Received: 19 February 2024 | Accepted: 16 July 2024

DOI: 10.1111/1365-2664.14756

Journal of Applied Ecology BRITISH ECOLOGICAL SOCIETY

RESEARCH ARTICLE

Resource limitation of compensatory responses in ecosystem processes after biodiversity loss

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Funding information
Natural Environment Research Council and Department for Environment, Food and Rural Affairs, Grant/Award Number: NE/L003279/1

Handling Editor: Fraser Andrew Januchowski-Hartley

Abstract

1. Biodiversity loss may result in the decline in important ecosystem processes. The effect of biodiversity loss on ecosystem functioning is determined by the functional contribution of the species lost and the compensatory responses of the remaining species. It is unknown to what extent the strength of the compensatory response of the remaining species depends on resources availability.
2. Here we evaluate how the primary production of an assemblage of salt marsh plants responds to a realistic sequence of species loss in an 7-year experiment, with and without the addition of fertiliser.
3. We found near-full compensation of progressive species loss in gross community primary production by the extinction-resistant species with fertiliser as long as one species (*Triglochin maritima*) remained. Without fertiliser, at least four species, including the particularly abundant species *Plantago maritima*, were needed to maintain gross community primary production.
4. These results suggest that the magnitude of the compensation by extirpation-resistant species for the decline in ecosystem processes associated with progressive biodiversity loss depends on the resource context, and that compensation after the loss of plant species can be accelerated by increasing resource availability. Ultimately, full compensation appears to be limited by the presence and abundance of species in the remaining community that possess traits that allow them to compensate for the species lost.
5. *Synthesis and applications*: These findings suggests that the conclusions of a large body of biodiversity-ecosystem experiments cannot be used for informing the management of natural systems because they do not simulate realistic extinction sequences and therefore cannot quantify the potential for compensation of ecosystem services in the real world.

KEYWORDS
biodiversity-ecosystem functioning relationships, compensation, ecosystem function and services, effect traits, recovery, removal experiment, response traits, species removal

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1 | INTRODUCTION

The relationship between biodiversity and ecosystem functioning (BEF) has been the focus of a major body of research since the 2000s (Duffy et al., 2007; Hooper et al., 2005; Reiss et al., 2009; Schmid et al., 2009). Most work focused on short-term experimental studies where biodiversity was manipulated in ways that implicitly assumed that species are lost at random—necessitated by the desire to test generalisable hypotheses about the role of biodiversity in supporting ecosystem services (Cardinale et al., 2009). The general pattern that was observed in these studies was that there existed, on average, a saturating relationship between biodiversity and ecosystem functioning, which implies that there will be little loss in ecosystem functioning even when quite a large fraction of species are lost (Hooper et al., 2005; Loreau et al., 2001). These insights were however, challenging to translate into the real world because they ignored critical ecological processes invoked when asking questions about the consequences of biodiversity loss for ecosystem functioning. In the real world, species are likely to be lost deterministically according to biological response traits that make them more or less resilient to disturbance, and the maintenance of ecosystem function depends on the ability of those species that remain to compensate for loss of biomass and/or function (Larsen et al., 2005). The 'mass–ratio' hypothesis suggests that dominant species control the rate ecosystem processes because species contributions to ecosystem processes in natural communities correlate closely to their abundance (Grime, 1998). This is supported by the fact that previous studies have shown that the direction and strength of compensation are highly dependent on the order in which species disappear (Pan et al., 2022; Thomsen et al., 2019).

Compensation by the remaining, resistant, species therefore plays an important role in shaping the biodiversity-ecosystem function relationship in nature.

In nature, species are not lost at random but differ in their sensitivity to perturbances, and in their contribution to ecosystem functioning (Davies et al., 2011; Larsen et al., 2005). This means that if species that make a large contribution to ecosystem functioning (EF) are also the most sensitive to disturbance, EF may collapse with even a small biodiversity loss. If those species are resistant to disturbance, EF may not show much of a response to biodiversity loss until most species have been lost (Davies et al., 2011, 2012). In other words, when response (to disturbance) and effect (contribution to EF) traits are positively correlated, the vulnerability of ecosystem functioning to disturbance increases. In contrast, ecosystem functioning is likely to be more resilient when response and effect traits correlate negatively (Heilpern et al., 2018).

The effect of biodiversity loss on ecosystem functioning depends on the strength of the compensatory responses of the species that are remaining in the community (Chaves & Smith, 2021). Compensatory responses are likely to occur when the remaining species are released from competition over resources, such as prey, nutrients, water or light. The processes through which such compensation can occur include the increased efficiency in functioning of the organisms already there, the increase in growth and therefore size of the remaining organisms, and the recruitment of new individuals. These three processes are not independent from each other and are likely to occur over different timescales, with increases in efficiency likely to occur fastest and recruitment of new individuals taking longest. Very few BEF experiments have been long enough to allow all three processes to reach a new equilibrium. For example, for a tallgrass prairie grassland, such experiments would need to last for at least 4 years (Chaves & Smith, 2021). A natural grassland in Yukon Territory, Canada, needed at least 5 years or more for full biomass compensation depending on what functional groups were removed (McLaren & Turkington, 2011). Given that many research projects only receive funding for a few years, such long-term studies are rare, and we may be underestimating the potential for compensation of ecosystem functioning after biodiversity loss.

The lack of full compensation in some ecosystems, even after many years, has led to the hypothesis that resources availability may affect compensatory response (Chaves & Smith, 2021; Davies et al., 2012). If species that are more resistant to extinction are poor competitors for resources, the removal of more efficient resource using species may not allow full compensation of EF. Even if the resistant species are equally efficient, a higher resource availability may allow a faster compensatory response. For example, Chaves and Smith (2021) showed that compensation after the loss of a dominant plant species can be accelerated by increased resource availability.

Here we investigate if extirpation-resistant species can compensate for the decline in ecosystem processes associated with biodiversity loss, and whether this depends on resource availability in a 7-year recovery study of saltmarsh plant communities. Manipulations were performed to simulate a realistic sequence of species loss, based on observed sensitivity to disturbance. The effect of resource availability was quantified by adding fertiliser to half the manipulated plots from year 4 to 7. This addition of fertiliser helps us understand to what extend the results from the experiment are generalisable or depend on the local resource situation. Changes in biomass and primary production of extirpation-resistant species were monitored over 7 years.

2 | MATERIALS AND METHODS

2.1 | Experimental treatments

Following a previous study by Davies et al. (2012) on algal impact in salt marshes, this paper investigates how plant communities respond to the gradual loss of species caused by increasing fucoid algae deposits. Ninety 1-m^2 experimental plots spaced ~3 m apart were established in an area of transitional low salt marsh in the Cefni estuary, Anglesey, Wales, UK (53°10′12″ N: 4°23′39″ W). In June 2009, the undisturbed assemblage of salt marsh plants was manipulated. A central 40 × 40 cm area of each of 32 plots was randomly allocated to a stage in the extirpation sequence of species in response to increased volumes of fucoid algae deposited on the marsh surface (see

Davies et al., 2012). While algal mat deposition occurs frequently in many European salt marshes (Van Hulzen et al., 2006), natural algal deposits did not occur on experimental plots during the study period. Such deposits occurred infrequently on the salt marsh and were restricted to the pioneering zone. We were therefore confident that the experimental assemblage was not previously structured by algal mat deposition. Species were removed on a species-by-species basis following the derived extirpation sequence (*Salicornia ramosissima* J. Woods, < *Puccinellia maritima* (Huds.) Parl. < *Armeria maritima* (Mill.) < *Limonium humile* Mill. < *Plantago maritima* L. < *Aster tripolium* L. < *Triglochin maritima* L., from least to most extirpation resistant). Adopting this approach allowed us to test whether compensation for loss of biomass and primary production occurs at each stage of community disassembly. Some species were patchy in their distribution and did not occur in all experimental plots (i.e. *Spergularia marina* (L.) C.Presl and *Halimione portulacoides* (L.) Aellen), preventing a uniform gradient in species composition being generated from the manipulations. Hence, these species were removed in all treatments except an 'all' species treatment (unmanipulated plots), which allowed us to compare how plots in which species were removed varied in biomass and primary production in comparison with the natural plant assemblage. The resulting design represented a single extirpation sequence from eight to one salt marsh plant species ($n = 4$ per treatment). To avoid disrupting soil properties, species were removed by breaking off the above-ground biomass just below the soil surface as opposed to weeding. Removal of above ground biomass accurately simulates how saltmarsh plants die back during algal disturbance events. For the majority of species, root systems produced no new shoots following above ground biomass removal, however some rarer species required regular removal (Davies et al., 2012).

The experiment lasted for 7 years from 2009 to 2017. The results for 2009 to 2011 were reported by Davies et al. (2012). Four years after the start of the experiment, in 2013, compensation seemed very limited. The saltmarsh soil at this location is sandy and likely low in nutrients, and this may have been limiting the possibility for compensation by the remaining species. To quantify whether compensation was context dependent and limited by nutrient availability, half the plots for each treatment ($n = 2$ per treatment) where fertilised while the rest of the plots (n = 2 per treatment) were left unfertilised. Fertilisation was carried out by spreading 50 g of Osmocote slow release fertiliser pellets per 40 × 40 cm plot on 07 May 2013. These pellets were not visible anymore in 2015 and therefore the treatment was repeated on 28 May 2015. The experiment was finished after 7 years in 2017.

Permission to carry out the fieldwork was given by Natural Resources Wales.

2.2 | Measurements

During every summer growth season, one or more samples were collected for each replicate treatment plot in each year to provide an average value of gross community productivity and % cover per plant species over the peak of each growing season. At the end of the experiment in 2017, the biomass of each plant species in each plot was also measured destructively.

Gross community productivity (GCP, a measure of primary production) was quantified once or more in every year during June, July, August and/or September (dates given in SM). Gross community productivity (GCP) was estimated as CO_2 flux recorded using an LI-840 CO_2/H_20 gas analyser (LI-COR Biosciences, Lincoln, NE, USA) connected to a clear plexiglass chamber (0.09 m^2 internal base area, 0.19 m high, internal volume = 17.1 L). GCP was estimated using the rate of CO_2 flux recorded during consecutive light and dark measurements representing net community productivity (NCP, CO_2 utilisation by photosynthesis plus CO_2 production by respiration) and community respiration (CR, CO_2 production during respiration), respectively. GCP was then estimated as GCP = NCP-CR and expressed at the community level as mmol CO_2 uptake $m^{-2} h^{-1}$. CO_2 flux measurements were recorded in a stratified random order between 10:00 h and 14:00 h BST during a neap tidal cycle on days with low cloud cover to minimise imprecision caused by the effect of abiotic factors on photosynthetic rates. In addition, GCP measurements were recorded only where light levels exceeded 700 μmol PPFD $m^{-2} s^{-1}$, a previously observed threshold above which variation in ambient light level has minimal impacts on primary production in this salt marsh community.

Total dry-weight biomass by species was measured at the end of the experiment in September 2017 by clipping all vegetation at soil level. Species biomass could only be estimated before the end of the experiment as this required destructive sampling. To estimate a proxy for total community biomass before the end of the experiment, the abundance of each species in each plot was assessed as % cover using a 0.3 × 0.3 m point quadrat (49 point intersections) in July and/or August. The vegetation cover and GCP were not measured in 2015.

2.3 | Analysis

For biomass at final harvest, full compensation would be evident if there is no longer a relationship between species richness and total community biomass, while partial compensation would be evident if the biomass of an individual species decreases as species richness increases. Because we expected a saturating curve of the response variable total community biomass in response to species richness, we fitted a GAM (biomass ~ Species richness, separately for fertilised and unfertilised plots). For the individual species, a linear relationship was fitted (biomass ~ Species richness, separately for fertilised and unfertilised plots). The number of data points for each species varied, because some species were not supposed to be present in particular treatments. If a species was found to be present anyway when sorting the samples (which was only ever recorded in very low abundances), the data is plotted but ignored in the linear regressions.

For GCP and % cover, full or partial compensation of species loss can be deducted from a decrease in the difference between

treatments with fewer species versus treatments with more species over time. GCP measurements were combined per one or 2 year period, and a non-linear saturating curve was fitted using logistic growth curve using a non-linear regression separately for fertilised and unfertilised plots (GCP ~ c/(1 − exp(−b*(Species richness − a))), where c indicates the maximum estimated GCP, b indicates the steepness of the curve and a the species richness at the midpoint of the curve). The GCP at SR = 0 was not included in this analysis. The parameters describing the non-linear curves were estimated using Bayesian statistics using the Rethinking package in R (McElreath, 2018). This enabled the estimation of the mean as well as the credible intervals around the ratio of GCP at SR = 1 in comparison to higher levels of SR. For the analyses, where the data was analysed separately for fertilised and unfertilised plots (GCP and biomass at final harvest), the number of replicates plots per treatment is limited to two and therefore the statistical power of to detect effects is also likely to be limited (but for some measurements, repeated measurements were taken within a year to increase the precision of estimates).

Repeated measurements of % cover collected in each year were averaged to provide one value per replicate species richness plot in each year.

The effect of species richness (SR), recovery time (Year) and fertilisation (yes/no) and all their interactions on the summed % cover was analysed using a generalised linear squares regression, which has a Gaussian error structure, correcting for the temporal autocorrelation correlation structure of year using the corAR1 function (Zuur et al., 2009). Measurements from 2009 to 2012 from plots that were fertilised in 2013 were included as 'fertilisation: yes' in the analysis because the effect of fertilisation itself would be capture by the two-way interaction of fertilisation and year and the three-way interaction of fertilisation, year and species richness.

3 | RESULTS

Photos of the experimental plots at the end of the experiment in 2017 (Figure 1) show that the % cover of vegetation increases with increasing species richness up to a SR ~ 4 for both fertilised and non-fertilised plots. This pattern is confirmed by the analysis of the % cover measurements of plants (Figure 2, Table 1). Although total % cover for all plant species combined significantly increased over the duration of the experiment for some of the low SR treatments and for the fertilised plots, this increase in cover was fairly modest for most treatments.

From the harvested biomass at the end of the experiment, there was evidence of compensation of biomass by the most resistant species, *Triglochin*, with fertilisation (indicated by an increase in biomass of this species with decreasing species richness, linear regression, $R^2 = 0.48$, $F_{1,14} = 12.92$, $p = 0.003$, Figure 3b) and without fertilisation ($R^2 = 0.36$, $F_{1,14} = 7.8$, $p = 0.014$) but not for any of the other species ($p > 0.05$, Table 2). This modest compensation in biomass by a single species did not result in a compensation of total community biomass at low SR, and 4–5 species were needed to reach full biomass of around 50 g DW per plot for both fertilised and non-fertilised plots (Figure 3a).

A long-term decline in gross community productivity (GCP) for the undisturbed community was observed (Figure 4), and therefore the best way of evaluating the existence of compensation is to compare the difference in GCP at different levels of species richness, within years. We found that the difference in GCP between low and high species richness treatments decreased over time, and particularly so for the fertilised plots, because the GCP in the low species richness treatments increased and the GCP in the high species richness treatments decreased over time. This suggests that the addition of fertiliser speeded up the compensation for species loss. This is illustrated by examining the ratio of GCP at SR = 1 relative to the GCP at SR = 8 (Figure 5a), where a ratio of 1 would indicate full compensation. The ratio increased over time and was higher for fertilised plots, and by 2017 was about 0.9 for fertilised plots, but only 0.4 for non-fertilised plots. The ratio of GCP at SR = 4 relative to the GCP at SR = 8 (Figure 5b) indicated near-full compensation for the non-fertilised plots by the end of the experiment for plots where at least 4 species remained (*Triglochin*, *Aster*, *Plantago*, *Limonium*).

4 | DISCUSSION

We found near-full compensation of species loss in gross community primary production by the extinction-resistant species, with fertiliser, as long as the most resistant species (*Triglochin maritima*) remained. Without fertiliser, at least four species, including the normally dominant species *Plantago maritima*, were needed to maintain gross community primary production. At least three species were needed to maintain biomass, regardless of the resource additions. These results suggest that the magnitude of EF compensation by extirpation-resistant species for the decline in ecosystem processes associated with progressive biodiversity loss depends on the resource context. Compensation after the loss of plant species can by accelerated by increasing resource availability in nutrient limited systems. Ultimately, full compensation appears to be limited by the presence and abundance of species in the remaining community that possess traits that allow them to compensate for the species lost. In the unmanipulated plant community, *Plantago maritima* was dominant in biomass and cover and made the largest contribution to GCP, while *Triglochin maritima* was a minor contributor in all these three parameters. This shows that the dominant species that are most important for ecosystem functioning under undisturbed conditions are not necessarily important for ecosystem resilience. We detected these effects despite a low level of replication in the experiment ($n = 2$) and these effects are therefore likely to emerge in real ecosystems.

These results show that while after three growing seasons extirpation-resistant species did not compensate for the loss of either biomass or primary production associated with the removal of extirpation-prone species (Davies et al., 2011), seven growing seasons were enough to achieve near-complete compensation. These

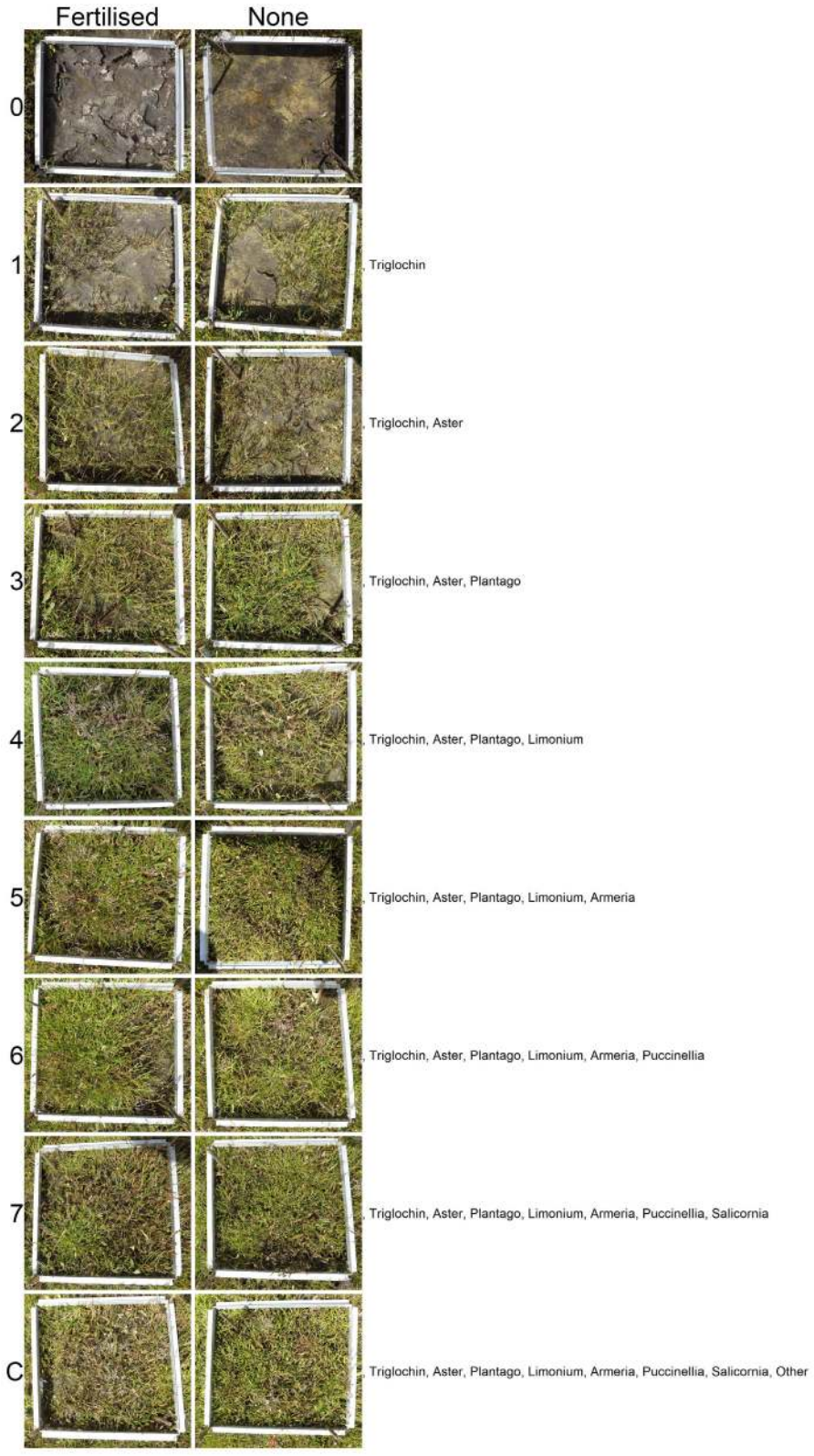


FIGURE 1 Photos of examples of each treatment in August 2017 at the end of the experiment. Species richness increases from the top to the bottom of the figure, and the species present are listed next to the photos. The frame measures 40×40 cm.

results show that 3-year experiments, that are long relative to the 'normal' duration of most field experiments, may severely underestimate the potential for compensation of ecosystem functioning after biodiversity loss. These results align with those of previous long-term compensation experiments, where partial compensation was observed in the short-term, while full biomass compensation of the community was observed in the long term (e.g. Bret-Harte et al., 2004, 2008; McLaren & Turkington, 2011).

It was surprising that near-full compensation of GCP for loss of species was possible with only a single species remaining. This was particularly surprising as this compensation of GCP was not accompanied by a compensation of biomass or % cover (i.e. the GCP per

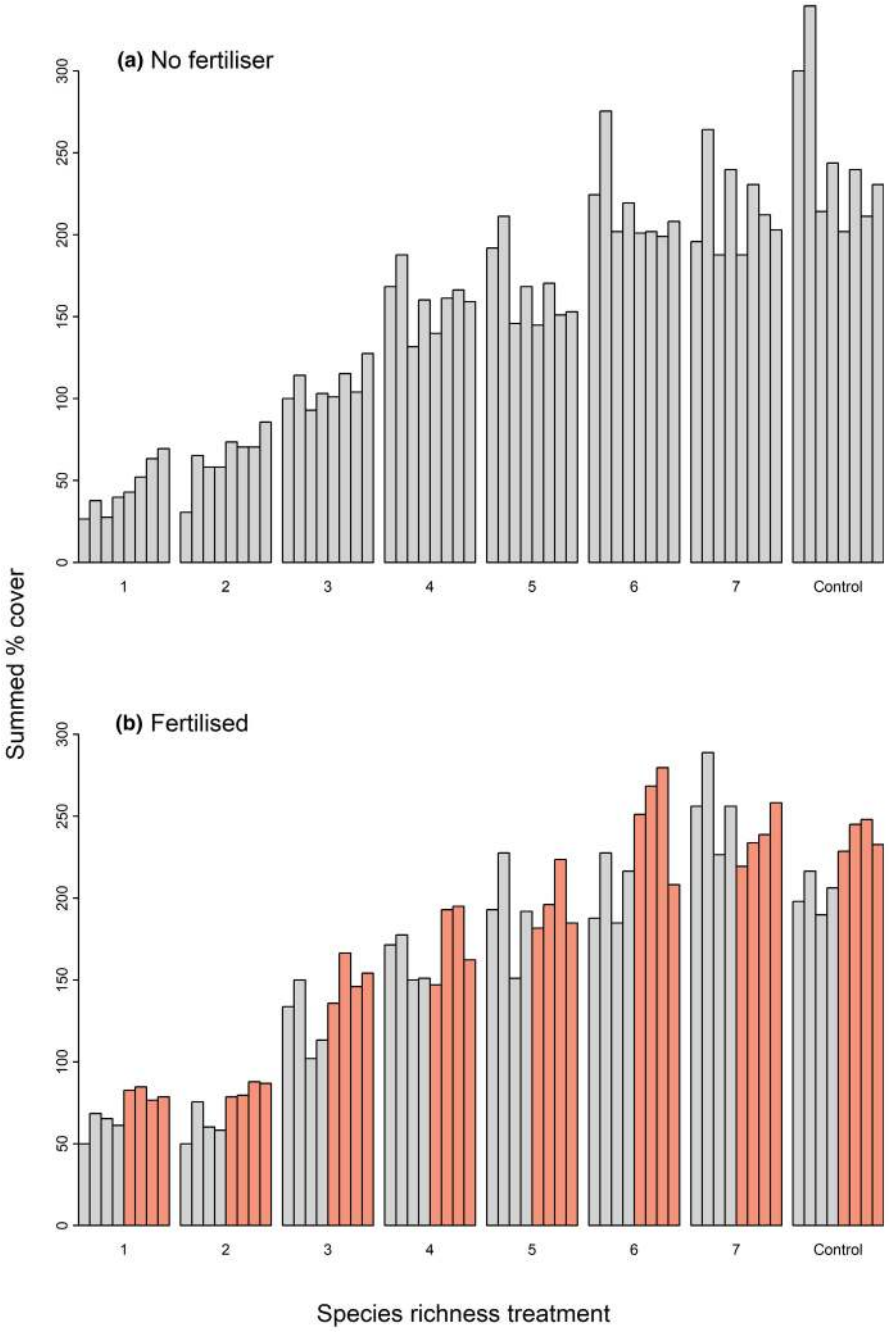


FIGURE 2 The recovery of % cover over 8 growing seasons in a salt marsh plant community undergoing community disassembly. The bars show the summed % cover of all plant species combined over time. The bars from left to right show data for 2009 to 2017 but excluding 2015 when no measurements were taken. The % cover can be >100% because of overlapping plants on the same point. Red bars represent the fertilised plots in those years that fertiliser was present. Where present, compensation can be recognised as an increase in cover over time in the lower species richness treatments. (a) Plots without fertiliser, (b) plots that were fertilised.

unit of biomass increased substantially with species loss). There are two processes that may have contributed to this observed increase in efficiency. First, the reduction in shading and competition for nutrients and water may have allowed *Triglochin* to increase its photosynthetic efficiency. Secondly, the contribution of the algal mat that covers the 'bare' sediment to the overall photosynthesis may have increased. However, the GCP of algal mat only (species richness = 0) was only about 20% of the GCP with *Triglochin* only, and this second process therefore does not seem to contribute much to the observed patterns. It seems likely that GCP declined due to larger scale processes that were outside the parameters examined here. For example, the time frame of the study coincides with the emergence from a period of very wet to drier summers (Hoy et al., 2017).

The high level of compensation may also be related to the conditions under which GCP was estimated. GCP measurements were taken only when light levels were assumed to be high enough not to be limiting (700 µmol PPFD $m^{-2} s^{-1}$), on the implicit assumption that plant biomass would be limiting GCP in such conditions. These results suggest that another factor may instead have been limiting GCP. Measurements were generally carried out on sunny, dry days and during neap tides to avoid inundation of the saltmarsh during and before measurements (seawater also absorbs CO_2 which could bias GCP estimates). Saltmarsh plant primary production can be negatively affected by high soil salt concentration (Janousek & Mayo, 2013). This suggests that these conditions may have meant that soil salt levels were limiting GCP,

rather than community biomass. *Triglochin maritima* is not a particularly salt-tolerant plant, however, compared to the other species in the community, which rank from low to high salt tolerance as *Plantago*, *Armeria*, *Triglochin*, *Aster*, *Puccinelia*, *Limonium* and *Salicornia* (Hill et al., 1999), and it does not seem that GCP limitation by salt could explain the strong compensatory responses observed.

TABLE 1 ANOVA table. The effect of species richness (SR), recovery time (Year) and fertilisation (yes/no) on the summed % cover, analysed using a generalised linear squares regression, correcting for the temporal autocorrelation of year.

	df	*F*	*p*
Year	1, 248	1.03	0.31
SR	1, 248	494.94	<0.0001
Fertiliser	1, 248	6.69	0.0104
Year:SR	1, 248	5.82	0.0165
Year:Fertiliser	1, 248	3.60	0.0592
SR:Fertiliser	1, 248	1.67	0.1962
Year:SR:Fertiliser	1, 248	4.93	0.0273

4.1 | Implications and synthesis

The importance of biodiversity in sustaining ecosystem functioning remains controversial. There is evidence from both experiments and observational studies is that biomass production increases with species richness (Duffy et al., 2017). Our results however suggests that the conclusions of a large body of published biodiversity-ecosystem experiments may not be particularly useful for informing the management of natural systems because neither random extinctions nor the lack of compensation that are implicit in many of those experiments are likely to lead to realistic projections of the effect of species loss. Although such experiments will have provided useful insights in the mechanisms that are underpinning

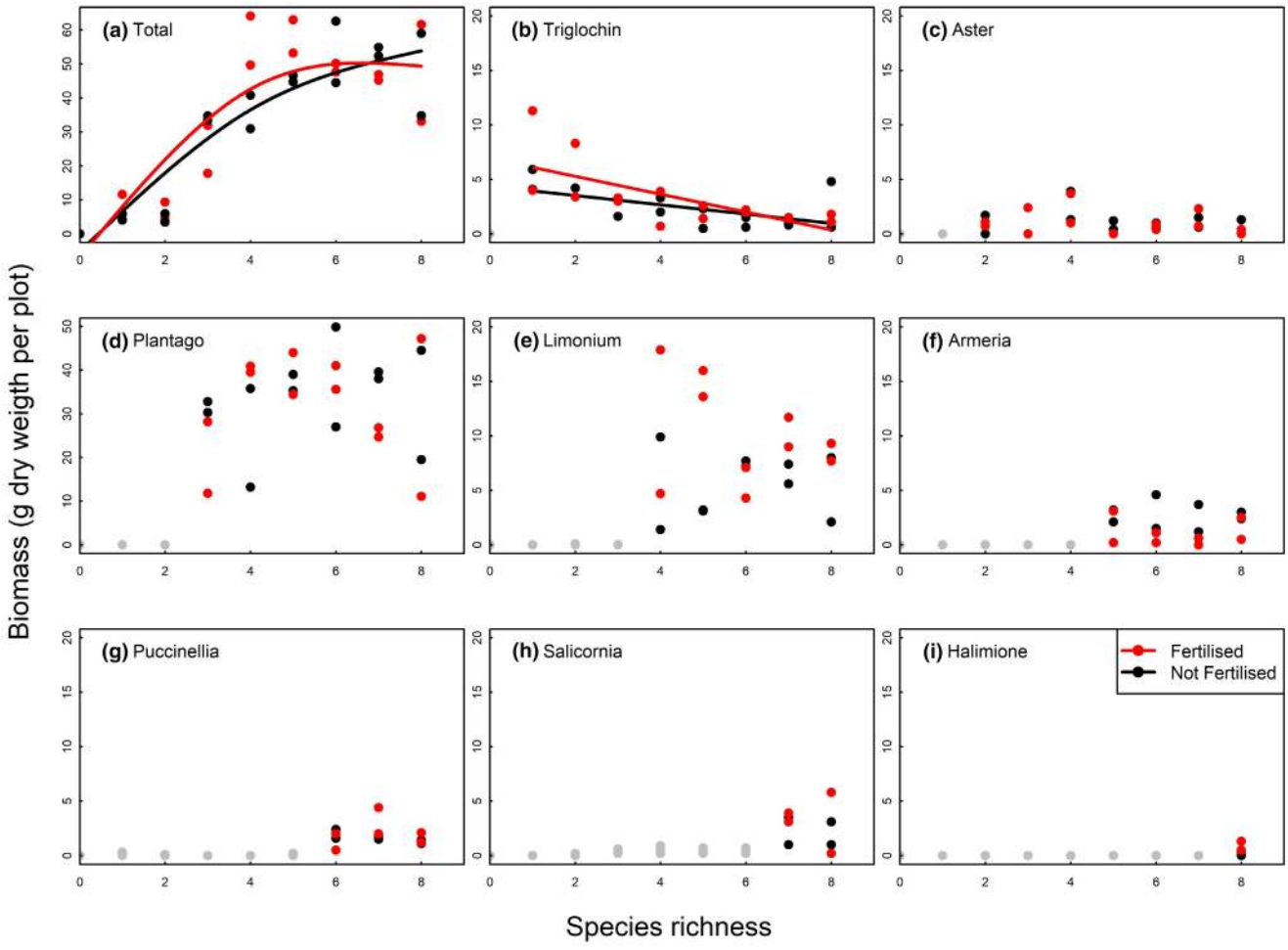


FIGURE 3 The biomass in a salt marsh plant community undergoing community disassembly. The biomass by species and for the full community at the end of the experiment in September 2017. Coloured points indicate fertilised (red) and non-fertilised plots (black). Grey points indicate biomasses at treatments where a species was not supposed to be present and that were not used in the analysis. Only significant regression lines are plotted. If compensation occurs, a flat line is expected in panel (a), and in panels (b–i), decreasing slopes are expected.

TABLE 2 The relationship between species richness and biomass for each species at the final harvest in 2017, for fertilised and non-fertilised plots. Outputs from a linear regression.

	Not fertilised				Fertilised			
Species	R^2	*F*	df	*p*	R^2	*F*	df	*p*
Triglochin	0.36	7.8	1,14	0.014	0.48	12.92	1,14	0.003
Aster	0.00	0.01	1,12	0.942	0.05	0.58	1,12	0.463
Plantago	0.05	0.57	1,10	0.468	0.00	0.00	1,10	0.984
Limonium	0.01	0.1	1,8	0.762	0.11	0.95	1,8	0.358
Armeria	0.00	0.01	1,6	0.912	0.01	0.04	1,6	0.846
Puccinellia	0.58	5.48	1,4	0.079	0.02	0.08	1,4	0.797
Salicornia	0.01	0.02	1,2	0.914	0.02	0.03	1,2	0.876

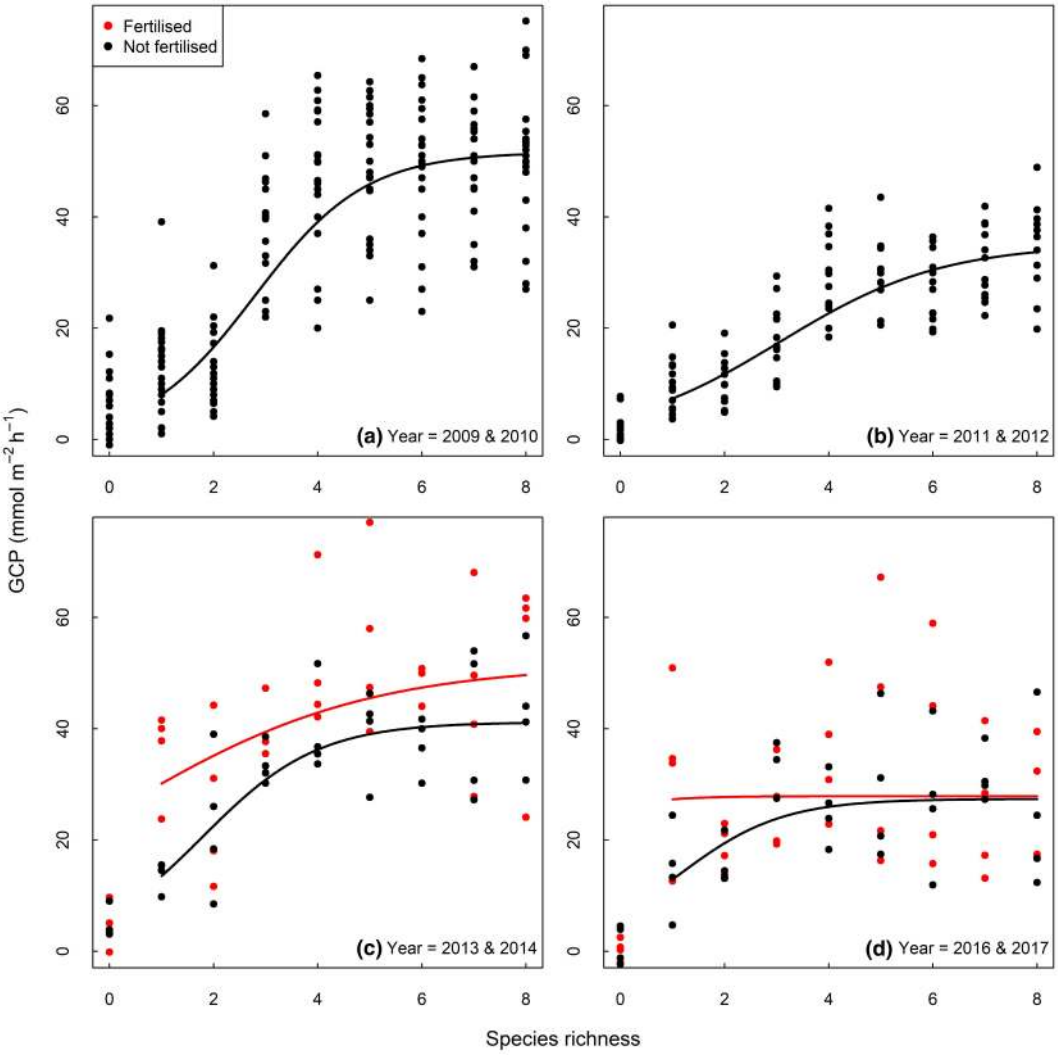


FIGURE 4 The recovery of GCP over eight growing seasons in a salt marsh plant community undergoing community disassembly. The development of the relationship between GCP and species richness over time per 2-year period, for fertilised and non-fertilised plots, with fitted logistic curves. Each plot combined all measurements for all months for two years of data to increase the accuracy of the estimated relationships. (a) Data for 2009 & 2010. (b) Data for 2011 & 2012. (c) Data for 2013 & 2014. (d) Data for 2016 & 2017.

the effect of biodiversity loss on ecosystem functioning, our results suggest that the observed BEF relationships for randomised species loss in short-term experiments are unlikely to be useful in guiding decisions on what level of species loss needs to be avoided to maintain functioning in the management of ecosystems. For the maintenance of EF, it is most important to avoid the extinction

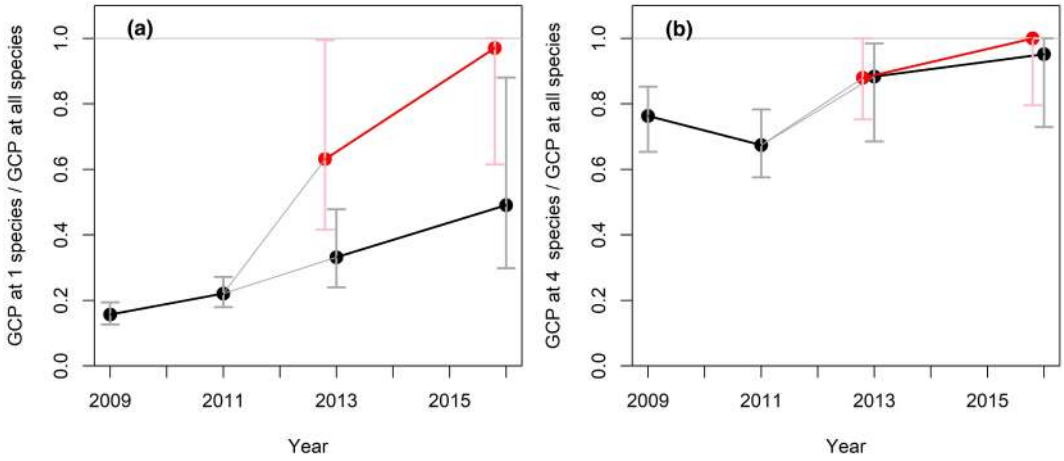


FIGURE 5 The ratio of GCP at SR = 1 (a) or SR = 4 (b)/GCP at SR ≥8 from the predicted values from the fitted logistic curves in Figure 4. Red points are fertilised plots in those years, and black points are unfertilised years and plots. A ratio = 1 would indicate full compensation of GCP by the last remaining species *Triglochin*. Error bars are 95% credible intervals, which do not go above 1 because of the saturating nature of the fitted curves in Figure 4 (GCP at SR = 1 is never predicted to be larger than GCP at SR > 1).

of species that are the strongest compensators and to know how this depends on the resource context. Current knowledge does not provide any generally applicable predictions of which species will be these essential compensators.

AUTHOR CONTRIBUTIONS

Jan Geert Hiddink and Thomas W. Davies conceived, designed and performed the experiments, analysed the data and wrote the paper.

ACKNOWLEDGEMENTS

Our thanks to Natural Resources Wales and the Forestry Commission for granting the relevant access permissions for work to be carried out on the salt marsh of the Cefni Estuary. This work was supported by the Natural Environment Research Council and Department for Environment, Food and Rural Affairs (grant No. NE/L003279/1, Marine Ecosystems Research Programme). We thank Rachel Kingham and many others for their help in data collection.

CONFLICT OF INTEREST STATEMENT

The authors have no conflict of interest to declare.

DATA AVAILABILITY STATEMENT

Data available from the Dryad Digital Repository https://doi.org/10.5061/dryad.12jm63z6j (Hiddink & Davies, 2024).

STATEMENT OF INCLUSION

Our study brings together authors from the UK and includes scientists based in the country where the study was carried out.

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SUPPORTING INFORMATION

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

Table S1. Months in which GCP was estimated in each year. In the earlier years repeated measures were taken within a single year.

Table S2. Months in which % cover was estimated in each year. The earliest measurements were taken on 9 July, and the latest measurements on 7 August.

How to cite this article: Hiddink, J. G., & Davies, T. W. (2024). Resource limitation of compensatory responses in ecosystem processes after biodiversity loss. *Journal of Applied Ecology*, *61*, 2382–2391. https://doi.org/10.1111/1365-2664.14756