interactions found in all instances (Table 4). MaxSST was further found to cause consistent antagonistic effects when interacting with SOI, another climate related stressor (Table 4). Sediment mud content was found to be the most dominant stressor causing synergistic effects, with 90 % of interactions identified as synergistic, of which 78 % were found to be with climate related stressors (maxSST, SOI, or Exposure) (Table 4). SOI was most often causing antagonistic effects (70 % of interactions), of which 72 % were antagonistic interactions with other climate stressors (maxSST or Exposure) (Table 4).

Significant multiplicative effects between stressor pairs were visualised and assessed, with examples for *Austrovenus stutchburyi* and *Magelona dakini* used to highlight the main effects observed (Figs. 1 and 2), which were consistent with shapes and effect for the remaining species (Supplementary Materials, Figs. S2–7). For *Austrovenus* significant multiplicative interactions were found for Mud:maxSST and Exposure:N-load, which were both

identified as synergistic from the coefficient-based assessment (Table 4). In both cases, 3D-PDPs confirm the synergistic nature of the interactive effect, with a steeper and more pronounced drop in abundance when both stressors increased, reflecting a ‘bowl’ shaped effect (Fig. 1). Compared to the 3D-PDP from the additive model, both stressor pairs showed a clear pattern with high predicted abundances in the multiplicative model when either (or both) stressors were low. For Mud:maxSST, this is clearly characterised by the high (red) edges along the low stressor gradients (Fig. 1B) compared to the drop along both low stressor edges in the additive model (Fig. 1A). For the Exposure:N-load interaction, the drop with increasing N-load along the low exposure edge is reduced compared to the additive model, but this effect is weaker along the low N-load gradient with an increase in exposure (Fig. 1C & D).

For *Magelona*, multiplicative effects between stressors included combinations of Exposure with local stressors (Mud, OM and N-load). 3D-PDP showed clear peaks in abundance in the multiplicative model whereas the additive model predominantly showed the effect of exposure, covering the general trend that abundances were highest in exposed sites (Fig. 2).

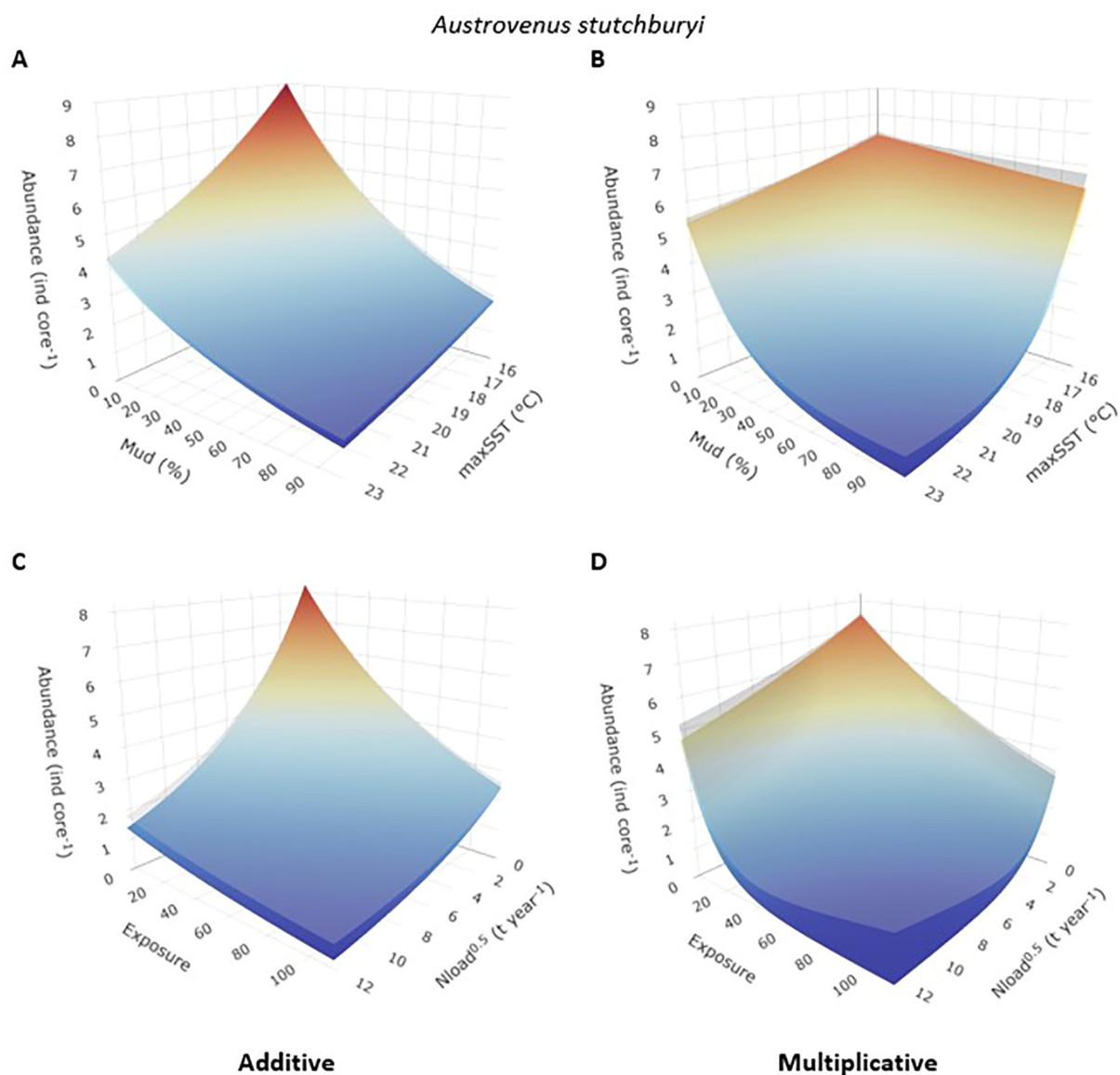


Fig. 1. Three-Dimensional Partial Dependence Plots (3D-PDP) for stressor pairs with significant interactive terms in multiplicative models for *Austrovenus stutchburyi*. For each combination of the stressor pair, abundance is predicted using the additive or multiplicative model (left and right column respectively), whilst keeping all other variables at their mean. Upper confidence bound (grey overlaid) reflect the Standard Error (SE). Multiplicative terms in the model include Mud:maxSST (A & B) and Exposure:N-load (C & D) interactions. Note colour scales continuously for all stressor pairs, whereas z-axes are scaled for each stressor pair.

Magelona dakini

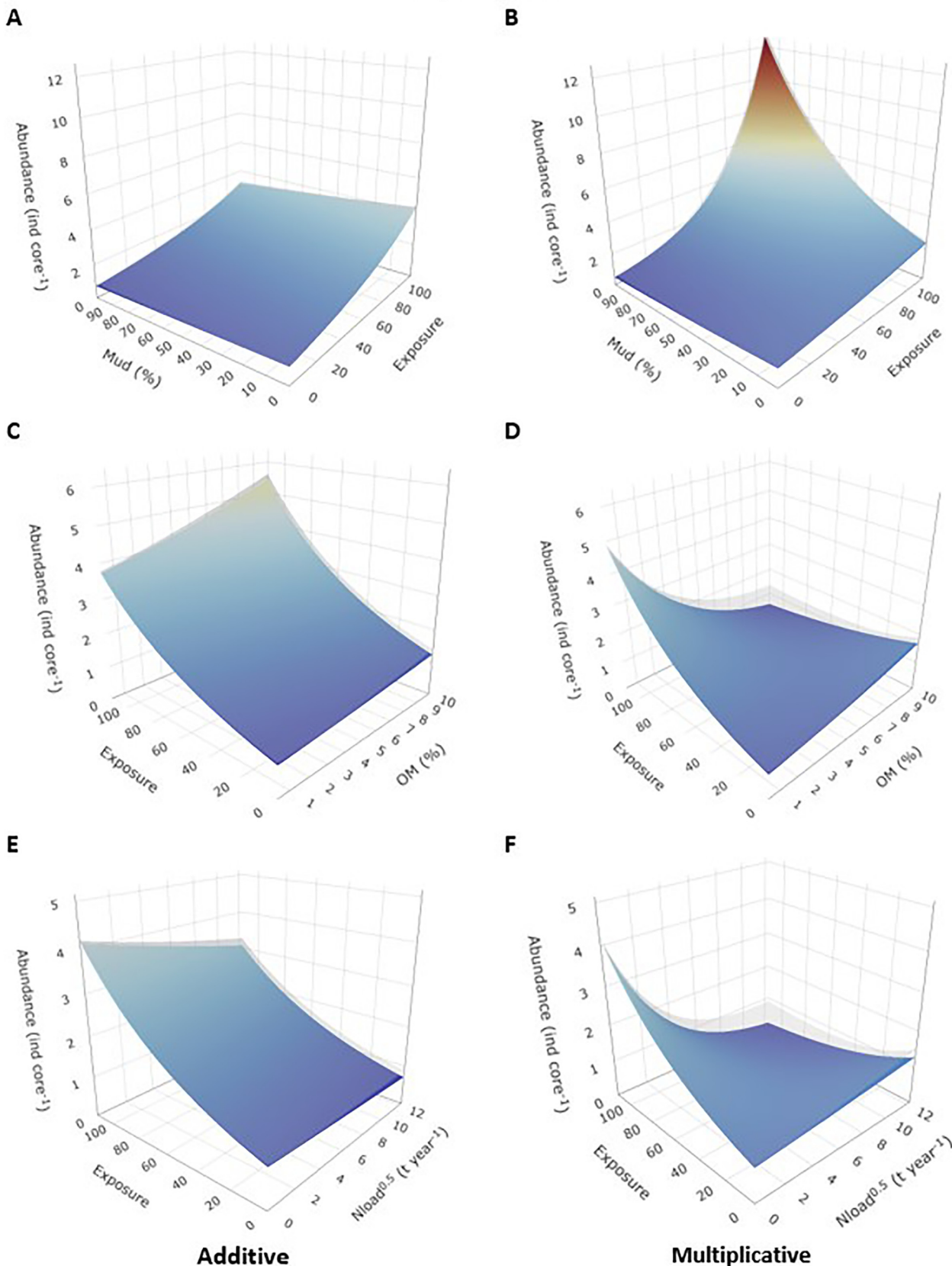


Fig. 2. Three-Dimensional Partial Dependence Plots (3D-PDP) for stressor pairs with significant interactive terms in multiplicative models for *Magelona dakini*. For each combination of the stressor pair, abundance is predicted using the additive or multiplicative model (left and right column respectively), whilst keeping all other variables at their mean. Upper confidence bound (grey overlaid) reflect the Standard Error (SE). Multiplicative terms in the model include Mud:Exposure (A & B), Exposure:OM (C & D), and Exposure:N-load (E & F) interaction. Note colour scales continuously for all stressor pairs, whereas z-axes are scaled for each stressor pair.

Coefficient-based assessments identified the Mud:Exposure interaction as synergistic, whereas the Exposure:OM and Exposure:Nload were characterised as antagonistic (Table 4). 3D-PDP illustrated that the nature of these interactions depends on the position of the (primary) peak. For synergistic effects a peak was found in the high-high corner (Fig. 2B), and antagonistic effects in the low-high corner (Fig. 2D & F). 3D-PDP further showed that the magnitude of stressor impacts differed substantially for the three stressor pairs with the biggest change in abundance predicted for the Mud:Exposure interaction, as shown by the difference in colour gradient in Fig. 2. Furthermore, both Exposure:OM and Exposure:N-load interactions showed a ‘saddle-shaped’ effect, with a small secondary peak and a directionality shift from an initial positive effect with increasing stressors shifting to a negative effect on abundance past the ‘saddle’ (Fig. 2D & F). Response surfaces showed lower predicted abundances and steeper gradients of change where both stressors were high than expected from the additive model, and contradicted the antagonistic classification (Fig. 2C–F). Directionality shifts were found for other species, and can occur with a large secondary peak (e.g. *Macomona* or *Aonides* in Figs. S2 and S5).

3.3. Uncertainty

Standard errors from model predictions reflected modelled uncertainty from data availability for multiplicative models compared to additive effects of the same stressor pair. For *Austrovenus*, Mud:maxSST had SE up to 0.3 or 0.6 in the additive and multiplicative model respectively (Fig. 3A

& B). SE were higher for the Exposure:N-load interaction, with SE ranging up to 0.5 in the additive and 1.6 in the multiplicative model which showed a strong increasing trend with increases in both stressors (Fig. 3C & D). For *Magelona*, uncertainty in all additive panels were low with SE up to 0.2 for Exposure with Mud and N-load (Fig. 4A & E), and 0.3 for Exposure:OM (Fig. 4C). Multiplicative models had higher SE, with highest observed values for Exposure:OM at a maximum of 0.8 when both OM and Exposure were high (Fig. 4D). For both *Austrovenus* and *Magelona*, an interactive effect between Exposure and N-load was observed, for which SE contours were similar in shape, but the magnitude of the SE varied between species with a much higher uncertainty for *Austrovenus* for the same stressor pair (Figs. 3D & 4F).

In general, additive models had lower SE than their multiplicative counterpart for all species and reflect the data availability per stressor, which are shown as rug plots along the x and y axis (Figs. 3 & 4, and Figs. S8–13). SE was generally low in additive models when both stressors were low, reflecting the data availability for low stress environments. SE increased when data became sparser along either axis, as was most noticeable for Exposure:N-load for *Austrovenus* (Fig. 3C). SE in the multiplicative models captured the data availability for stressor combinations instead of data availability for individual stressors. This always resulted in higher SE and clearly reflected the distribution of data points in the multi-stressor space of the uncertainty figures (Figs. 3 & 4, Figs. S8–13). Overall, N-load and Exposure were the stressors with highest uncertainty, which was found in both the SE contours as well as the Error estimates in the model summary

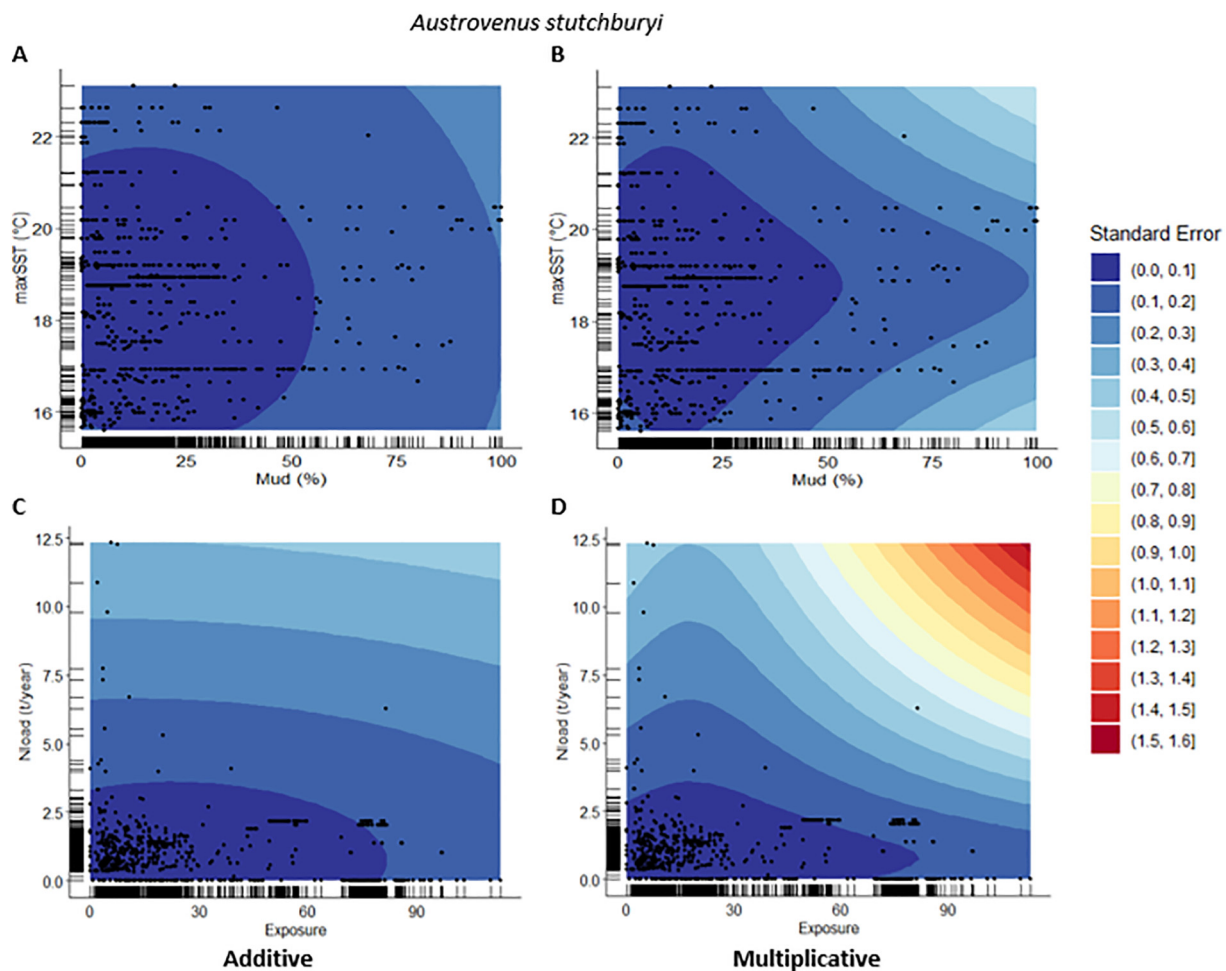


Fig. 3. Standard Error predictions for significant stressor combinations from additive and multiplicative models for *Austrovenus stutchburyi*. Figure contours capture the standard error with data availability displayed as rugs along the x and y axis for each of the individual stressors, and dots in the combined stressor space. Stressor interactions include effects between Mud:maxSST (A & B) and Exposure:N-load (C & D).

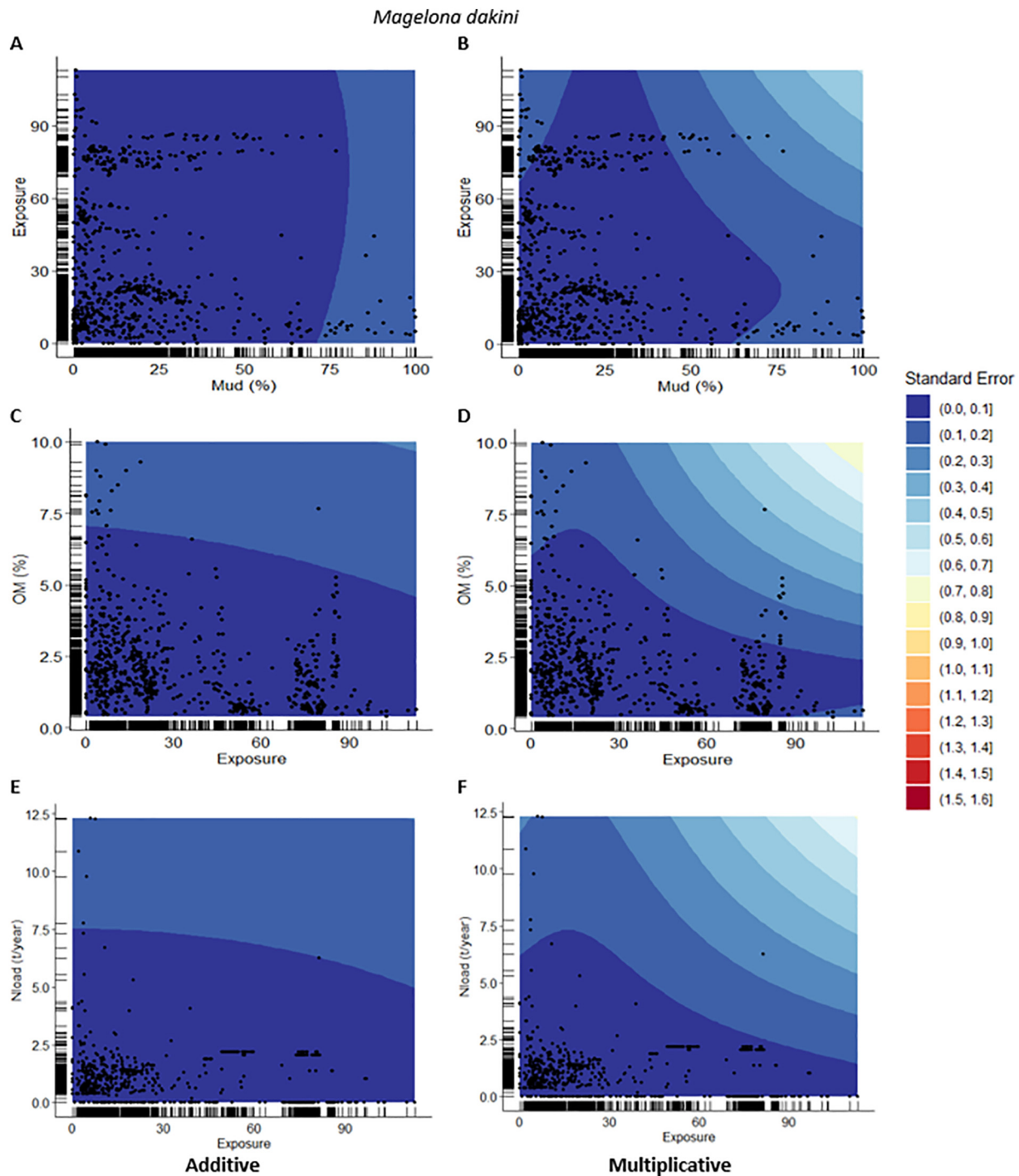


Fig. 4. Standard Error predictions for significant stressor combinations from additive and multiplicative models for *Magelona dakini*. Figure contours capture the standard error with data availability displayed as rugs along the x and y axis for each of the individual stressors, and dots in the combined stressor space. Stressor interactions include effects between Mud:OM (A & B), Exposure:maxSST (C & D), and Exposure:SOI (E & F).

(Table S1). SOI on the other hand was associated with lowest overall uncertainty in SE contour plots and model Error estimates, as data availability generally covered the combined stressor space well.

4. Discussion

In this study, regression models were applied to compare how the inclusion of multiplicative interaction terms, as opposed to simple additive effects, impacted the assessment of species responses to multiple stressors and how this altered our understanding of the associated risk and uncertainty. Firstly,

species models accounting for multiplicative stressor interactions outperformed additive models in all examples and showed that non-additive stressor effects dominated. Models that analyse multiple stressors using ecosystem data can assess real-world complexities, and identify consistencies in stressor interactions. Most noticeably, proxies for climate stressors (e.g. sea-surface temperature) were frequently included in multiplicative terms, often creating a synergistic effect in combination with local stressors (e.g. sedimentation). Secondly, 3D-PDP provide insight in the direction, magnitude and gradients of change, and were critically important to identify directional shifts where the nature of the interaction changed along increasing stressor

gradients. Coefficient based assessments, which simply provide one effect term for a stressor pair, were not able to capture the complexity observed in 3D-PDP and are at risk of mis-identifying interaction types. Finally, despite this increased understanding and reduced risk from missed or mis-identified stressor effects, including multiplicative effects in models did not lead to decreased uncertainty in model parameters, but rather better captured the true uncertainty generated by data availability.

4.1. Multiple stressors in a risk and uncertainty framework

In situations where the consequences of a threat are unknown or not well understood, uncertainty arises that must be identified and evaluated in risk assessments (Stelzenmüller et al., 2020). Through modelling species responses to stress, insight was gained from real-world patterns to minimise these unknown consequences. Models with higher explanatory power can reduce epistemic uncertainty, originating from an imperfect understanding of the system, and provide new insights to better manage stressors. By comparing models with additive and multiplicative stressor effects, we identified how much our understanding increased (i.e. increase in explanatory power) by accounting for multiplicative stressor interactions. In the comparison between additive and multiplicative models, the latter always resulted in higher explanatory power, ranging from 2.5 to 9.1 % increase in variance explained. However, the relationships between stressors and species abundance overall remained weak (between 10.3 and 34.8 % variance explained), which is in line with R^2 values from previous soft sediment stressor studies (e.g. Thrush et al., 2008b; Ellis et al., 2017a). The use of proxies for stressors (such as modelled data), most of which are integrative over space/time, may contribute to unexplained variability in the models. Furthermore, ontological uncertainty (i.e. natural variability) is high due to the ecological complexity in estuarine systems and the many drivers that influence the distribution and abundances of species besides their response to stress (Soberón and Peterson, 2005). In ecology, the importance of weak relationships is however recognised (Kneib, 1991; McCann, 2000; Thrush et al., 2008b), where studies that explain 10 % or more of the variance in empirical and modelling studies are recognised as ecologically meaningful. However, it is worth noting that this means much variance remains unexplained, and uncertainty persists.

In this study, non-additive effects dominated (Table 4). Especially for synergistic effects, a small change in a stressor can cause a disproportionately large effect and should result in more conservative management limits. Risk can arise when the actual consequences of (multiple) stressors deviate from what was previously expected (ISO, 2009). Past management criteria for acceptable stressor levels were often set for single stressors, like setting catch quotas to manage fisheries (Copes, 2019) or nutrient limits to mitigate eutrophication (Schiel and Howard-Williams, 2015). Newly identified stressor interactions are critical as they will predict altered responses to stress, and previously set thresholds may no longer work. For example, a synergistic effect between Mud and maxSST was found in 50 % of the species models where 3D-PDP showed steeper changes in species abundance compared to additive predictions. MaxSST was used as a proxy for increasing ocean temperatures (Sutton and Bowen, 2019), which impacts environments and communities globally (e.g. Sorte et al., 2010; Rogers-Bennett and Catton, 2019; Strydom et al., 2020). Sedimentation, causing increased mud content, was found to be a dominant local stressor that caused synergistic effects in 90 % of cases and is known to be an important driver of communities along estuarine gradients (e.g. Ysebaert et al., 2002; Thrush et al., 2003; Gimenez et al., 2005; Robertson et al., 2015). By identifying priority stressors, management practices can be updated, and in the short-term, focussing on local stressors can maximize effectiveness of management actions (Brown et al., 2013; Gurney et al., 2013; Weijerman et al., 2018). In the long-term however, the bigger issues, like climate change, need to be tackled as the frequency with which synergistic effects from climate stressors were found indicates they pose a high risk. The precautionary principle provides a robust strategy when dealing with deep uncertainty in stressor interactions to avoid ecological surprises (Côté et al., 2016; Gladstone-Gallagher et al., 2019a).

There is an ongoing debate about the classification and (mis-)identification of interaction types, and in particular sub-types (e.g. Brook et al., 2008; Piggott et al., 2015; Côté et al., 2016). A meta-analysis by Piggott et al. (2015) found that depending on the classification, different interaction types could be identified from the same datasets. This is problematic for management and consistency is needed. Previous studies using regression models distinguish additive, antagonistic, and synergistic effects from model coefficient estimates (but see Feld et al., 2016). To aid transparency and consistency in categorising stressor interactions, visualisation of stressor effects through 3D-PDP reduces the risk of mis-interpretation by showing the direction, magnitude, and gradients of change (Feld et al., 2016). The categorisation of antagonistic and synergistic effects from model coefficient estimates did not always match the complexity of patterns shown in the plots, which also showed the magnitude of the interaction changing along the stressor's gradient. Moreover, even when the same interaction type was identified, the shapes and gradients of change in response surfaces could differ, as exemplified by the synergistic effects for *Austrovenus* ('bowl' shaped) and *Magelona* ('peak' shaped). Gradients of change can identify tolerance to one or multiple stressors and a transition zone where steep and pronounced drops in abundance occur (e.g. yellow band for *Austrovenus*, Fig. 1) and tolerance is lost.

More importantly, some plots showed 'saddle' shapes, created by a change in the nature (antagonistic/synergistic/additive) of the interaction along the stressor gradients. For *Magelona*, where most stressors interactions were originally classified as 'antagonistic' effects (i.e. the combined effect of two stressors is smaller than was predicted additively), a directionality shift occurred for some stressor pairs from a positive effect with increasing stressors to a negative effect. The 3D-PDPs clearly showed the complex pattern with limited conditions for abundance when both stressors are low, a preferred range of conditions (which depends on the sensitivity to the other stressor, e.g. Hewitt et al., 2016), and a pronounced drop in abundance past these conditions (synergistic). 3D-surfaces are therefore critically important to identify directional shifts, as the complexity cannot be readily captured from coefficient-based assessments which simply provide one effect term calculated across the whole range of stressor gradients (or combinations), and require additional attention in risk-assessments and management.

This study focussed on pairwise stressor effects for selected single species responses. The visualisation of response surfaces in 3D-PDP provides a helpful asset when communicating complex stressor effects to managers and decision makers. However, they are limited to display two stressor effects simultaneously, whilst models contained more than two stressors and interactions between three or more stressors are possible. This is a particular limitation for certain stressor types, such as chemical pollutants, which often include a vast number of substances. Visualising the effect of any additional stressors would therefore require other techniques, like multidimensional scaling plots (e.g. from Principal Component Analysis or other ordination approaches). Although more complex effects from any number of stressors can be captured through dimensionality reduction or composite variables (e.g. Esselman et al., 2011; Clark et al., 2020), detailed information on changes along gradients is lost and it is more difficult to define stressor limits for management application. Furthermore, while selected single species models were used to identify consistencies in priority stressors, decision makers face the fact that they are not managing for a single species, but for an ecosystem. Novel methods exist that are better equipped to deal with multivariate (e.g. community) data, including Generalized Dissimilarity Matrices (GDM; Ferrier et al., 2002), Gradient Forests (GF; Ellis et al., 2012), and Joint Species Distribution Models (JSDM; Ovaskainen et al., 2017), but these are less intuitive in how stressor interactions are modelled and identified. The high-priority stressor interactions identified from single species models could be applied in JSDMs that account for environmental and biological variables driving communities through hierarchical modelling of species communities (HMSC; Ovaskainen and Soininen, 2011).

4.2. Uncertainty and data availability

Uncertainty for cumulative stressor models is rarely considered in the literature, despite a transparent treatment of uncertainty being critical to inform decision making (Stelzenmüller et al., 2018; Marcot, 2020). Uncertainty is a multi-dimensional concept, and the origin of uncertainty relates to the nature (epistemic vs. ontological), level, and location within the model (Walker et al., 2003). The impact of data availability on statistical uncertainty estimates was considered, acknowledging that there are other sources of uncertainty that were beyond the scope of this study (Stelzenmüller et al., 2020). Interestingly, for models including multiplicative stressor interactions, the decrease in epistemic uncertainty from increased explanatory power (as discussed above) did not translate to a decrease in model parameter uncertainty. On the contrary, the prediction errors were larger (as compared to the additive model uncertainty contours) and showed clearly the areas that were uncertain when data in the combined stressor space was lacking. Additive models, which are also predicting multiple stressor effects, were unable to capture this uncertainty and only picked up the uncertainty along individual stressor gradients. When models are derived from limited data for stressor combinations they will produce highly uncertain outputs, similar to extrapolations into unsampled space (Thuiller et al., 2004; Fitzpatrick and Hargrove, 2009; Zurell et al., 2012). Although the uncertainty measure was higher in multiplicative models, it's a more genuine reflection of the uncertainty that exists from data availability and is more informative for risk management

Transparent communication about model uncertainty therefore requires not only a direct measure of uncertainty itself, but also an understanding of the origin and the accurate representation of the type of uncertainty. Error contour plots enable communication and simultaneously provides feedback for environmental monitoring programs to ensure sampling efforts are conducted across the combined stressor space and highlights areas of insufficient data. Acknowledging that some combinations of stressors may not naturally occur in real-world systems (Williams and Jackson, 2007). Data limitations mostly occurred where both stressors were high, and better data cover will contribute to more robust modelling and potentially a reduction of uncertainty of cumulative stressor effects in the future. Alternatively, experts can be consulted to validate underlying (ecological) mechanisms to increase confidence in the predicted response (Singh et al., 2017). Overall, acknowledging uncertainty in management is critical, and together with 3D plots showing steep gradients of change, the higher uncertainty in model predictions in multiplicative models urges more conservative limits to be set for management that account for risk and uncertainty in multiple stressor effects.

5. Conclusion

There is an increasing awareness of the many complex cumulative effects that occur between multiple stressors, influencing the ways we manage marine ecosystems and the species therein. The risks and uncertainties that are associated with the analysis of stressor impacts receives little attention in the scientific literature, but a transparent treatment of risk and uncertainty is essential for informed decision making. Multiplicative stressor interactions were found to have an important effect when predicting the abundance of estuarine macrofauna species, and outperformed additive models for all species of interest. Here we argue that applying multiplicative models, visualising stressor interactions, and explicitly acknowledging the model uncertainties from data availability, provides a meaningful way to improve transparency and communication of risk and uncertainty from multiple stressor effects. Visualising the predicted response in the combined stressor space can reduce the risk of mis-identifying interaction types by revealing the direction, magnitude and gradients of change for important stressor pairs. It thereby provides insight in priority stressors, the tolerance of a species to stress, and appropriate limit setting for management that takes risk and uncertainty into account. Similarly, visualising model uncertainty demonstrated that although error terms were higher for multiplicative models, they were a more appropriate reflection of the uncertainty

originating from data availability. Although these models were applied to estuarine macrofauna, the need to implement multiple stressor research into risk and uncertainty frameworks extends to other ecosystems and the approach can be adopted in regression models in other environments to improve transparency and communication about cumulative stressor effects.

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CRedit authorship contribution statement

Vera Rullens: Conceptualization, Data curation, Methodology, Formal analysis, Visualisation, Writing original draft, **Fabrice Stephenson:** Conceptualization, Methodology, Writing – Review & Editing, Funding acquisition, **Judi Hewitt:** Conceptualization, Methodology, Writing – Review & Editing, Funding acquisition, **Dana Clark:** Data curation, Writing – Review & Editing, **Conrad Pilditch:** Writing – Review & Editing, **Simon Thrush:** Writing – Review & Editing, **Joanne Ellis:** Conceptualization, Methodology, Writing – Review & Editing, Supervision, Funding acquisition.

Declaration of competing interest

The authors declare that they have no known competing financial interests or personal relationships that could have appeared to influence the work reported in this paper.

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Appendix A. Supplementary data

Supplementary data to this article can be found online at <https://doi.org/10.1016/j.scitotenv.2022.156877>.

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