

# Compensation alters estimates of the number of species required to maintain ecosystem functioning across an emersion gradient: A case study with intertidal macroalgae

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## Abstract

1. Whether more species are required to maintain ecosystem functioning as spatial scale increases or across environmental gradients has frequently been studied by examining whether different species drive ecosystem functioning in different sites. However, this approach does rule out the counterfactual scenario where a few species could potentially maintain ecosystem functioning across sites as this requires examining which species can (or cannot) compensate for the loss of others.
2. Here, I used an observational study and a field-based transplant experiment to examine the effects of species loss on biomass productivity in an intertidal marine macroalgal system. I calculated the number of species required to maintain biomass productivity across four depth zones reflecting a water emersion gradient using two commonly used observational approaches. Then, I combined hypothetical simulated extinction scenarios with field-based transplant data of relative growth rates of all species across the four depth zones to explore how the number of species required to maintain biomass productivity across depth zones changed under counterfactual scenarios where species compensated for species loss.
3. The observational analyses suggested that between three and four species were required to maintain productivity across the depth zones. The simulated extinction scenarios did not. Rather, decreases in biomass productivity due to the loss of some species (e.g. *Fucus spiralis*, *Ascophyllum nodosum*) were easily compensated by other species (e.g. *Fucus vesiculosus*). However, for some species like *F. vesiculosus*, the extinction simulations suggested that compensation would be unlikely.
4. Commonly used observational approaches may overestimate the number of species required to maintain ecosystem functioning across environmental gradients and spatial scales.

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## KEYWORDS

biodiversity, compensation, ecosystem process, intertidal, scale

## 1 | INTRODUCTION

Both theory and empirical work have shown that biodiversity loss can negatively affect the functioning of ecosystems (Cardinale et al., 2012; Tilman et al., 2014). But, most of the ecological work linking the loss of biodiversity to ecosystem functioning (e.g. productivity, grazing rates etc.) has taken place at small spatial scales (Gonzalez et al., 2020; Isbell et al., 2017). In these small-scale studies, the rates of single ecosystem functions can frequently depend on one or a few dominant and high functioning species (Cardinale et al., 2011; Leibold et al., 2017; Smith et al., 2020; Smith & Knapp, 2003) although there is some evidence that more species are required when considering a variety of different ecosystem functions (Hector & Bagchi, 2007; Zavaleta et al., 2010). Large spatial scales are typically associated with high levels of environmental heterogeneity (Hart et al., 2017). If species respond to that environmental heterogeneity and dominate in different environmental conditions, more species may be required to maintain the rate of any given ecosystem function at large spatial scales (Gamfeldt et al., 2023; Isbell et al., 2018; Loreau et al., 2003).

Whether more species are required to maintain single ecosystem functions at large compared to small spatial scales or across environmental gradients has been studied by examining if different species drive ecosystem functioning in different sites. This has been done using both experimental (Isbell et al., 2011) and observational data (Genung et al., 2023; Schiettekatte et al., 2022; Simpson et al., 2022; Winfree et al., 2018) in a variety of ecological systems. For example, Isbell et al. (2011) showed that different grassland plant species drove productivity in different spatial locations; Winfree et al. (2018) showed that different bee species pollinated the same crops in different parts of a landscape; and Schiettekatte et al. (2022) showed that many ecosystem functions performed by coral reef fish (e.g. herbivory and N-excretion) are dominated in a given site by a few species but that the identity of those species tends to vary across sites. Some of these studies (Isbell et al., 2011; Winfree et al., 2018) suggest that, because different species are associated with functioning in different parts of a landscape, more species may be required to maintain ecosystem functioning at large compared to small spatial scales.

An issue with this approach is that it does not rule out the counterfactual scenario that one or a few species could potentially maintain ecosystem functioning across sites. For example, if a dominant species goes extinct at one site but gets compensated by a different, less abundant species in the community or a species that colonises from another site, ecosystem functioning across sites may not be strongly affected (Diaz & Ernest, 2022; Fetzer et al., 2015; Leibold et al., 2017; Schrofner-Brunner et al., 2023). Many of the observational studies cited previously provide defensible arguments for

why compensation may be unlikely (e.g. lack of evidence for spatial density compensation, Winfree and Kremen (2008) or potentially high levels of environmental specialisation among different species, Simpson et al. (2022)). However, in my view, this assumption has not been properly scrutinised in the context of biodiversity–ecosystem functioning research.

A range of evidence suggests that some species could compensate for the loss of others in some ecological systems. First, experiments where species are removed from an intact community often find substantial compensation of individual density or biomass by other species (Kardol et al., 2018). Second, in natural systems, asynchrony in species' population fluctuations, which suggests compensation among species, is observed frequently even though population synchrony seems to be more common overall (Gonzalez & Loreau, 2009; Houlihan et al., 2007; Lamy et al., 2019; Vasseur et al., 2014). Third, species are often absent from certain sites because of competition and not due to an innate inability to survive, grow and reproduce (Germain et al., 2018; Kraft et al., 2015; Schrofner-Brunner et al., 2023; Wisheu, 1998). In line with this last point, many competition models predict that species do not perform (i.e. survive, grow and reproduce) best where they are found to be most abundant (Fox, 2012; Rosenzweig, 1981). Rather, either many species perform best under similar environmental conditions (Rosenzweig, 1981), or species performance is decoupled from abundance due to complex species interactions (Fox, 2012). These models have substantial empirical support. For example, the growth rates of North American trees are decoupled from both abundance (McGill, 2012) and probability of occurrence metrics derived from species distribution models (Bohner & Diez, 2020; Midolo et al., 2021). Thus, even if the high levels of compensation following species loss are not the norm as some have suggested (Gonzalez & Loreau, 2009; Winfree & Kremen, 2008), there is enough evidence of species compensation to warrant a critical view of its consequences for understanding whether more species are required to maintain ecosystem functioning at large compared to small spatial scales or across environmental gradients.

I used an observational study along with a field-based transplant experiment to study the effects of species loss on biomass productivity in a marine intertidal system. The system consists of communities of four furoid marine macroalgae species in four depth zones which reflect a water emersion gradient on the Swedish West Coast. To do this, I first analysed the number of species required to maintain biomass productivity across the four depth zones using two observational approaches. I then examined the sensitivity of biomass productivity to species loss across depth zones by simulating counterfactual scenarios of species loss with different levels of compensation from other species. Species responses to the depth zone in the counterfactual scenarios were based on data from a field-based

transplant experiment. The observational analyses suggested that between three and all four species were required to maintain biomass productivity across the depth zones. In contrast, the simulated counterfactual scenarios showed that decreases in biomass productivity due to the loss of some species can often be compensated by other species. However, this was not always the case and these counterfactual simulations suggested that biomass productivity due to the loss of certain species would probably not be compensated by other species in this system. Nevertheless, in this case study, using only observational data would probably lead to an overestimation of the number of species required to maintain biomass productivity across the depth zones.

## 2 | MATERIALS AND METHODS

### 2.1 | Data collection

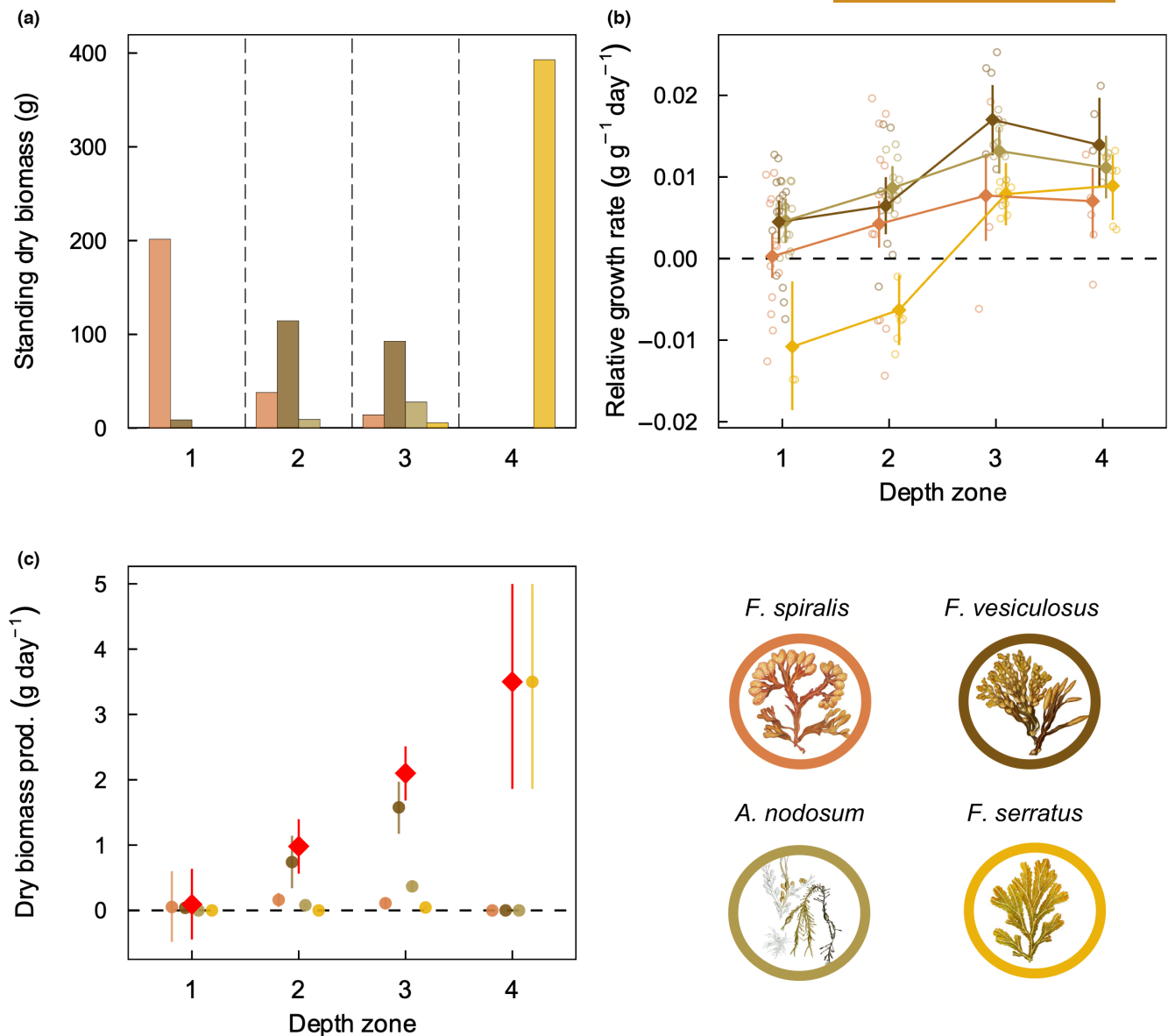
The data were collected on the Swedish West Coast (Tjärnö Marine Laboratory, Latitude: 58.875 DD; Longitude: 11.145 DD). I had permission to do fieldwork in the Kosterhavet National Park by the Swedish county administrative board (permit: 521-8021-2021). Between June and September (2021), I measured the depth distribution of four furoid macroalgae species using a set of five transects on a granite island (Latitude: 58.88506 DD, Longitude: 11.11854 DD): *Fucus spiralis*, *Fucus vesiculosus*, *Ascophyllum nodosum* and *Fucus serratus*. For this, I laid out measuring tape parallel to the rocky shore and used a random number generator (<https://www.random.org/>) to select five transect positions (nearest centimetre). At each transect position, I placed a transect perpendicular to the shore running into the water. Starting at 10 cm distance from the uppermost algae at the transect position, I recorded the identity, total length and circumference (sensu Åberg, 1990) of all individuals greater than 10 cm in length of the four species within 15 cm left and right of the transect. I measured the depth from the water surface to the substrate where the holdfast of each individual was attached using a measuring stick. Concurrently with the water depth measurements, I recorded the water level relative to the RH2000 standard based on the closest monitoring station (Kungsvik, Latitude: 58.996 DD; Longitude: 11.127 DD, Swedish Meteorological and Hydrological Institute, <https://www.smhi.se/>). I accessed the data using the Viva mobile application (<https://www.sjofartsverket.se/en/>). I then calculated the depth of each individual algae relative to the RH2000 standard as: [water level RH2000 + measured depth from water surface].

I converted each individual algae to standing stock dry biomass (SSDB) using previously developed allometric equations that relate dry biomass (g) to total length (cm) and circumference (cm) for each species (see Appendix S1: Tables S2 and S3; Figure S1 for further validation). Using the depths relative to the RH2000 standard, I divided each transect into four depth zones from shallowest to deepest which were separated by 2 cm depth: zone 1: [-2, -10 cm], zone 2: [-12 to -20 cm], zone 3: [-22 to -30 cm] and zone 4: [-32 to -40 cm]

(referred to as *depth zones* hereafter). The shore slopes on each transect were relatively consistent (*personal observation*) which means that the equal interval depth zones reflect a similar overall habitat area. Within each of these depth zones in each transect, I summed the standing dry biomass for each species. I then summed the standing dry biomass across transects for each species. This left me with data on the SSDB of *F. spiralis*, *F. vesiculosus*, *A. nodosum* and *F. serratus* in the four depth zones (Figure 1a).

Converting the individual SSDB to dry biomass productivity (DBP) requires dry biomass growth rate data. I measured dry biomass growth rates by transplanting adult individuals of all four species to four different depths relative to the RH2000 standard: -5, -12, -28 and -40 cm. These depths are within the four depth zones in which I measured SSDB. Full details of this transplant experiment are described in Schrofner-Brunner et al. (2023) but, in brief, I placed 16 different 30×30 cm granite tiles (one tile at the four depths for each of the four species) on two sandy beaches on the same island where the transects were taken. One of the sandy beaches was 2 m away from the shoreline where the transects were taken (Latitude: 58.88506 DD, Longitude: 11.11854 DD). The other sandy beach was approximately 200 m away and directly adjacent to a different rocky shore with a similar macroalgae community (*personal observation*, Latitude: 58.88715 DD, Longitude: 11.11664 DD). Each tile had nine adult individuals of one of the four species attached to it. Before deploying the tiles, I measured the maximum length (to 1 mm accuracy), the wet weight (Balance: VWR PBP5201I-1S-FCECN 611-4828, to 0.1 g accuracy) and took a flattened photograph on a light-board (ARTOGRAPH LightPad 950) using a digital camera mounted on a tripod (Panasonic, Waterproof 4k Compact Camera LUMIX DC-FT7). I used ImageJ 1.53r (Schneider et al., 2012) to measure the surface area.

After approximately 60 days, I collected all tiles. Experimental losses left me with 33, 32, 44 and 20 individuals of *F. spiralis*, *F. vesiculosus*, *A. nodosum* and *F. serratus* (of an initial 72 individuals of each species). Experimental losses were mainly due to ropes severing the attachment point on the stem (Schröfner-Brunner et al., 2023). However, with this subset of the data, tiles had an average of four individuals and all tiles had at least one individual (see Schrofner-Brunner et al., 2023 for additional details). For all individuals, I measured the maximum length, wet weight and surface area on all individuals as previously. I dried the individuals at 60°C for 48 h and measured the post-experiment dry weight with a precision of 0.001 (Sartorius, BP 211S). I chose to measure growth rate as the change in dry weight as it is the most direct and accurate measure of biomass (Bickel & Perrett, 2016) and because I measured standing stock of individuals as dry biomass (Figure 1a). To do this, for each algae (*i*), I used a linear model to obtain the expected initial dry weight values ( $E(DW_{i,t_0})$ ). The linear model (Appendix S1: Model S1) was fit to the post-experiment dry weight data with maximum length, wet weight and surface area as predictor variables and had an  $r^2$  value 0.98 (see Appendix S1 for further validation). Using this model along with each individual algae's initial maximum length, wet weight and surface area, I obtained the expected initial dry weight values ( $E(DW_{i,t_0})$ ). I



**FIGURE 1** Background data of standing stock dry biomass (SSDB) and relative growth rates (RGRs) used to calculate dry biomass productivity (DBP). (a) SSDB (g) of *Fucus spiralis*, *Fucus vesiculosus*, *Ascophyllum nodosum* and *Fucus serratus* (different colours) in the four different depth zones (1 shallowest to 4 deepest) summed across five different transects. Vertical dashed lines separate the four depth zones for clarity. (b) Modelled expected RGRs (g g<sup>-1</sup> day<sup>-1</sup>, mean and PI90%) for each species across the four depth zones based on a transplant experiment. Observed data are overlain as unfilled circles. (c) DBP (g day<sup>-1</sup>, mean and PI90%) in each depth zone calculated by multiplying the SSDB (a) by the expected RGRs (b) and summing across species (red diamonds, Equation 2). DBP of each species (mean and PI90%) is also shown as filled circles.

used the expected initial dry weight values ( $E(DW_{i,t_0})$ ) and the measured, post-experiment dry weight values ( $DW_{i,t_N}$ ) to quantify relative growth rate (RGR, g g<sup>-1</sup> day<sup>-1</sup>) as (Equation 1):

$$RGR_i = \frac{DW_{i,t_N}}{E(DW_{i,t_0})} \times \frac{1}{\text{days}}. \quad (1)$$

I then fit a random effect generalised linear model with normally distributed errors to the RGR data with species (S: *F. spiralis*, *F. vesiculosus*, *A. nodosum* and *F. serratus*) and depth zone (DZ: 1–4) coded as categorical variables. I fit separate intercepts as correlated random

effects for each species and depth zone combination which allowed the effect of the four depth zones on RGR to vary by species. The full random effect generalised linear model with weakly informative priors is presented below in the non-centred parameterisation (Model 1, see Appendix S3 for Stan code). I estimated the posterior distribution using Stan's No-U-Turn Sampler Hamiltonian Monte Carlo algorithm (<https://mc-stan.org/>) with four separate chains. I implemented this in R v4.1.2 (R Core Team, 2021) using the *rstan* package (Stan Development Team, 2021). I assessed model convergence by inspecting trace plots, R-hat values and effective samples sizes (see Appendix S3: Table S4 and Figure S3 for full model diagnostics).

Model 1	
$RGR_i \sim \text{Normal}(u_i, \sigma)$	[likelihood]
$\mu_i = \alpha_{S[i],DZ[i]}$	[linear model]
$\alpha_{j,k} = \bar{\alpha}_j + v_{j,k}$	
$v = (\text{diag}(\tau) \times \text{cholesky}(\mathbf{R}) \times \mathbf{V})^T$	
$\sigma \sim \text{Exponential}(1)$	[priors]
$\tau_j \sim \text{Exponential}(1)$ for $j \in 1 \dots 4 \text{ DZ}$	
$V_{j,k} \sim \text{Normal}(0, 1)$ for $j \in 1 \dots 4 \text{ DZ}$ for $k \in 1 \dots 4 \text{ S}$	
$\bar{\alpha}_j \sim \text{Normal}(0, 1)$ for $j \in 1 \dots 4 \text{ DZ}$	
$R_{j,j} \sim \text{LKJCorr}(2)$ for $j \in 1 \dots 4 \text{ DZ}$	

The model fit the data well ( $r^2=0.45$ ). Using 3000 samples from the posterior distribution, I obtained 3000 estimates of the expected RGR (i.e.  $u_i$ , Model 2) for each species in the four depth zones (Figure 1b). I then multiplied these 3000 expected RGR estimates for each of the four species (S) and each of the four depth zones (DZ) by the SSDB of each species (k) before summing across species within each depth zone (j) to obtain the total DBP ( $\text{g day}^{-1}$ ) for each depth zone (Equation 2):

$$DBP_j = \sum_{i=1}^{DZ} \sum_{k=1}^S SSDB_{j,k} \times RGR_{j,k} \quad (2)$$

for  $j \in 1 \dots 4 \text{ DZ}$   
for  $k \in 1 \dots 4 \text{ S}$

Therefore, for each of the four depth zones, I obtained a distribution of DBP ( $\text{g day}^{-1}$ ) estimates for the 60 days of the transplant experiment (Figure 1c). It is important to note that this method assumes that the growth rate of individual algae does not depend on total length. However, the algae individuals in the transplant experiment were initially between 12.5 and 50.5 cm in length. This does not fully cover the range of lengths observed in the transects (between 10 and 105 cm, median = 25 cm). But the expected RGR ( $\mu_i$ , Model 2) for a given species and depth zone combination represent the average RGR of algae of a variety of different initial lengths which I consider reasonable.

## 2.2 | Observational analyses

I used the species and depth zone-specific estimates of DBP (Figure 1c) to examine the number of species required to maintain biomass productivity across the four depth zones. To do this, I first used the approach proposed by Winfree et al. (2018). The approach calculates the minimal set of species required to reach a certain level of functioning (F) at a particular site (Appendix S2: Figure S2a). The approach then considers another site and asks if species other than those required at the first site are required to reach F. If other species are required to reach F in the second site, then the number of species required at the first site ( $S_1$ ) is

lower than that required across both sites ( $S_2 > S_1$ ), (Appendix S2: Figure S2b). This is done for all sites and the order of sites is randomised to prevent single trajectories from affecting the results. In the original paper, F was defined as 25%, 50% and 75% of the average level of functioning (in their case pollination) across all sites.

With my data, functioning was measured as DBP and the different sites correspond to the four different depth zones. I defined F as per the original paper which, in my case, is 25%, 50% or 75% of the average DBP (summed across species) across the four depth zones. I repeated this for all possible orders of the four depth zones and for the whole distribution of DBP values for each species based on the uncertainty in the estimations of RGRs (see Figure 1c).

A similar approach to Winfree et al.'s (2018) method is to examine whether different species are responsible for most of the functioning (in this case DBP) in different sites (e.g. Isbell et al., 2011; Schiettekatte et al., 2022). To do this, I calculated the proportion of species that were functionally dominant in at least one of the depth zones as per one of the analyses presented in Schiettekatte et al. (2022). Specifically, I calculated the contribution (C) of each species (k) to DBP in each depth zone (j) as:

$$C_{k,j} = \frac{DBP_{k,j}}{\sum_{k=1}^{DZ} DBP_k} \quad (3)$$

for  $j \in 1 \dots 4 \text{ DZ}$   
for  $k \in 1 \dots 4 \text{ S}$

A species was defined as functionally dominant in a depth zone if its contribution to DBP was greater than expected. A species' expected contribution in a depth zone was defined as  $1/R$  where R is the number of species present at a given site. If, however, one species was completely responsible for all DBP at a site (i.e.  $C=1$ ), I also defined it as dominant (unlike Schiettekatte et al. (2022) because they did not have any sites with just one species). I then calculated the proportion of the four species that were dominant in at least one of the depth zones. I performed these calculations using the whole distribution of DBP values (Figure 1c). While I chose to use the methods proposed by Winfree et al. (2018) and Schiettekatte et al. (2022), there is very little difference with other, similar approaches (e.g. Isbell et al., 2011).

## 2.3 | Counterfactual extinction-compensation simulations

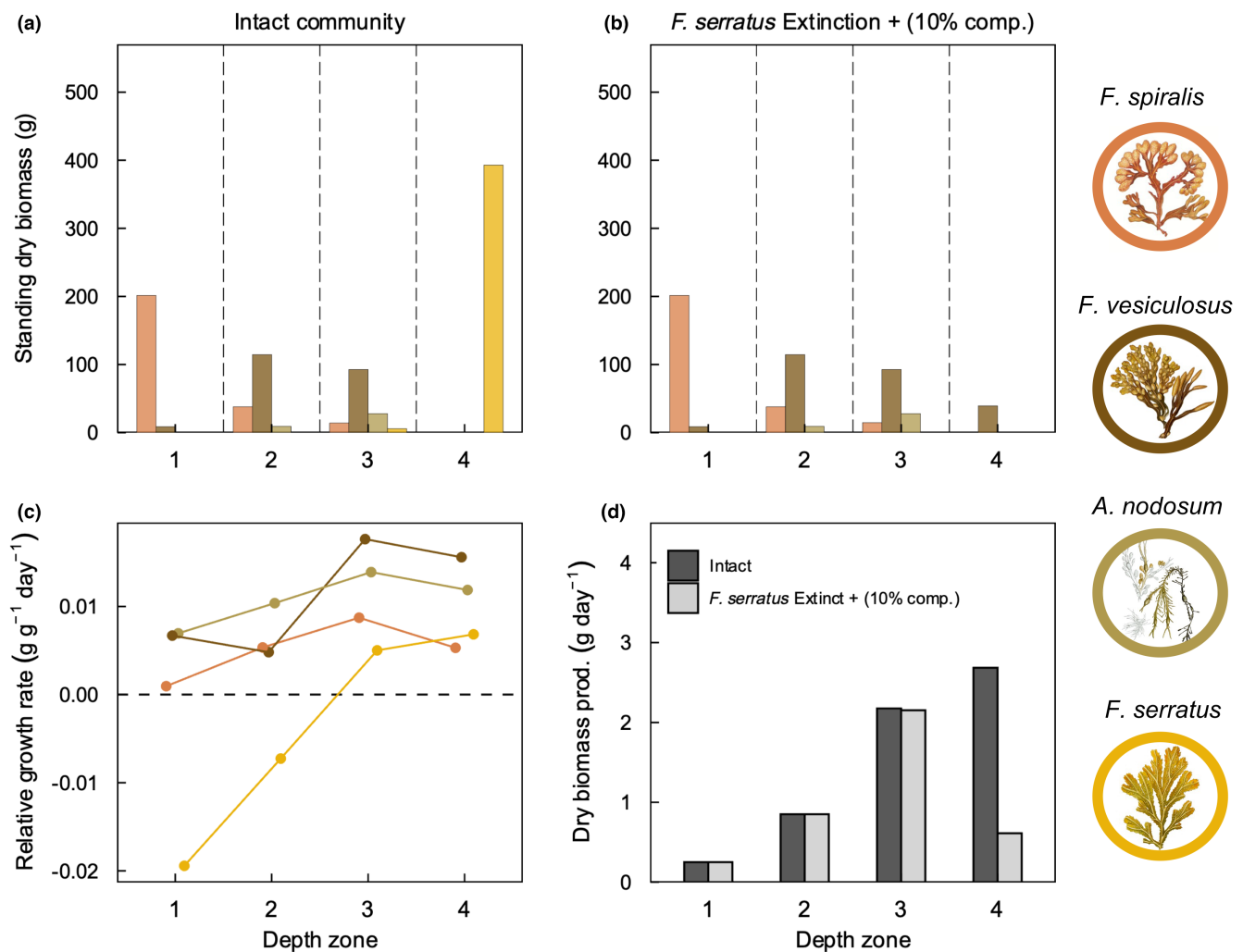
The observational approaches that I used (see previous section) do not make specific predictions about the consequences of losing different species and, therefore, cannot answer counterfactual queries such as what would happen if *F. spiralis* went extinct across the four depth zones due to, for example, a species-specific disease? Would we lose all the DBP provided by *F. spiralis* or would other species be able to compensate for its loss? Answering such queries requires directly simulating losing different species and studying changes in DBP under different scenarios of potential compensation by other

species. I use this intertidal macroalgae data to illustrate the potential of this latter approach.

To simulate counterfactual extinction and compensation scenarios, I took the following approach. First, I assumed that one of the four species went completely extinct across the four depth zones. Therefore, the extinct species' *SSDB* goes to zero in each of the four depth zones. Second, I assumed that some percentage of this lost *SSDB* in each depth zone could be compensated by other species. To do this, I chose a level of compensation (e.g. 10%) and then chose a species that has both a positive growth rate in that depth zone and some *SSDB* in an adjacent zone (i.e. *F. spiralis* has zero standing stock biomass in the second deepest depth zone and, therefore, cannot compensate for *F. serratus* loss in the deepest zone). Therefore, I replaced some percentage of the lost *SSDB* of the extinct species with other species in each depth zone (see Figure 2a,b for an example assuming extinction of *F. serratus* and 10% compensation).

Using this extinction–compensation scenario of *SSDB* (e.g. Figure 2b) and a sample of *RGRs* of each species in each depth zone (Figure 2c), I calculated *DBP* as described previously (Equation 2). I then compared the *DBP* of intact communities where all species were present across the depth zones to the *DBP* of communities with one species extinct and some assumed level of compensation by other species (Figure 2d). I repeated this assuming the loss of each of the four species independently and assuming three different levels of compensation (10%, 50% and 90%). In addition, I performed these calculations using *RGRs* derived from all 3000 samples from the posterior distribution (Model 1) to incorporate the uncertainty in these measurements.

Unless previously specified, all analyses were conducted in R v4.1.2 (R Core Team, 2021). In addition to the R-packages cited previously, I used *dplyr* (Wickham, François, et al., 2022), *tidyr* (Wickham & Girlich, 2022), *broom* (Robinson et al., 2023) and *readr* (Wickham, Hester, & Bryan, 2022) for data handling, *ggplot2* (Wickham, 2016) for



**FIGURE 2** Example of a simulated extinction–compensation scenario using one of the 3000 samples of relative growth rates (*RGRs*). The standing stock dry biomass (*SSDB*) (g) of (a) the intact community containing all four species and (b) a hypothetical community where *Fucus serratus* is extinct but other species (in this case *Fucus vesiculosus*) compensate 10% of the *SSDB* of *F. serratus* in each depth zone. (c) Using one sample from the posterior distribution and obtaining *RGRs* ( $\text{g g}^{-1} \text{day}^{-1}$ ) for each species across the four depth zones, I calculated (d) the dry biomass productivity (*DBP*) ( $\text{g day}^{-1}$ ) of each depth zone for the intact community and the hypothetical community where *F. serratus* is extinct. Under this extinction compensation scenario, *DBP* declined in the two deepest zones but was unaffected in the two shallow zones.

plotting, *ggpubr* (Kassambara, 2020) and *cowplot* (Wilke, 2020) for plot arrangement and *renv* (Ushey, 2023) for package version management.

### 3 | RESULTS

#### 3.1 | Observational analyses

The first observational approach (i.e. Winfree et al., 2018) showed that more species were required to maintain *DBP* at 25%, 50% and 75% of the average across the four depth zones as the number of depth zones increased (Figure 3a). Indeed, at a 50% threshold,  $2.1 \pm 1.4$  (mean  $\pm$  SD) species were required in one depth zone and all four species ( $\pm 0.01$  SD) were required in all four depth zones.

The second observational approach (i.e. Schiettekatte et al., 2022) showed similar results. The proportion of species that were dominant in their contribution to *DBP* in at least one depth zone was high (mean, [PI<sub>90%</sub>]: 0.64, [0.5–75]). And, for most samples of modelled growth rates, three of the four species were dominant in at least one depth zone (i.e. 75%, Figure 3b).

#### 3.2 | Counterfactual extinction–compensation simulations

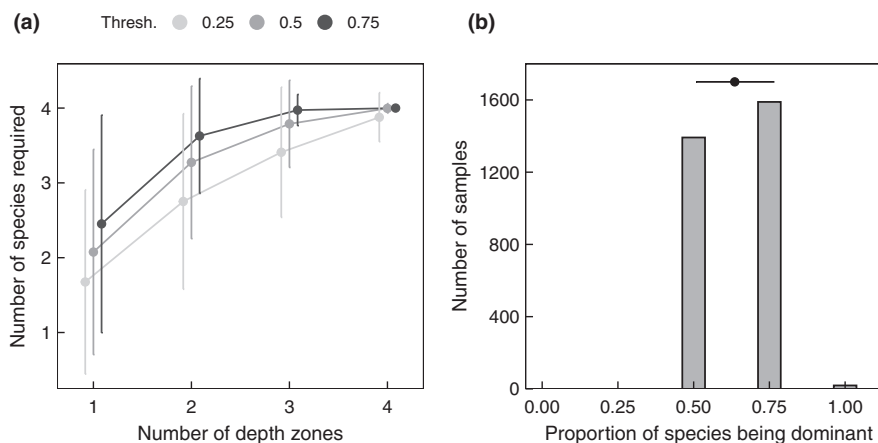
The counterfactual extinction–compensation scenarios showed that the extinction of both *F. spiralis* and *A. nodosum* had limited effects on *DBP* across the four depth zones (Figure 4a,c). The simulated extinction of *F. spiralis* led to increases in *DBP* across all zones unless I assumed low compensation of 10% (Table 1). Moreover, only depth zones 2 and 3 were affected by the simulated extinction of *A. nodosum* with average drops of between 4.3% and 16% depending on the assumed level of compensation (Appendix S4: Table S5). Thus, *DBP*

was relatively insensitive to the counterfactual scenarios where *F. spiralis* and *A. nodosum* went extinct.

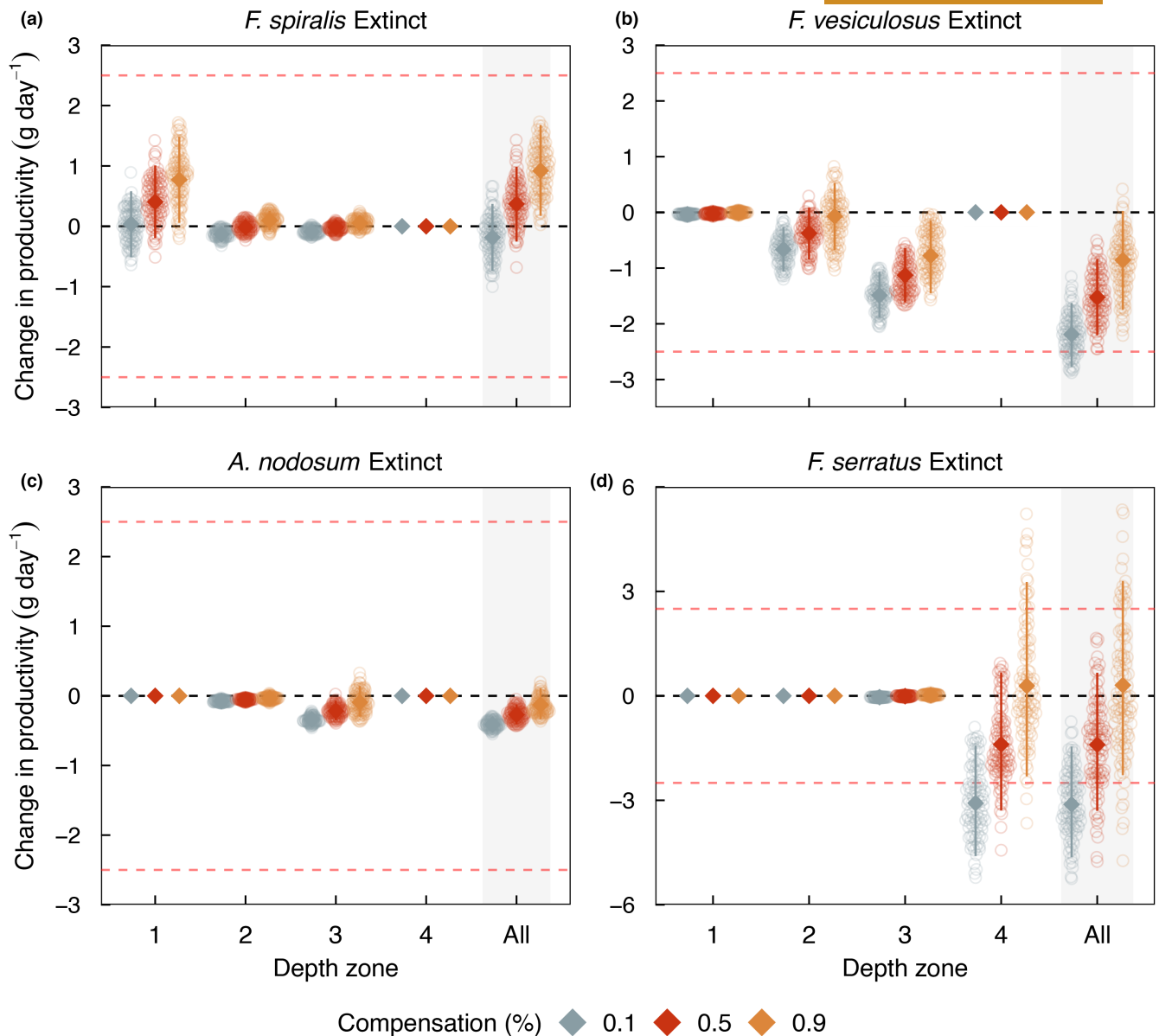
The results differed under the counterfactual scenarios where *F. vesiculosus* and *F. serratus* went extinct. The simulated extinction of *F. vesiculosus* caused *DBP* to decrease by 36% on average in depth zone 3 even under 90% compensation (Figure 4b). In depth zone 2, average decreases of more than 30% were predicted unless compensation reached 90% (Appendix S4: Table S5). For the simulated extinction of *F. serratus*, *DBP* in depth zone 4 dropped considerably (–87% on average) when compensation was assumed to be 10%. But, at higher levels of compensation (i.e. 50% and 90% compensation), this effect disappeared (Figure 4d). At 90% assumed compensation following simulated *F. serratus* extinction, *DBP* increased across zones (Table 1) because *F. vesiculosus* has high RGRs in depth zone 4 (Figure 1b).

### 4 | DISCUSSION

Are more species required to maintain ecosystem functioning at larger compared to smaller spatial scales or across environmental gradients as suggested by several observational studies (Genung et al., 2023; Isbell et al., 2011; Schiettekatte et al., 2022; Simpson et al., 2022; Winfree et al., 2018)? In this intertidal macroalgae system, analyses based solely on observational data suggested that between three and four species were required to maintain *DBP* across depth zones reflecting a water emersion gradient (Figure 3). But, using counterfactual scenarios of simulated extinction and compensation, the answer was more complicated. *DBP* was potentially very sensitive to the loss of *F. serratus* and *F. vesiculosus* in some depth zones (Figure 4b,d) but was relatively insensitive to the loss of both *A. nodosum* and *F. spiralis* across all depth zones even under relatively low levels of assumed compensation (–50%, Figure 4a,c). These results suggest that during the study period (which only lasted 60 days), all four species were not



**FIGURE 3** (a) The number of species required (maximum is all four macroalgae species) to achieve 25%, 50% and 75% (different shades) of the average dry biomass productivity (*DBP*) across depth zones increases with the number of depth zones. Reported are the mean  $\pm$  SD for each number of depth zones (see Section 2 for details of the uncertainty calculations). (b) The proportion of the four macroalgae species that are dominant in their contribution to *DBP* in at least one of the four depth zones. Each sample represents one of the 3000 sets of modelled relative growth rates. The circle and error bar are the mean and 90% percentile interval.



**FIGURE 4** Change in dry biomass productivity given the simulated extinction of (a) *Fucus spiralis*, (b) *Fucus vesiculosus*, (c) *Ascophyllum nodosum* and (d) *Fucus serratus* for three different counterfactual scenarios of standing stock dry biomass compensation: 10%, 50% and 90%. Data are shown for each depth zone and for all depth zones combined (All—indicated by shaded grey bar). Diamonds and error bars are the mean and 90% percentile interval representing the uncertainty in the relative growth rates. In addition, a sample of 100 individual data points are plotted. Dashed black horizontal line is the zero change line. The y-axes are on different scales but the two red, dashed horizontal lines represent  $-2.5 \text{ g day}^{-1}$  and  $2.5 \text{ g day}^{-1}$  to aid as a shared frame of reference among the four plots (a–d).

**TABLE 1** Percentage change in dry biomass productivity given the simulated extinction of *Fucus spiralis*, *Fucus vesiculosus*, *Ascophyllum nodosum* and *Fucus serratus* under three different counterfactual scenarios of standing stock dry biomass compensation by other species (10%, 50% and 90%) across the four depth zones.

Species extinct	10% compensation	50% compensation	90% compensation
<i>Fucus spiralis</i>	-2.6 [-11 to (6.3)]	6 [-3.5 to (17.1)]	14.4 [2.6 to (28)]
<i>Fucus vesiculosus</i>	-33.5 [-45.5 to (-23.8)]	-23.3 [-35 to (-12.7)]	-13 [-27.1 to (0.4)]
<i>Ascophyllum nodosum</i>	-6.4 [-8.9 to (-4.5)]	-4.2 [-6.9 to (-1.8)]	-2 [-5.5 to (1.6)]
<i>Fucus serratus</i>	-45.8 [-59.2 to (-28.3)]	-19.5 [-42.9 to (12.4)]	6.9 [-32 to (59.2)]

Note: The mean and 90% percentile interval are reported representing the uncertainty in the RGRs.



necessarily required to maintain *DBP*. Thus, it is possible that, in some cases, observational analyses may overestimate the number of species required to maintain ecosystem functioning as larger spatial scales with more environmental heterogeneity are examined.

The observational approaches described implicitly assume that species cannot compensate for the loss of other species. In the extinction–compensation simulations, I assumed that compensation was possible. But is this a valid assumption? In the case of these four furoid macroalgae species, compensation is likely for two reasons. First, the field-based transplant experiment showed that most species could maintain positive growth rates outside the zone that they naturally occur in (Figure 1b). Second, previous work has shown that *F. vesiculosus* can colonise parts of the upper shore if *F. spiralis* is removed (Hawkins & Hartnoll, 1985) and deeper depth zones if other species are removed (Lubchenco, 1980). Thus, it seems reasonable to assume that there will be some compensation in a species loss scenario in this system.

Even if we can assume some compensation, how much we should assume requires further work. This can be partially dealt with by assuming different levels of compensation as I did here (10%, 50% and 90% compensation), but detailed knowledge in different systems would be required to refine these estimates. Moreover, even if compensation occurs, it will not be instantaneous which I assumed in these models. It is more likely that compensation will occur during species loss and only reach maximum potential levels after some lag time. Indeed, it has been shown in grasslands that even after many decades following agricultural abandonment, plant biodiversity had still not recovered to the levels of biodiversity observed in fields never used for agriculture (Isbell et al., 2019; Ladouceur et al., 2023). The lag in compensation will probably depend on the generation times of the species and the degree to which the environment has been altered. Nonetheless, a lag in recolonisation could lead to long periods of decreased functioning which is an undesirable outcome even when compensation is possible (Buschke & Brownlie, 2020).

In other systems, including those that used the observational approaches I implemented, compensation may be less likely than observed in this intertidal macroalgae system for at least two reasons. First, the depth zones in this study vary mostly across one environmental dimension, namely, water emersion (although this also correlates with changes in light and temperature; Schrofner-Brunner et al., 2023). This may explain the relatively high rates of compensation I observed. If this study was done across a broader range of environmental conditions, I may have observed lower rates of compensation. Second, in some systems, there may be much higher levels of environmental specialisation than in this macroalgae system. For example, Winfree and Kremen (2008) found no evidence for spatial density compensation among wild bee species in two North American crop data sets. This lack of spatial density compensation among species suggests that assuming low or no compensation in this system (the same system analysed by Winfree et al., 2018) may be reasonable. Similarly, in coral reef fish, Mouillot et al. (2014) found that many coral reef fish species in a given geographical area have unique traits that would make compensation following extinction unlikely. Thus, in coral reef fish (the system studied by Schiattkatte et al., 2022), it

may also be reasonable to assume that compensation may not be very high. Nevertheless, what these extinction–compensation analyses show is that compensation can be important and assessing the potential for compensation in future studies is important for understanding the consequences of species loss on ecosystem functioning.

A strength of using these extinction–compensation scenarios compared to the observational approaches described is that it allows one to assess the sensitivity of a landscape to the loss of different species directly. It is commonly asserted within trophic levels that the loss of either the dominant species (Díaz et al., 2007) or functionally unique species (O’Gorman et al., 2010) should have the greatest effects on ecosystem functioning and many studies have found evidence for this (Brun et al., 2022; Smith et al., 2020). However, in this system, this is not what I found. Even though *F. seratus* dominated the *SSDB* in the deepest zone, its loss was relatively easily compensated by other species (Figure 4d) due to their high growth rates in these depth zones. Similarly, *A. nodosum* is the most functionally unique of the four species (Cappelatti et al., 2019), but *DBP* was least sensitive to its loss compared to the loss of other species because it had low *SSDB* at this site (Figure 4c, *A. nodosum* can sometimes attain very high standing stock biomass). The point is that these simple heuristics relating to the consequences of species loss for ecosystem functioning did not necessarily hold in this system.

I used these data to illustrate a potentially useful approach to studying the consequences of species loss for ecosystem functioning across environmental gradients or at large scales as an alternative or complement to observational analyses. However, these results may not be directly relevant in this system. None of the four furoid algae species that I studied are at risk of extinction in the region and it is unlikely that there would be considerable local extinctions in the future. However, in the 1990s, there were concerns that *Sargassum muticum*, which had invaded the Swedish west coast, could replace or negatively affect some of these furoid species (Karlsson & Loo, 1999). This modelling approach can be easily adapted to studying how invasive species might affect ecosystem functioning under this kind of scenario whereby the invader replaces some percentage of the biomass of the standing community (Teagle & Smale, 2018). Similarly, the approach is not limited to species loss per se. The approach could be used to investigate how assumed decreases in abundance or performance of species under, for example, climate change might affect ecosystem functioning under different compensation scenarios. Recent work suggests that furoid species in this region may be vulnerable to climate change pressures like warming and acidification (Kinnby, Toth, & Pavia, 2021; Kinnby, White, et al., 2021) and this approach could be used to explore the potential consequences of these pressures on ecosystem-level productivity. Thus, this approach has the potential to address diverse questions around functional biodiversity.

These analyses used growth rates that were measured over a relatively short period (ca. 60 days) to estimate *DBP*. It is important to note that just because some species exhibit high growth rates across many depth zones in a short-term study does not necessarily mean that they would be able to maintain those growth rates over the long term. Moreover, the observed distribution of standing stock biomass could be due to differential survival of species

due to infrequent events like ice-scouring (Cervin et al., 2004) or prolonged periods of desiccation. Biomass stocks themselves are important features of ecosystem, especially in these types of habitat-forming species. While we provide a first step, understanding compensation in this and other ecosystems requires understanding long-term responses across life stages of these species.

Another notable caveat of these results is that I focused on a single ecosystem function: *DBP*. Species differ in their traits and there is considerable evidence that species differ in their ability to drive different ecosystem functions (Dooley et al., 2015; Hector & Bagchi, 2007; Zavaleta et al., 2010). Although *DBP* can covary strongly with a variety of other functions like nutrient uptake (Hein et al., 1995), only considering one function may cause compensation to be overestimated. This could occur if, for example, one or a few species with unique traits are almost completely responsible for driving a certain function. A classic example of this may be nitrogen-fixing plants. Nitrogen fixation is only present in a few plant families (e.g. Fabaceae, Tedersoo et al., 2018) and, as a result, the loss of nitrogen-fixing species may completely alter functions related to nitrogen cycles that are unlikely to be compensated by other species. Future work may consider the ability of species to compensate for multiple ecosystems and the simulation-based approach used here could be easily adapted to do so.

I suggest that these simulated counterfactual scenarios of extinction and compensation, which linked growth rate measurements with the patterns of standing stock biomass (or, e.g. other measures of abundance), can be a useful tool for assessing the consequences of species loss. This type of analysis has precedents (Larsen et al., 2005; Solan et al., 2004; Thomsen et al., 2017, 2019), but it is not very frequently used and has not been applied across several communities as I did across the four depth zones. It is important to note that I am not suggesting that the observational approaches discussed in this article are useless or that they should not be used. Rather, I am suggesting that these methods may overestimate the number of species required to maintain ecosystem functioning. My goal was to illustrate the potential importance of compensation for understanding the consequences of species loss for ecosystem functioning across environmental gradients or at large compared to small spatial scales. The counterfactual approach presented here may be a useful alternative or complement to these observational approaches in the future.

#### AUTHOR CONTRIBUTIONS

James G. Hagan conceived the idea, collated the data, performed the analysis and wrote the paper.

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#### CONFLICT OF INTEREST STATEMENT

I have no conflicts of interest to declare.

#### DATA AVAILABILITY STATEMENT

All data used in this study and all code required to reproduce the analysis can be found in the following repository on Zenodo: <https://doi.org/10.5281/zenodo.10257262>.

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## SUPPORTING INFORMATION

Additional supporting information can be found online in the Supporting Information section at the end of this article.

**Appendix S1.** Quantifying standing stock dry biomass and relative growth rates.

**Appendix S2.** Additional details regarding the first observational data analysis approach.

**Appendix S3.** Full Stan code and diagnostics for Model 1.

**Appendix S4.** Extended results.

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