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Co-extinctions and co-compensatory species responses to climate change moderate ecosystem futures

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Abstract

Consensus has been reached that the sequential loss of biodiversity leads to a non-linear and accelerating decline in ecosystem properties. The form of this relationship, however, is based on theory and empirically derived observations that do not include species co-extinctions. Here, we use data from marine benthic invertebrate communities to parameterise trait-based extinction models that adjust the probability of species extirpation and compensation by including the dependencies between different species across a gradient of climate-driven environmental change. Our simulations reveal that the inclusion of static co-extinctions leads to more pronounced declines in the trajectories of sediment bioturbation - a process of great importance to the functioning of marine ecosystems - than those observed with sequential losses of single species. Compensatory mechanisms and allowance of the formation of new interactions derived from local and regional species pools moderate the compounding influence of co-extinction, but introduce additional variability in community response depending on the composition and functional role of incoming and outgoing species. Our observations emphasise the importance of accounting for local and regional community dynamics, especially in highly connected systems that are prone to extinction cascades, when projecting the ecosystem consequences of altered biodiversity.

37 Introduction

38 Localised species loss is generally expected to reduce ecosystem functioning (Cardinale et al. 2012). Evidence
39 consistently indicates that the magnitude and trajectory of species loss will reflect the relative vulnerabilities
40 of species to extinction (Payne et al. 2016), the covariance between extinction risk and the functional traits
41 of individual species (Solan et al. 2004), and the influence of post-extinction community dynamics (McIntyre
42 et al. 2007; Thomsen et al. 2017; Thomsen et al. 2019). Whilst the inclusion of these sources of variation can
43 lead to more relevant and realistic ecological projections (Naeem, 2008), they remain insufficient to explain
44 observed patterns in the biodiversity-function relationship. This is because the ecological consequences of
45 biodiversity adjustments are also expressed through longer-term changes in species interactions (Hughes,
46 2012), including those related to niche emergence (Cazzolla et al. 2018), that are disconnected from the
47 initial cause of extinction (Brook et al. 2008). Co-extinctions of obligate species, likely the most common (Koh
48 et al. 2004) but under-appreciated (Stork & Lyal, 1993) form of extinction, can arise during and after the
49 initial wave of primary extinctions (Koh et al. 2004; Dunne & Williams, 2009; Brodie et al. 2014) and have
50 additional functional consequences (Luza et al. 2024). Yet, the ecosystem implications of these secondary
51 extinctions (Sanders et al. 2015; Valiente-Banuet et al. 2014; Strona & Bradshaw, 2018; Strona & Bradshaw,
52 2022) have not been measured directly (Kehoe et al. 2020; Raine et al. 2018; Blanchard & Munoz, 2022),
53 compared to those of singular extinctions (Ives et al. 2004) or been incorporated into projections of the
54 ecosystem consequences of biodiversity loss (Cardinale et al. 2012). Theory suggests that the ecosystem
55 effects of co-extinctions are a reflection of network connectivity and community structure (Thébault et al.
56 2007; Dallas & Cornelius, 2015; Morton et al. 2022), but conflicting conclusions exist regarding how co-
57 extinctions affect functional diversity (Vieira et al. 2013; Petchey et al. 2008) and redundancy (Sanders et al.
58 2018; Biggs et al. 2020), making it challenging to determine the most likely ecosystem consequences of
59 biodiversity loss.

60

61 Failure to adopt a full community perspective and consider processes, such as co-extinction and co-
62 compensation, means that the generalised biodiversity-function curve is unlikely to generate robust
63 estimates of future ecosystem properties (Thomsen et al. 2017; Naeem, 2008; Garcia et al. 2021). Post-
64 extinction performance of a surviving community will depend not only on the absolute loss of species, but
65 on how associated adjustments to network connectivity and structure alter species interactions (Morton et
66 al. 2022) and the likelihood and/or expression of compensatory mechanisms (Thomsen et al. 2017; Thomsen
67 et al. 2019; Gonzalez & Loreau, 2009; Pan et al. 2016) across different contexts (Garcia et al. 2021). Species
68 with a low population density, slow life history, high trophic level and small geographical range size tend to
69 be associated with a high extinction risk (Purvis et al. 2000) and low compensatory capacity because the
70 species' range and niche are out of equilibrium (Sheth & Angert, 2018). In contrast, the number and
71 probability of extinction cascades are minimised in regions exhibiting high levels of geographic isolation
72 (Albouy et al. 2019) and maximised when species are most connected (Eklöf & Ebenman, 2006; Curtsdotter

et al. 2011; Baumgartner et al. 2020). The ecosystem consequences of species loss, compensation and secondary extinctions, however, do not necessarily reflect modifications to community structure (Thomsen et al. 2019; Brodie et al. 2014). Rather they reflect the extent to which alterations to functional roles (Fetzer et al. 2015), trait expression (Wohlgemuth et al. 2017; Cassidy et al. 2020; Sanders et al. 2024), and adjusted interactions with the environment (Dolbeth et al. 2019) and other species (Bimler et al. 2018) are presented over time (months to years; (Godbold & Solan, 2013; Touchton & Smith, 2011)). Hence, a species with a low (or high) probability of co-extinction may have a high (or low) potential to compensate through interactions with other surviving species (Vieira et al. 2014) but, in terms of ecosystem functioning, may deliver no compensation (Davies et al. 2012), partial, complete, or overcompensation (Pan et al. 2016). Should a species survive primary and secondary bouts of extinction, emergent compensatory responses (e.g. competitive release, alterations to resource partitioning, assemblage reorganisation (Thomsen et al. 2017; Thomsen et al. 2019)) increase the likelihood of alternative ecosystem outcomes (Thomsen et al. 2017) both within, and across, a range of spatio-temporal contexts (Thomsen et al. 2017; Albouy et al. 2019; Cassidy et al. 2020; Wardle & Zackrisson, 2005).

Here, we use data from marine benthic invertebrate communities from a region of the Barents Sea currently facing amplified climatic forcing (Lind et al. 2018) to parameterise trait-based extinction models that adjust the probability of species extirpation and compensation by including the dependencies between different species across an environmental gradient (Solan et al. 2020). In doing so, we explicitly recognise that the sequential loss of species is ordered, first, by extinction risk associated with the transition to increasingly boreal environmental conditions (Wang et al. 2020), and second, by the likelihood that the modified diversity and structure of the community associated with primary extinctions will lead to interaction-driven co-extinctions followed by numeric compensation from multiple taxa. We also assume, should compensation from the local species pool not be realised, that immigration of boreal-adapted species from the regional pool will introduce new interactions that revise extinction probabilities and modify local community dynamics (Albouy et al. 2019; Grebmeier, 2012; Kortsch et al. 2015) and associated ecosystem properties (Csapó et al. 2021; Ingvaldsen et al. 2021). In line with expectation, we find that including co-extinctions in our simulations hastens the decline in sediment bioturbation - a process crucial to the functioning of marine communities - regardless of extinction scenario. However, we show that the influence of co-extinction depends on location-specific interdependencies (Garcia et al. 2021; Albouy et al. 2019) between species interactions (Bimler et al. 2018), their vulnerability to change (McLean et al. 2019) and the degree of functional redundancy in the community (Thomsen et al. 2017; Naeem & Wright, 2003). We had anticipated that the influence of co-extinction on bioturbation would be maximised at the polar front, an area where boreal and polar communities converge, but the form of the biodiversity-function relationship varies along the length of the environmental gradient, reflecting differences in species turnover and community structure. Our models also reveal that the greatest declines in sediment bioturbation occur at low levels of

environmental forcing, despite elevated numbers of compensating species, presumably because species are close to, or at, the limit of their range distribution (Boakes et al. 2017). These findings emphasise the importance of including the full suite of species responses to perturbations when attempting to project the most likely ecosystem consequences of environmental forcing.

Methods

Study location and environmental gradient

We use macroinvertebrate data (Data Records S1, (Solan et al. 2020)) collected as part of a benthic survey of 6 stations (B17, B16, B15, Xs, B14, B13) each sampled four times using 0.1 m² USNL (United States Naval Laboratory) box cores in the North-western part of the Barents Sea shelf (Supplementary Data S1, Fig. S1), to parametrise models that predict how alterations to biodiversity associated with climate-driven change in environmental conditions affect seabed function. To minimize the effect of non-climatic drivers of change, stations were selected with comparable water depths (228–360m), sediment type and bottom fishing activity along the 30° E meridian. The transect of stations – from B13 in the south to B17 in the north, and with station Xs located between B14 and B15 at the location of the average southernmost extent of sea ice (Supplementary Fig. S1) intersects an established polar front (Jørgensen et al. 2015; Loeng, 1991) and exhibits a clear North-South separation in faunal assemblage structure (Solan et al. 2020). Although the precise physical location of the front is contested (Oziel et al. 2016; Oziel et al. 2017), the zone exhibits a relatively stationary behaviour (Onarheim & Teigen, 2018) and is becoming more persistent (Barton et al. 2018). We argue that this transect serves as a present-day gradient of climate-driven change, and use it to parameterise models that predict how associated stepped changes in biodiversity affect seabed function. We investigate differences in the magnitude and extent of forcing by parameterising our models with sequential station-to-station species vulnerabilities (based on inter-station transitions from: B17-B16 | B16-B15 | B15-Xs | Xs-B14 | B14-B13) and compared these simulations to equivalent extinctions based on change across the entire gradient (B17-B13). Hence, the most northerly (B17) and most southerly (B13) stations in our transect represent the most polar and most boreal community, respectively. In stepped scenarios between neighbouring stations, we assume a northward advance of climate change forcing such that the northernmost station represents the pre-extinction community (closest to pole), and the southernmost station represents the post-extinction community (closest to boreal).

Probabilistic modelling

We developed a probabilistic trait-based model to explore the effects of local extinction scenarios and the associated compensatory response of natural communities (Solan et al. 2004), and to predict how altered diversity associated with climatic-driven environmental change may affect seabed functioning in the Arctic. We establish the relationships between an index of community-level bioturbation potential (BP_c , Solan et

al. 2004), estimated from *per capita* contributions of sediment-dwelling invertebrates to sediment reworking (Supplementary Fig. S2) based on root-transformed mean body-size (across the entire transect; $B_i^{0.5}$, range: 0.008 – 1.225), abundance (A_i , range: 6 – 1350), predefined mobility (M_i , range: 1 – 4) and sediment reworking mode (R_i , range: 1 – 4):

$$BP_i = B_i^{0.5} \times M_i \times R_i$$

$$BP_p = BP_i \times A_i$$

$$BP_c = \Sigma BP_p$$

where BP_i is the bioturbation potential of an individual, BP_p is the bioturbation potential of a population of individuals and BP_c is the bioturbation potential of the community (Solan et al. 2004). Following Solan et al. (Solan et al. 2004), we use BP_c as a means to generate benthic ecosystem processes under novel scenarios. A summary table of species-specific $B_i^{0.5}$, A_i , M_i and R_i is provided in Supplementary Table S1.

As climate-driven changes across the Arctic will transform benthic communities through the selective removal of vulnerable taxa (Jørgensen et al. 2019), subsequently triggering compensatory responses, co-extinctions and increasing dominance of boreal-adapted taxa (Csapó et al. 2021), we selectively eliminate taxa from the pre-extinction species pool before calculating the response of the surviving community through compensatory mechanisms established for the regional species pool. As specific tolerances of Arctic invertebrates to climatic drivers are scarce (Degen & Faulwetter, 2019), we derive probability-based orders of species extinction and, reciprocally, their likelihood to compensate, from ranked vulnerabilities calculated across each pair of neighbouring stations based on the percentage difference in biomass between the pre- and post-extinction community for all taxa in the regional species pool (Supplementary Table S2, Code S1). Hence, a taxon with a high vulnerability score (i.e. highest biomass at the pre-extinction station and lowest biomass or absence at the post-extinction station) would have both a high probability of going extinct and a low probability to compensate. In adopting this approach, we explicitly recognise realistic, non-random changes in biodiversity that emerge as forcing progresses through multiple stages to avoid having to prescribe a single directional species-specific vulnerability that spans the entirety of the forcing (Bracken et al. 2008).

As taxa are sequentially extirpated and the surviving community numerically compensates to replenish biomass, a revised BP_c is calculated and taxa-specific contributions to BP_c are modified when they increase or decrease in abundance. At each iteration we calculate *per capita* contributions (BP_p) for all taxa in the regional community and run our simulations ($n = 500$ per scenario) until all taxa become locally extinct. However, each simulation is only valid to the level of biodiversity typically observed at the respective post-extinction station. That is, we assume the median species richness of each station reflects the existing local community which, in turn, is regulated within their temporal fluctuations (Gotelli et al. 2017). Similarly, we only allow for species to compensate up to the median abundance observed within the regional cluster of

northern versus southern stations (Northern cluster: B17, B16; Southern cluster: B15, Xs, B14, B13; Supplementary Fig. S3; Solan et al. 2020) to prevent any taxa increasing in abundance to improbable levels (Supplementary Code S2). As any alteration in local communities associated with climate change may be offset by more resilient taxa from a wider area (Ingvaldsen et al. 2021), we allow for taxa present in regional cluster species pools that were not present in the pre-extinction assemblage to be introduced and compensate (Garcia et al. 2021). This allows for the possibility that taxa from the regional pool can arrive and increase species richness, as would occur in a natural system.

Correlations, Co-extinctions and Co-compensations

As biotic interactions build up complex ecological networks through which the loss of one species can alter the vulnerability of other species (co-extinction, Sanders et al. 2015; Valiente-Banuet et al. 2014; Strona & Bradshaw, 2018; Strona & Bradshaw, 2022), we estimated interactions between taxa from positive and negative correlations in biomass across all station replicates ($n = 24$) and for each species (abundance > 1 , $n = 69$, Supplementary Fig. S4a). Whilst it has been argued that species correlations carry limited information on network interactions (Pinto et al. 2022; Loreau & de Mazancourt, 2013), they nevertheless provide a conservative starting point in the absence of such information. Hence, as correlation does not necessarily indicate co-dependency, we adopted a prudent approach by only selecting correlations that were 1.5 standard deviations outside the mean correlation score (0.0397; Supplementary Fig. S4b Table S3; 466 correlations, Supplementary Code S3). This reasonably assumes that the strongest correlations are more likely to indicate a genuine biotic interaction, as opposed to spurious and/or environmentally-driven taxa co-occurrences. Within each extinction iteration, we used these positive correlations to calculate the co-extinction risk of other taxa (multiple taxa can be simultaneously selected, Supplementary Code S4) or, in the absence of co-extinction, to reduce their probability of compensating. This approach ensures only the highest correlations are selected whilst allowing for indirect effects, such as competitive and/or predator release. To account for the greater chance of surviving taxa contributing to compensation following co-dependent release, we recalculate the probability of compensation within the community using the negative correlations of the extirpated co-dependent taxa (Supplementary Code S5). Following local extinction, we assume conditions are no longer supportive (Supplementary Code S5) to avoid compensation through re-introduction. The model is constrained to secondary extinction and compensatory mechanisms to avoid an uncontrollable cascade from the primary cause of extinction.

We acknowledge that multiple species can contribute to compensation, particularly when lost biomass is not entirely replaced by the initial responding species (Supplementary Code S6; Fig. S5). To improve the realism of our simulations of biodiversity change (Naeem, 2008), we limit the amount of compensation of each taxon to the median abundance observed in the regional species pool to allow several compensators to respond to an extirpation. In doing so, we avoid overinflation of the total biomass following compensation whilst

allowing biomass to vary with the removal and addition of species. When the median abundance of all taxa is reached during a simulation, biomass is lost from the system and a sequence of uncompensated extinction events is initiated until the next taxon from the regional species pool is introduced into the system. This follows the expectation that climate change will have negative consequences for seafloor biomass (Jones et al. 2013).

Statistical analyses

To examine the effect of extinctions on ecosystem functioning, we ran Generalised Additive Models (GAMs) with BP_c as the response variable given the non-linear nature of biodiversity-function relationships (Gross & Cardinale, 2005). A smooth term of species richness within each extinction scenario (by = scenario), and a smooth term of species richness in isolation were the main explanatory variables of interest. The extinction scenario was also included as a factorial covariate and the model was estimated using the fast Restricted Maximum Likelihood (REML) method, which is designed for fitting Generalised Additive Models (GAMs) on large datasets (Wood et al. 2015). The interaction was included to investigate whether the effect of extinctions differs with each spatially explicit extinction scenario (Supplementary Code S7). To deduce the best GAM fit, we conducted a backward stepwise selection on models estimated with the Maximum Likelihood (ML) method, informed by the Akaike Information Criteria (AIC), the deviance explained, and inspection of model residual patterns using the *visreg 2.7.0* and *lmtest 0.9-40* packages (Breheny & Burchett, 2017; Zeileis & Hothorn, 2002; Supplementary Table S4). To improve result standardisation and comparability, we ran linear models with the same structure of the best GAM estimated with fREML, and visually compared the partial estimated slopes of BP_c as a response to species richness using the *lm* function in base R (Supplementary Fig. S6).

To investigate differences in emergent adjustments to extinction probabilities as species are lost from the community within each extinction scenario, we used a series of linear models to examine changes in the climate vulnerability of all species going extinct ($_{ALL}$), species still present within the community ($_{PRESENT}$), species going extinct as a result of climate vulnerabilities ($_{CLIMATE}$) and species going extinct as a result of species co-dependencies ($_{CO-EXT}$) as species richness declined (Supplementary Table S5). All statistical analyses, data exploration and plotting were performed using the R statistical and programming environment (R Core Team, 2023) and the R packages ‘qgraph’ (visual correlation networks; Epskamp et al. 2012), ‘MetBrewer’ (formatting graphical outputs; Mills, 2022), ‘mgcv’ (Generalised Additive Models; Wood et al. 2015; Wood, 2011; Wood, 2017), ‘parallel’ (cluster computing of GAMs; R Core Team, 2023), ‘stats’ (correlation calculations and matrices; R Core Team, 2023) and ‘tidyverse’ (data exploration and plotting; Wickham et al. 2019). Code for creating model output figures can be found at the end of the supplementary information (Supplementary Code S8).

Results

Simulated ecosystem futures

In the absence of co-extinction and compensatory dynamics (Fig. 1a-f), we find that the form of the biodiversity-function curve approximates expectations (accelerating reductions in functioning with declining species richness) with notable climate-dependent differences in the form of the curve. Our simulations also commonly feature (except B15 to Xs, Fig. 1c) step changes within the species-function trajectory that reflect the loss or gain of species that disproportionately contribute to function. These become more pronounced when extinctions, ordered by climate vulnerability, incorporate co-extinctions (Fig. 1g-l). Co-compensatory mechanisms, however, temper the functional consequences associated with species loss (Fig. 1m-r), even when the proportion and number of compensating species increases with species loss (station Xs to B14, station B14 to B13; Fig. 2d and 3e). We also find that the taxa contributing most to community-level ecosystem functioning (% BP_c) transition from an Annelid dominated pre-extinction community (solid green line Fig. 3a-e) to a more diverse post-extinction community (dashed red line Fig. 3a-e), and that there is higher functional redundancy across the polar front (station B15 to Xs and Xs to B14; Fig. 2c).

Our simulations reveal differences in the form of the biodiversity-function curve for each of our scenarios (Table 1), and we observe non-linear changes in the rate and magnitude of function as species loss progresses (Table 2) that decrease as species loss extends below the level of biodiversity typically observed at the post-extinction station (dashed red vertical line, Fig. 2). Tube dwelling (Fig. 2m-r) and surficial modifying species (Fig. 2s-x) are lost first, whilst epifauna, deeper burrowers and conveyer belt lifestyles are preserved (Fig. 2m-x). A transect-wide transition from B17 to B13 exhibits a shallow biodiversity-function trajectory with minimal differences in uncertainty achieved between the pre-extinction and most likely post-extinction levels of species richness (Fig. 2f). Note, however, that the distribution of uncertainty across the species richness gradient does vary between each step of the extinction transition (compare panels Fig 2a-f). As compensation establishes, biodiversity levels may rise above pre-extinction species richness (= solid green vertical line, Fig. 2), although the extent of such an increase and any associated effect on functioning is scenario dependent. Within the most likely post-extinction levels of species richness window (area between the red and green vertical lines, all figures), both the range of the proportion of compensating species (%) and the level of species richness where compensating species is minimised or maximised varied between scenarios (Table 3, Fig. 2g-l), as did the mean ($\pm$ s.d.) number of compensating species (Table 3, Fig. 2g-l). Hence, the number, composition and proportion of compensating species are dependent on local circumstance, with the greatest capacity for compensation occurring in communities south of the polar front (Xs-B14 and B14-B13, Table 3, Fig. 2g-2l).

286 **Co-extinction and climate vulnerability**

287 Our simulations show that the incorporation of extinction probabilities related to climate vulnerabilities that
288 lead to primary extinctions, and species co-dependencies that lead to co-extinction, moderate ecosystem
289 outcomes based on differences in emergent adjustments to extinction probabilities. We find that, regardless
290 of whether species loss reflects bouts of primary or secondary extinctions, the taxa most vulnerable to
291 climate-driven change are preferentially removed (purple lines, Fig. 4a–f), although the rate of functional loss
292 does vary with scenario. As a result, the extinction probability of the surviving taxa adjusts and tends to be
293 lower than prior to extinction (compare purple to grey lines, Fig. 4a–f). Importantly our simulations reveal an
294 interplay between primary and secondary extinctions (compare blue to yellow lines, Fig. 4g–l) that can alter
295 the sequence of species loss, with synergistic, antagonistic or neutral ramifications for ecosystem functioning
296 (yellow lines, Fig. 4g–l). Indeed, the inclusion of co-extinction can either increase (B17–B16, Xs–B14, B14–B13
297 and B17–B13), decrease (B15–Xs) or have little effect on the preferential removal of the most vulnerable
298 species (compare blue to yellow line slopes, Fig. 4g–l). Thus, realised extinction risk is a product of both co-
299 dependency and climate driven forcing.

300

301 **Discussion**

302 Our simulations show that the ecological consequences of species loss associated with climate change reflect
303 the extent to which species traits covary with extinction risk (Solan et al. 2004), the compensatory response
304 of the surviving species (Thomsen et al. 2017; Thomsen et al. 2019) and the modifying role of environmental
305 context (Garcia et al. 2021; Albouy et al. 2019). However, they also emphasise the previously unaccounted
306 role of co-extinction in adjusting the number of species simultaneously being established and/or extirpated,
307 the realised level of extinction risk, and the order of sequential species loss, each having substantive
308 repercussions for ecosystem functioning (Luza et al. 2024). This is important because, when species co-
309 dependencies are acknowledged, they lead to different biodiversity-function trajectories to those that are
310 currently anticipated, lending support to the view that improved levels of ecological realism are necessary to
311 support the generation of robust environmental futures (Naeem, 2008; Garcia et al. 2021; Dolbeth et al.
312 2019; Gammal et al. 2020). Here, we embraced the modifying effects of biotic interactions on ecological
313 performance (Montoya & Raffaelli, 2010; Blois et al. 2013), where the rearrangement of species traits and
314 changes in dominance patterns (Wohlgemuth et al. 2017) within the post-extinction community are not
315 solely a function of specific extinctions and associated compensatory responses by the surviving community.

316

317 Co-extinctions are expected to hasten species loss (Dunn et al. 2009; Memmott et al. 2004) and minimise
318 functional diversity (Sellman et al. 2016). Our model simulations reveal amplified, sharper losses of
319 biodiversity and, subsequently, ecosystem functioning, indicating an erosion of functional capacity. Though
320 this is in broad agreement with global simulations (Strona & Bradshaw, 2018; Strona & Bradshaw, 2022), we
321 recognise that the effects of secondary extinctions on ecosystem functioning are likely to vary between

322 populations and environmental settings (Wohlgemuth et al. 2017). Nevertheless, species that are assumed
323 to be resilient based on single risk factors (Leonardsson et al. 2015; Ducatez & Shine, 2017; Di Marco et al.
324 2018), but are co-dependent on other species, may be compromised (Sanders et al. 2024) or lost earlier than
325 anticipated. Such resequencing may lead to divergent levels of ecosystem functioning depending on how
326 functionally pivotal the extirpated species are within the same context (Fetzer et al. 2015). In regions
327 experiencing amplified levels of climate change such as the Arctic, whether the functional architecture of
328 communities lead to the decline, maintenance or enhancement of ecosystem functioning will also be
329 dependent on the extent of species immigration, post-borealisation species interactions (and resulting
330 compensatory responses) are (Thomsen et al. 2017; Thomsen et al. 2019), and the level of functional
331 redundancy within replacement taxa (Garcia et al. 2021). Here, we find that incorporating multi-taxa
332 compensatory mechanisms sufficiently reduces the ecological consequences of species loss in each of our
333 scenarios and lessens the effect of losing dominant, highly productive species from local communities with
334 low functional redundancy. Further, we note that the rate of introduction of species from the wider species
335 pool can match or exceed the rate of extinction experienced within the same habitat (Ellis et al. 2012; Sax et
336 al. 2002), leading to stasis or an increase in local biodiversity, with concomitant effects on functioning. As
337 higher diversity is often assumed to have a positive effect on ecosystems, a naïve evaluation might view the
338 latter as a positive, albeit unintuitive, ecosystem response to external forcing (Salo & Gustafsson, 2016; Arese
339 Lucini et al. 2020). Yet, our results indicate that the effect of increased biodiversity on ecosystem functioning,
340 particularly when above the currently observed species richness, can be highly variable and, likely, transitory,
341 as changing circumstances further moderate species co-dependencies and final carrying capacity
342 (Woodworth-Jefcoats et al. 2017). For example, species introductions can exacerbate native species
343 extinctions (Catford et al. 2018), especially when introduced species are predators or pathogens (Pyšek et al.
344 2017) and/or cause competitive release (Castorani et al. 2005). The latter, however, is not expected to be
345 widespread (Davis, 2003) and will be influenced by the effects of environmental context (Melbourne et al.
346 2006).

347
348 While our simulations predict a decline in ecosystem functioning with increased "borealisation" across all our
349 scenarios, the weakest effect occurs at the polar front transition. One explanation might be that the mixing
350 of species and functional groups from the northern and southern species pools (Solan et al. 2020) delay a
351 reduction in functional diversity (Frainer et al. 2017; Frainer et al. 2021). Yet, it is also possible that
352 environmental variation associated with the juxtaposition of water masses will condition resilience (Keith et
353 al. 2008; Renes et al. 2020; Hillebrand et al. 2010). This finding is important because it argues that complex
354 relationships exist between temporal patterns of species turnover and extinction risk reinforcing the view
355 that species can endure climate change associated extinction by persisting in spatio-temporal refugia
356 (Maclean et al. 2015). As our study design allowed us to compare the response of northern and southern
357 species pools (Solan et al. 2020; Jørgensen et al. 2015), we were able to establish that a subset of taxa

dominates species contributions to functioning and that, despite high numbers of compensating species, the greatest functional losses tend to occur at low levels of perturbation. Hence, the potential for compensatory and co-dependent mechanisms to buffer the consequences of biodiversity loss will depend on the level and extent of functional redundancy (Naeem & Wright, 2003) - here, maximised at the polar front - and the net functional role of ingoing and outgoing taxa (Garcia et al. 2021). Interventions aimed at maintaining or improving ecosystem functioning may, therefore, be best placed at the outermost edges of the species pool and/or where environmental conditions are less stochastic (Gerber et al. 2003).

A contemporary focus in ecology is deciphering variations in the relationship between biodiversity and ecosystem function across local and regional spatio-temporal scales (Gonzalez et al. 2020). Our findings reveal that the shape, magnitude, and variability of post-extinction community functioning are moderated by local environmental conditions (Ratcliffe et al. 2017) and acknowledge the significance of environmental heterogeneity (Wohlgemuth et al. 2017; Bulling et al. 2008; Boyd et al. 2016; Gammal et al. 2020), species arrangement (Wohlgemuth et al. 2016), vulnerability (Kortsch et al. 2015), and the differential expression of response traits (Cassidy et al. 2020; Sanders et al. 2024; Williams et al. 2024). We contend that management and conservation efforts will benefit from considering how and when species responses to external pressures result in changes to extinction risk and alter functional outcomes. Progression in this area will require a transition from conducting before-after extinction assessments to undertaking stepwise assessments that consider the full and graduated extent of progressive forcing (Fukami & Wardle, 2005). It will also require assembly of detailed information about multitrophic network interactions for communities of interest, and empirical tests of model findings to refine model construction. As we demonstrate here, the functional consequences of biodiversity loss appear to be gradual and cumulative, but the rate, direction and magnitude of ecological change can be positively or negatively modified by species co-dependencies even as the expression of pressures intensifies (Hillebrand et al. 2010).

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Ethics declarations

392 This study was approved by the University of Southampton Animal Welfare and Ethical Review Body (ERGO
 393 II, #64402). For the purpose of open access, the author has applied a CC BY public copyright licence to any
 394 Author Accepted Manuscript version arising from this submission.

395

396 **Competing interests**

397 The authors declare no competing interests.

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714

715 **Tables**

716 **Table 1** | Analysis of variance (ANOVA, two tailed) parametric coefficients generated from the generalised
717 additive model (GAM) of bioturbation potential loss. Except for one scenario (station B16 to station B15),
718 each local extinction event results in a biodiversity-ecosystem functioning curve that is significantly (***)
719 different to the regional extinction scenario (baseline, station B17 to station B13).

Pairwise comparison	Mean difference	Std. error	t value	Significance
B17-B13 to B17-B16	68.172	1.244	54.781	< 0.0001
B17-B13 to B16-B15	16.439	17.998	0.913	0.361
B17-B13 to B15-Xs	-329.480	5.864	-56.189	< 0.0001
B17-B13 to Xs-B14	185.129	0.888	208.460	< 0.0001
B17-B13 to B14-B13	-35.871	2.486	-14.427	< 0.0001

722 **Table 2** | Approximate significance of smooth term “species richness” in each extinction scenario used in
723 the generalised additive model (GAM) of bioturbation potential loss. The edf (effective degrees of freedom
724 of smooth terms) represents the complexity of the smoother, with an edf of 1 equivalent to a straight line
725 between x (species richness) and y (**BP_c**). The Ref.df and F columns are test statistics used in an ANOVA
726 (two-tailed) to determine overall significance (Sig.) of the smoother (unable to draw a horizontal line
727 through the 95% confidence interval of the GAM).

Extinction Scenario	edf	Ref.df	F	Sig.
B17-B13	8.813	8.987	45603	< 0.0001
B17-B16	8.022	8.253	29309	< 0.0001
B16-B15	8.486	8.738	27652	< 0.0001
B15-Xs	5.981	6.309	1567	< 0.0001
Xs-B14	8.699	8.932	24758	< 0.0001
B14-B13	7.092	7.364	9942	< 0.0001

730 **Table 3** | The range in the proportion of compensating species (%), the absolute number (mean ± s.d.) of
731 compensating species and the level of species richness where compensating species is minimised or
732 maximised (indicated by SR in subscript) between the most likely post-extinction levels of species richness
733 window (area between the red and green vertical lines, all figures).

Extinction Scenario	Compensating species			
	Proportion of total species (%)		Absolute number (mean $\pm$ s.d.)	
	min _{n,SR}	max _{n,SR}	min _{n,SR}	max _{n,SR}
B17-B13	5 _{n=395, SR=39}	15 _{n=201, SR=12}	1.46 $\pm$ 0.91 _{n=169, SR=11}	3.76 $\pm$ 3.64 _{n=3086, SR=51}
B17-B16	7 _{n=474, SR=51}	12 _{n=554, SR=18}	1.52 $\pm$ 0.54 _{n=443, SR=17}	4.67 $\pm$ 2.51 _{n=1816, SR=52}
B16-B15	5 _{n=2391, SR=42}	14 _{n=417, SR=15}	1.78 $\pm$ 0.61 _{n=427, SR=17}	2.54 $\pm$ 1.08 _{n=2159, SR=41}
B15-Xs	7 _{n=2060, SR=27}	9 _{n=1313, SR=16}	1.45 $\pm$ 0.44 _{n=1313, SR=16}	3.50 $\pm$ 1.70 _{n=1580, SR=40}
Xs-B14	9 _{n=1608, SR=40}	78 _{n=293, SR=11}	3.69 $\pm$ 2.40 _{n=1608, SR=40}	8.57 $\pm$ 3.81 _{n=293, SR=11}
B14-B13	15 _{n=4348, SR=26}	37 _{n=444, SR=16}	2.18 $\pm$ 0.96 _{n=79, SR=13}	5.95 $\pm$ 3.38 _{n=444, SR=16}

735 Figure legends

736 **Fig. 1 |** Changes in community bioturbation potential ($\log(BP_c)$) following climate-driven extinctions (upper
737 panels), combined with interaction-derived co-extinctions (middle panels) and post-extinction
738 compensations (bottom panels) associated with step-wise environmental transitions from stations **(a,g,m)**
739 B17- B16, **(b,h,n)** B16 -B15 **(c,i,o)** B15 -Xs **(d,j,p)** Xs-B14 **(e,k,q)** B14-B13 and the transect-wide transition from
740 stations **(f,l,r)** B17- B13 in the Barents Sea. Colour intensity (grey—blue) reflects an increasing density (low
741 to high) of data points with the pre-extinction species richness (vertical green solid line) and predicted post-
742 extinction species richness (vertical red dashed line) represented. Co-extinctions lead to an increase in colour
743 intensity along the main species-function trajectory, whilst compensations increase the spread of data
744 points. Simulations, $n = 500$ per panel.

745
746 **Fig. 2 |** Predicted biodiversity-ecosystem function relation curves (mean $\pm$ s.e., first row) represented with
747 a generalised additive model (GAM, solid lines) and the standard error (shaded areas). In the second row,
748 post-extinction compensations (mean $\pm$ s.e., number, in yellow) and the proportion of species (purple, >1
749 when the number of compensating taxa relies on greater influx from the regional species pool) are shown.
750 The reorganisation of functional groups characterised by their mobility (third row) and sediment reworking
751 (fourth row) associated with step-wise environmental transitions are shown between stations (B17-B16,
752 panels **a,g,m,s**; B16-B15, panels **b,h,n,t**; B15-Xs, panels **c,i,o,u**; Xs-B14, panels **d,j,p,v**; B14-B13, panels
753 **e,k,q,w**) and the transect-wide transition from stations B17-B13 (panels **f,l,r,x**) in the Barents Sea. The pre-
754 extinction species richness (vertical green solid line) and predicted (median of observed data) post-extinction
755 species richness (vertical red dashed line) define the upper and lower boundaries of the most ecologically
756 realistic output.

757
758 **Fig. 3 |** Taxonomic reorganisation during simulated extinction events following step-wise environmental
759 transitions from station **(a)** B17-B16, **(b)** B16-B15 **(c)** B15-Xs **(d)** Xs-B14 **(e)** B14-B13 and the transect-wide
760 transition from stations **(f)** B17-B13 in the Barents Sea. Colour shading (white, low—dark blue, high)
761 represents the relative contributions of individual taxa to BP_c at each sequential level of local extinction. The
762 pre-extinction species richness (vertical green solid line), predicted post-extinction species richness (vertical
763 red dashed line) and subset of twenty taxa that contribute most to functioning pre-extinctions are
764 represented. Contributions above 20% greyed.

765
766 **Fig. 4 |** Changes in mean extinction probability ($\log$) of species following step-wise environmental transitions
767 from station **(a-g)** B17-B16, **(b-h)** B16-B15 **(c-i)** B15-Xs **(d-j)** Xs-B14 **(e-k)** B14 B13 and the transect-wide
768 transition from stations **(f-l)** B17-B13 in the Barents Sea. Colours represent the extinction risk for all species
769 (purple), species still present within the community (grey), species going extinct because of climate

770 vulnerabilities (blue), and species going extinct as a result of species co-dependencies (yellow). The pre-
771 extinction species richness (vertical green solid line) and post-extinction species richness (vertical red dashed
772 line) are also shown.

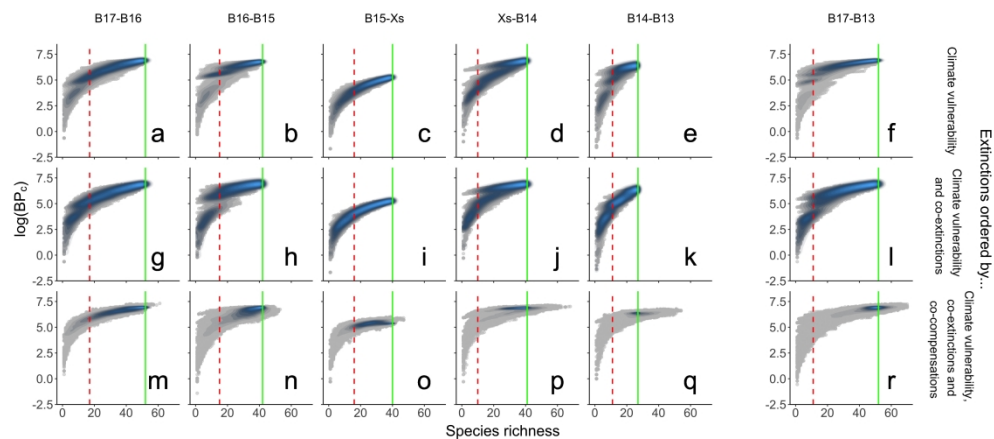


Fig. 1 | Changes in community bioturbation potential ($\log(BP_c)$) following climate-driven extinctions (upper panels), combined with interaction-derived co-extinctions (middle panels) and post-extinction compensations (bottom panels) associated with step-wise environmental transitions from stations (a,g,m) B17- B16, (b,h,n) B16 -B15 (c,i,o) B15 -Xs (d,j,p) Xs-B14 (e,k,q) B14-B13 and the transect-wide transition from stations (f,l,r) B17- B13 in the Barents Sea. Colour intensity (grey—blue) reflects an increasing density (low to high) of data points with the pre-extinction species richness (vertical green solid line) and predicted post-extinction species richness (vertical red dashed line) represented. Co-extinctions lead to an increase in colour intensity along the main species-function trajectory, whilst compensations increase the spread of data points. Simulations, $n = 500$ per panel.

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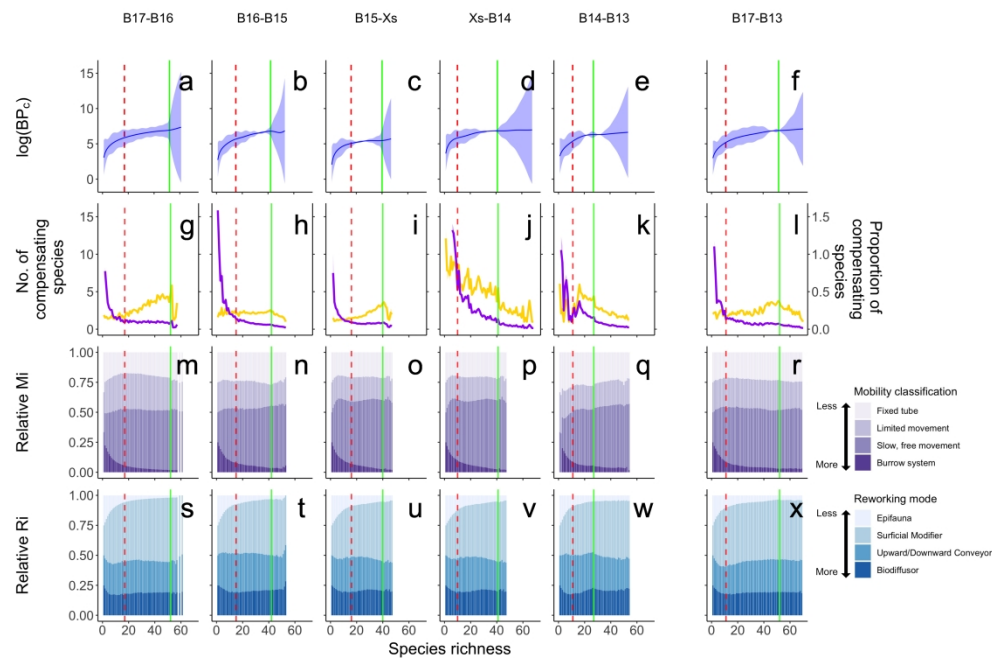


Fig. 2 | Predicted biodiversity-ecosystem function relation curves (mean $\pm$ s.e., first row) represented with a generalised additive model (GAM, solid lines) and the standard error (shaded areas). In the second row, post-extinction compensations (mean $\pm$ s.e., number, in yellow) and the proportion of species (purple, >1 when the number of compensating taxa relies on greater influx from the regional species pool) are shown. The reorganisation of functional groups characterised by their mobility (third row) and sediment reworking (fourth row) associated with step-wise environmental transitions are shown between stations (B17-B16, panels a,g,m,s; B16-B15, panels b,h,n,t; B15-Xs, panels c,i,o,u; Xs-B14, panels d,j,p,v; B14-B13, panels e,k,q,w) and the transect-wide transition from stations B17-B13 (panels f,l,r,x) in the Barents Sea. The pre-extinction species richness (vertical green solid line) and predicted (median of observed data) post-extinction species richness (vertical red dashed line) define the upper and lower boundaries of the most ecologically realistic output.

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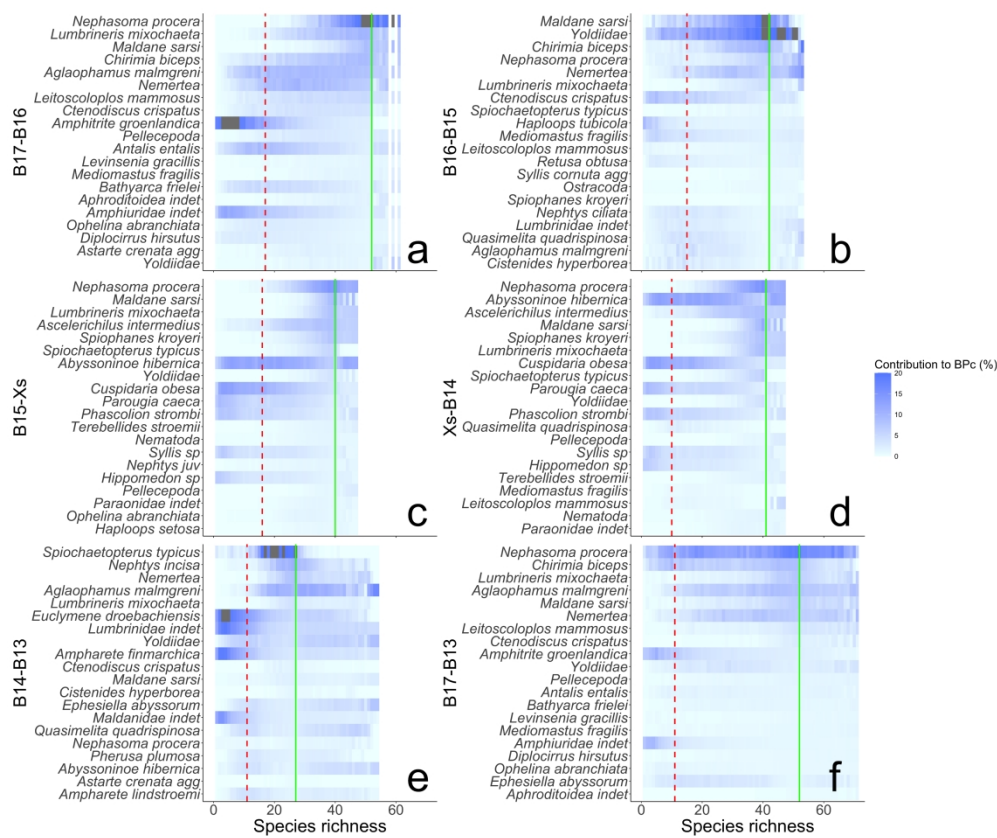


Fig. 3 | Taxonomic reorganisation during simulated extinction events following step-wise environmental transitions from station (a) B17-B16, (b) B16-B15 (c) B15-Xs (d) Xs-B14 (e) B14-B13 and the transect-wide transition from stations (f) B17-B13 in the Barents Sea. Colour shading (white, low□dark blue, high) represents the relative contributions of individual taxa to BP_c at each sequential level of local extinction. The pre-extinction species richness (vertical green solid line), predicted post-extinction species richness (vertical red dashed line) and subset of twenty taxa that contribute most to functioning pre-extinctions are represented. Contributions above 20% greyed.

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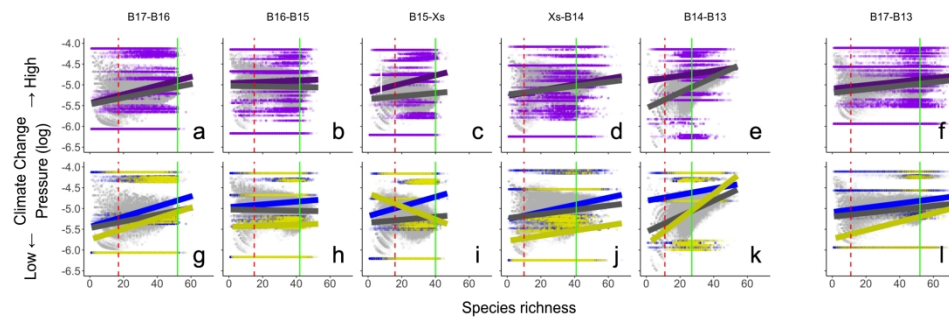


Fig. 4 | Changes in mean extinction probability (log) of species following step-wise environmental transitions from station (a-g) B17-B16, (b-h) B16-B15 (c-i) B15-Xs (d-j) Xs-B14 (e-k) B14 B13 and the transect-wide transition from stations (f-l) B17-B13 in the Barents Sea. Colours represent the extinction risk for all species (purple), species still present within the community (grey), species going extinct because of climate vulnerabilities (blue), and species going extinct as a result of species co-dependencies (yellow). The pre-extinction species richness (vertical green solid line) and post-extinction species richness (vertical red dashed line) are also shown.

254x99mm (300 x 300 DPI)