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LETTER

Linking changes in species composition and biomass in a globally distributed grassland experiment

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Abstract

Global change drivers, such as anthropogenic nutrient inputs, are increasing globally. Nutrient deposition simultaneously alters plant biodiversity, species composition and ecosystem processes like aboveground biomass production. These changes are underpinned by species extinction, colonisation and shifting relative abundance. Here, we use the Price equation to quantify and link the contributions of species that are lost, gained or that persist to change in aboveground biomass in 59 experimental grassland sites. Under ambient (control) conditions, compositional and biomass turnover was high, and losses (i.e. local extinctions) were balanced by gains (i.e. colonisation). Under fertilisation, the decline in species richness resulted from increased species loss and decreases in species gained. Biomass increase under fertilisation resulted mostly from species that persist and to a lesser extent from species gained. Drivers of ecological change can interact relatively independently with diversity, composition and ecosystem processes and functions such as aboveground biomass due to the individual contributions of species lost, gained or persisting.

KEYWORDS
aboveground biomass, biodiversity change, CAFE approach, ecosystem function, global change, grasslands, nutrient deposition, Price equation, The Nutrient Network, turnover

INTRODUCTION

Human pressures are changing the global environment in terms of species diversity and the functioning of ecosystems (Chaplin-Kramer et al., 2019; Moreno-Mateos et al., 2017). There are elevated extinction rates globally, but this is often not reflected in measures of species richness and diversity at local scales (Blowes et al., 2019; Dornelas et al., 2014). Instead, compositional change in species is predominant (Blowes et al., 2019; Hillebrand et al., 2018), with mixtures of winners and losers responding to anthropogenic pressures (Dornelas et al., 2019). Biodiversity, in general, positively influences ecosystem processes and functions such as biomass production, nutrient absorption and carbon sequestration (Cardinale et al., 2013; Hooper et al., 2005), all of which can be negatively affected by species loss (Genung et al., 2020; Isbell et al., 2013; Smith & Knapp, 2003). However, aggregate community measures of biodiversity and functioning, although somewhat interdependent, can also respond independently to external processes and pressures (Grace et al., 2016; Ladouceur et al., 2020). It is not well understood how compositional change resulting from global change pressures or disturbance affects ecosystem processes and functions.

A major driver of global biodiversity change is the increased inputs of biologically limiting nutrients to the environment from anthropogenic activities (Ackerman et al., 2019; McCann et al., 2021). In plant communities, fertilization can act independently on multiple resource-limited processes, which may interact with one another (Harpole & Tilman, 2007). Specifically, by altering trade-offs among species in competition for limited resources, nutrient enrichment changes the conditions for species coexistence, which can result in dramatic, long-term shifts in species richness and composition (Harpole et al., 2016; Midolo et al., 2019; Seabloom et al., 2020). Nutrient addition and resulting changes in biodiversity might further interact with changes in key ecosystem processes and properties such as the production of biomass (Fay et al., 2015), soil carbon content (Crowther et al., 2019), the balance of mutualist versus pathogenic fungi (Lekberg et al., 2021) and nutrient cycling (Hooper et al., 2005). Live aboveground biomass is a particularly important measure of ecosystem processes and function, as plant biomass is an important source of energy for most life on land (Yang et al., 2021) and is well-known to increase under nutrient deposition. However, the relationship between biodiversity and aboveground biomass under nutrient enrichment varies in direction and strength across contexts, systems and sites (Harpole et al., 2016). Understanding how biodiversity, species composition and aboveground biomass changes are interrelated is essential for anticipating the impacts of global change pressures on ecosystems and their functions.

Global change drivers, such as nutrient addition, can alter community assembly processes, community composition and ecosystem properties concurrently (Bannar-Martin et al., 2017; Leibold et al., 2017; Leibold & Chase, 2017). Small changes in species richness can be associated with large compositional changes, or not (Hillebrand et al., 2018; Spaak et al., 2017). Additionally, nutrient inputs can affect losses of existing species, gains of novel species and abundance changes of species that persist in unique ways via altered competitive and coexistence dynamics (Harpole & Tilman, 2007; Tilman, 1982). Because the contributions of colonising or increasing species to aboveground biomass may or may not offset the contributions of species that go locally extinct, species diversity and aboveground biomass change may be decoupled (Fay et al., 2015; Harpole et al., 2016).

Here, we apply an adaptation of the Price equation (Fox & Kerr, 2012; Price, 1970, 1972) to quantify the contributions of individual species to biomass change through time. The Price equation was originally developed in evolutionary biology (Price, 1970, 1972) but has been widely adapted and applied in many contexts to compare two samples and quantify what is unique in each, versus shared between the two (Lehtonen et al., 2020). In ecology, this approach has been used in a diversity of ways to examine the biological relationships that underpin variation among aggregate changes in species richness, composition and additive measures of ecosystem functioning (i.e. biomass, abundance) or traits (Genung et al., 2020; Lefcheck et al., 2021; Ulrich et al., 2021; Winfree et al., 2015). We use the three-part 'Community Assembly' Price partition proposed by Bannar-Martin et al. (2017) to link temporal changes in plant biodiversity to aboveground biomass. Additionally, we quantify absolute species losses and gains. By following experimental plots through time, we partition cumulative species compositional change and the associated with a change in aboveground biomass into that of species losses, species gains and species that persist through time (Figure 1).

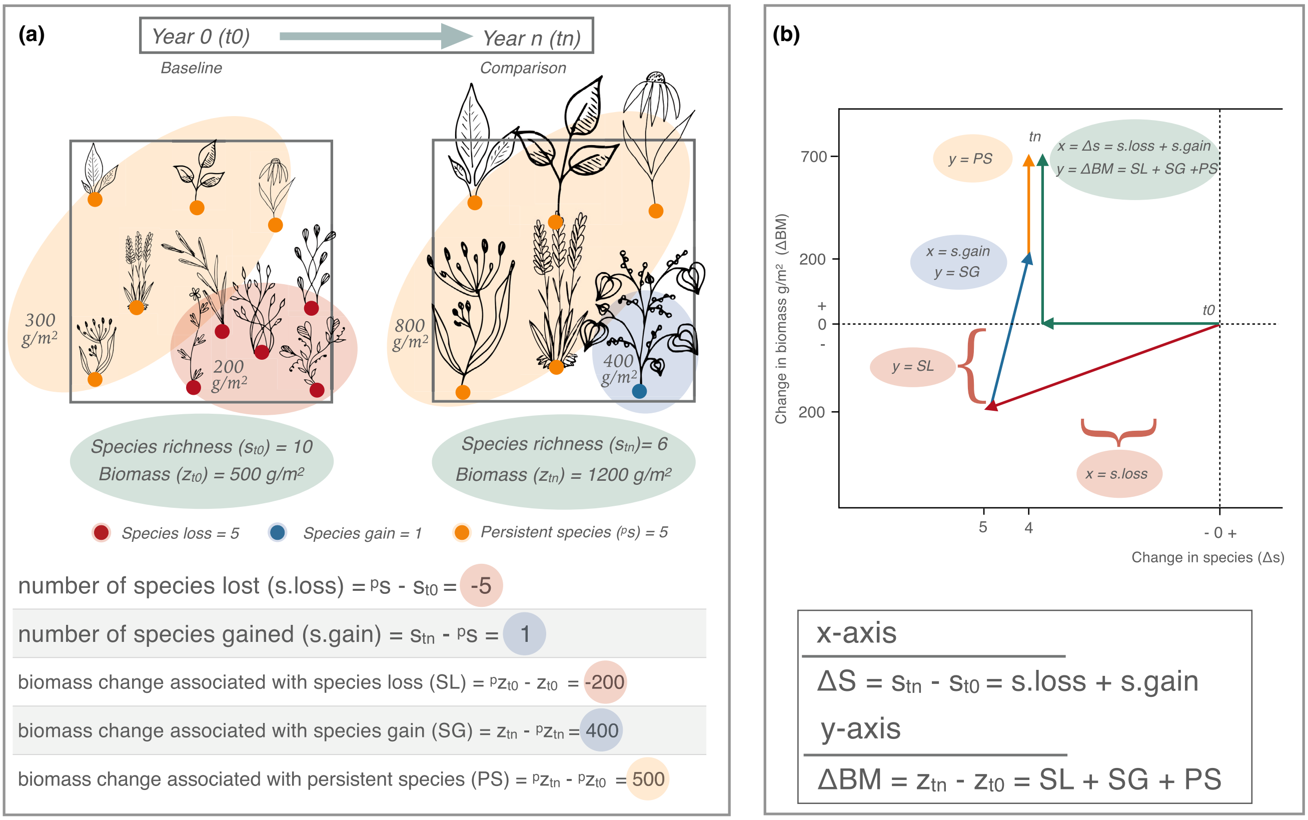
To quantify how community compositional change induced by nutrient addition contributes to altered aboveground biomass, we used data from sites within the Nutrient Network, a globally distributed nutrient addition experiment, replicated across grassland sites (NutNet; http://www.nutnet.org) (Borer, Harpole, et al., 2014). Specifically, we synthesize results from 59 experimental sites across six continents (two sites in Asia and four sites in Africa) comparing unfenced control plots and unfenced plots that were fertilised annually with a combination of nitrogen (N), phosphorus (P), potassium (K) and micronutrients (hereafter the NPK treatment).

Previous work has documented that on average, grassland communities experience reduced richness and increased aboveground biomass with fertilization, but the signs of this relationship can vary among sites (Borer et al., 2020; Borer, Seabloom, et al., 2014; Harpole et al., 2016) (Box 1). We expect that how a loss in richness will be associated with change in biomass likely depends on the biomass contributions of species lost, gained or persisting in the community. On the one hand, a weak response of persistent species or the loss of relatively abundant species could be associated with minimal changes or even reductions in biomass (Fay et al., 2015; Harpole et al., 2016). On the other hand, if biomass change associated with persisting and gained species exceeds that of lost species in response to nutrient addition, biomass may increase even if more species are lost than gained. Determining how components of compositional variation are associated with changes in biomass would advance understanding of how global change affects interdependent dimensions of natural and managed systems.

METHODS

Experimental design

The Nutrient Network (NutNet) is a distributed experiment replicated in herbaceous terrestrial systems across six continents, representing a range of grassland habitats (Borer, Harpole, et al., 2014) (Table S1, Figure S1). At each site, a factorial combination of nitrogen (N), phosphorus (P) and potassium (K with a one-time addition of micronutrients) is applied annually, alongside an unmanipulated control treatment with no added nutrients. Micronutrients were applied once at the start of the experiment to avoid toxic levels from over-application (Borer, Seabloom, et al., 2014) Plots are 5 × 5 m and



z = aboveground biomass

^{p}z = biomass of persistent species

z_{tn} = biomass at time(t) = n

z_{t0} = biomass at t = 0

s = # of species

^{p}s = # persistent species

s_{tn} = # of species at t = n

s_{t0} = # of species at t = 0

FIGURE 1 Schematic illustration of compositional change and the contribution to altered aboveground biomass based on the 'Community Assembly' 3-part Price equation partition suggested by Bannar-Martin et al. (2018). (a) A Nutrient Network plot at year 0 (t = 0, t0) on the left before nutrient addition, and on the right represents the same plot at a point in time after NPK addition (Year tn). Species losses (red), species gains (blue) and change in persistent species (orange) are additive components of the relationship between composition and biomass and each component affects measures of species richness and community biomass change. (b) Observed changes in species and changes in biomass within a community can be considered together to understand the joint response. This represents our expectations for the overall effect of NPK addition on change in species and biomass, and our expectations for partitioning this effect into biomass lost associated with species loss, biomass gained associated with species gain and biomass change associated with persistent species. Plant images by Alex Muravev, The Noun Project.

treatments are applied in a randomized block design, usually with three blocks (range 3–6 among sites). All sites have the same experimental design and sampling protocols.

For this study, we used data from two unfenced treatments: unmanipulated control (ambient conditions) and full fertilization (NPK) treatments. Unfenced plots are grazed by wildlife or livestock according to site-specific conditions, in the presence of a consumer food web. Sites with measurements for a year prior to fertilization (year 0) and for at least 3 years with fertilization were included in this analysis. The mean length of experiments across all sites included in this analysis is 8 years, with the maximum being 13 years. This resulted in 59 sites meeting all criteria, situated on every continent except Antarctica (Table S1, Figures S1 and S2).

Sampling

Aboveground plant biomass and plant community composition were sampled annually during the peak of the local growing season at each site. All aboveground biomass was clipped into two 0.1 × 1 m strips. Live (current year's growth) and dead (previous year's growth) biomass were separated, and live biomass was typically sorted into functional group categories (e.g. graminoid [including sedges], forb, legume, fern). All sites recorded total live biomass. Biomass was dried at 60°C and weighed to the nearest 0.01 g. The location of the biomass clip plot was moved every year within a subplot designated for biomass sampling. Community composition was sampled as absolute aerial cover in a permanent 1 × 1 m subplot close to biomass strips. The absolute cover was estimated

BOX 1

Thanks to a great deal of previous work on the effect of nutrient deposition on ecological communities, and after over a decade of the Nutrient Network (Borer, Harpole, et al., 2014), we know that the more resources (Nitrogen, Phosphorus and Potassium) that are added to grasslands, the more species richness declines and the more aboveground biomass and productivity increases (Fay et al., 2015; Harpole et al., 2016). We also know that there is an increasing effect of chronic nutrient enrichment on plant diversity loss and ecosystem productivity over time (Seabloom et al., 2020) and that species loss due to nutrient addition increases with spatial scale (Seabloom et al., 2021). Here, we use an updated data set that includes more sites and longer time series than in this previous work, so we analyse the relationship between the addition of multiple limiting nutrients (a combination of Nitrogen, Phosphorus and Potassium - NPK hereafter) on species richness over time and biomass over time as a reference point with this updated data set (Figure S5 and Tables S2–S5).

We then link changes in species composition and biomass using a partitioning approach to understand components of change contributing to these well-known aggregated plot-level effects. The ecological adaptation of the Price equation enables the partitioning of community change into five additive components, named the ‘5-part Price partition’ or alternatively into three components (Bannar-Martin et al., 2017; Fox & Kerr, 2012). This partition links changes in species with any related additive measure of an ecosystem property between two samples often referred to as ecosystem function in previous work (Bannar-Martin et al., 2017; Fox & Kerr, 2012). Here, we use the 3-part ‘Community assembly’ partition proposed by Bannar-Martin et al. (2017) to understand the effects of biomass change associated with all lost species unique in the baseline sample (SL), with all gained species in the comparison sample (SG), and changes in the function of shared species often referred to as the ‘Context Dependent Effect’ or CDE, but here called persistent species (PS) (Figure 1, Table below). This partition requires two comparable units to quantify additive pairwise differences between the two, to tell us how they vary and covary. Here, we compare every Nutrient Network plot included in this analysis at the year before experimental treatments began as a baseline (year 0 = t0) to itself at every point in time as a comparison (year *n* = tn) measured since experimental treatments began to quantify cumulative continuous temporal changes in each and every plot.

The version of the ecological Price equation used here (Figure 1) uses the number of species in each community (s_{t0} and s_{tn}), the number of species shared ($_{p}s$), the species-level biomass (i.e. function) in each community (z_{t0}, z_{tn}) and the biomass of species shared by the baseline ($^{p}z_{t0}$) and comparison communities ($^{p}z_{tn}$) as terms (Bannar-Martin et al., 2017). Here, we uniquely use the number of species shared between two samples in time (^{p}s), those unique in the baseline community (s_{t0}) to quantify the number of species lost (s.loss), and those unique in the comparison community (s_{tn}) to quantify the number of species gained (s.gain) (Figure 1). These are the same number of species used to quantify the impacts of these gains and losses on additive measures of biomass in this study (or any additive measure of ecosystem processes or functions) in the 3-part Price equation partition. Next, we use this 3-part ecological version of the Price partition to quantify aboveground vegetation biomass change associated with species loss (SL) ($^{p}z_{t0} - z_{t0}$), gains (SG) ($z_{tn} - {}^{p}zt_{n}$) and persistent species (PS) ($^{p}z_{tn} - {}^{p}z_{t0}$) (see methods and Figure 1). Slightly different language has been used to describe the components of the most commonly used 5-part Price equation partition for different applications and contexts in previous work. Below we describe these differences in relation to what is presented here.

Descriptions of Price equation components, the different short names of each component have been given in previous literature to address various contexts, and their acronyms are compared against the components used in this work. Acronyms for each component are in bold italic. Initials are used as a short reference for each paper that uses each acronym for each component (Fox & Kerr, 2012) = FK, (Winfree et al., 2015) = W, (Bannar-Martin et al., 2017) = BM, cited in the order they were published.

visually for each species, so that the summed cover of all species could exceed 100% to most accurately represent multi-layered grasslands. We excluded non-living litter and debris, woody species and non-vascular species such as bryophytes from the data for this analysis, as these categories were not consistently accounted for in living herbaceous biomass samples across sites.

Data preparation

We used live species relative cover and live aboveground biomass to estimate per species live biomass in two ways. In sites and years when biomass was sorted into functional groups, the species percentage cover was summed within those same functional groups and the relative cover of each species within a functional group

BOX 1 (Contiued)

5-part Price partition component description	5-part Price partition short names and acronyms used in other contexts	3-part Price partition component description and acronyms used in this work
Impact of species loss on ecosystem function, for average functioning species	a. Species richness effect of loss ***SRE.L*** (FK, BM), ***Rich-L*** (W)	a. Impact of species loss associated with aboveground biomass loss equal to the sum of (a) and (b) in the 5-part partition. ***SL*** (BM, this work)
Impact of species loss on ecosystem function, for non-average functioning species	b. Species composition/identity effect of loss ***SCE.L*** (FK), ***COMP-L*** (W), ***SIE.L*** (BM)	
Impact of species gain on ecosystem function of average functioning species	c. Species richness effect of gain ***SRE.G*** (FK, BM), ***RICH-G*** (W)	b. Impact of species gain on aboveground biomass. Equal to the sum of (c) and (d) in the 5-part partition. ***SG*** (BM, this work)
Impact of species gain on ecosystem function for non-average functioning species	d. Species composition/identity effect of gain ***SCE.G*** (FK), ***COMP-G*** (W), ***SIE.G*** (BM)	
The changes in ecosystem in the species shared between two samples	e. Context dependent effect/Abundance effect ***CDE*** (FK, BM), ***ABUN*** (W)	c. Biomass change associated with persistent species. Equal to (e) in the 5-part partition. **PS** (this work)

was multiplied by the sorted biomass of that functional group to estimate per-species biomass (Axmanová et al., 2012). This relates the species cover to biomass for different functional groups (Figure S3a) and accounts for differences in the mass to cover relationships among different life forms. For example, broadleaf forbs will likely have a higher cover-to-mass relationship as their leaves are more horizontal.

In sites and years where biomass was not sorted into functional groups, or in plots where samples of functional groups were not matched between the cover and biomass data (e.g. a legume recorded in cover measurements but not in biomass samples), total live biomass values were used to estimate per species biomass. In these cases, the cover of each species relative to the whole plot was multiplied by the total live biomass for the plot (Axmanová et al., 2012; Hautier et al., 2014; Isbell et al., 2015) (Figure S3b). We expect that the first method provides more accurate species-level estimates, so this method was used wherever possible. These approaches use the best available data from destructively sampled biomass strips to estimate species-level biomass from per cent cover data. We acknowledge that this is not an exact measure of per species biomass and introduces some uncertainty in our analyses. However, we compared both methods and found no major differences in estimates of overall biomass change associated with components of diversity change between major functional groups (Figure S3c). In addition, we examined whether using species' per cent cover instead of biomass as a response altered our inferences (Figure S4). Changes in species' per cent cover through time were qualitatively consistent with those estimated using biomass. However, the cover is a constrained and two-dimensional measure that does not fully describe growth in a plant community. We find that the rate of change in cover does not change as much as biomass in response to NPK, but still demonstrates turnover within communities, so when we relate biomass measures to cover to estimate per species biomass, biomass estimates are moderated by the cover and likely underestimated due to these differences (Figure S4).

Data analysis

After data were prepared and cleaned, species richness and total live biomass were quantified for every 1 m^2 subplot each year. To partition plot level measures into changes associated with species losses, gains and species persistence, we made pairwise comparisons between each plot pre-treatment (t0) to itself at every subsequent time point after nutrient addition treatments were applied (tn; Figure 1).

Quantifying components of change

To quantify changes in species and biomass through time, we compared the composition of each plot in the year before fertilization (year 0, t0) to itself at every subsequent time-step measured annually (comparison, year n, tn) using the R package priceTools (Bannar-Martin et al., 2017) (Figure 1). We used two approaches to quantify community change. First, we used an ecological adaptation of the Price equation (Bannar-Martin et al., 2017; Fox & Kerr, 2012) to partition overall biomass changes into those associated with species losses, species gains and persistent species between two samples in time in every plot (Figure 1). Specifically, we use the 'Community Assembly' 3-part partition approach suggested by Bannar-Martin et al., 2017 (Figure 1, Box 1). This equation quantifies additive differences between comparable units (e.g. plots). Here, this equates to additive species-level changes in aboveground biomass through time associated with specific changes in species composition, relative to the plot before experimental treatments began. Second, we used a complementary but separate approach to quantify absolute species losses and gains (Figure 1).

To quantify the absolute number of species loss (s.loss), the species richness of the plot at year 0 (s_{t0}) is subtracted from the shared species (^{p}s) between the two samples. That is, species lost are the species that are unique in the first sample at year 0 and are therefore not present in the sample at year n. For species gains (s.gain), the shared species (^{p}s) between two samples is subtracted from the species richness of the plot at year n (s_{tn}). Simply put, species gained are the species that are unique in the sample at year n but are not present at year 0. Persistent species are the species that are shared between year 0 and each point in time. In other words, species that were present at year 0 are still present.

The 3-part Price equation partition uses the same species terms to quantify components of biomass change (Bannar-Martin et al., 2017). Biomass change associated with species loss (SL) equates to the total biomass of the plot at year 0 (z_{t0}) subtracted from the sum of the biomass at year 0 of shared species ($^{p}z_{t0}$) between two samples. Biomass change associated with species gains (SG) is equal to the sum of the biomass of shared species ($^{p}z_{tn}$) between two samples at year n, subtracted from the total biomass of the plot year n (z_{tn}). Biomass change in persistent species (PS), is the sum of the biomass of shared species at year 0 ($^{p}z_{tn}$) subtracted from the sum of the biomass of shared species at year tn ($^{p}z_{t0}$). The full details of the 3-part Price equation partition (and a 5-part partition used in previous works but not used here) can be found in Bannar-Martin et al. (2017) (summarised in Figure 1).

There are different options to arrange the pairwise comparisons required to employ the Price equation depending on the question being asked. Previous work has examined temporal changes using between-site temporal variance as a metric of change (Genung et al., 2017) or by comparing all years to the highest functioning year within a site as a relative metric of temporal change (Winfree et al., 2015). We follow the original temporal approach taken by George R. Price (Price, 1970, 1972) that quantifies change by comparing the same unit to itself continuously through time to track changes continually. In the context of the Nutrient Network, this quantifies the cumulative change in each local plot across time, and means we can contrast component changes relative to the starting point of the plot before experimental fertilization began and between the NPK treatment and the control. We calculated species and biomass partitions that sum additively to the exact change in richness and change in biomass quantified between two plots in time (Figure 1).

Species composition and biomass in each plot were partitioned into five continuous components. Species compositional changes consisted of the (1) number of species lost (s.loss, species unique in baseline [t0] compared to same plot at another point in time [tn]), (2) number of species gained (s.gain, species unique in comparison plot [tn] compared to species in baseline [t0]). Biomass was partitioned using the 3-part Price equation into (3) biomass change associated with SL, year 0, (4) biomass change associated with species gains (SG, year tn) and (5) biomass change associated with persistent species (PS, species shared between comparisons year t0 and year tn) (Figure 1, Box 1). We compare control plots to themselves through time, and NPK plots to themselves through time to examine component changes under ambient conditions and under fertilisation. These pairwise comparisons resulted in continuous response metrics for every year after year 0 (t0) that we modelled as a function of time. We use this approach to estimate (1) the average total (or cumulative) change in each component at the end of the time series (i.e. the predicted value at year 13); (2) the overall rates of change (slope parameters) for each metric component and (3) pairwise relationships (i.e. correlations) among the changing components.

Statistical models

We examined how nutrient addition (NPK treatment) influenced species losses and gains, and the three components associated with the Price equation partition, using multi-level linear regression models. We fitted five separate univariate multi-level linear regression models, one to each metric. We also examined species richness and plot-level biomass across time using the largest data set coming from the Nutrient Network to date (version May 6, 2021) (Box 1. Figure S5).

Responses were untransformed and we fit models that assumed the additive (natural) scale of the partition. Each univariate model included treatment (NPK or Control) as a categorical fixed effect, time since the experimental start as a mean-centred continuous fixed effect (in years), and their interaction. These same covariates were also allowed to vary as random intercepts and slopes among sites, blocks (nested within sites) and plots (nested within blocks). Species richness was modelled with a Gaussian distribution, and all other responses used the Student *t* distribution (Table S3).

To quantify the joint response of these metrics to NPK treatments across time, we also fitted two multivariate multi-level linear regression models that included multiple response variables in the same model. The first multivariate model was fitted to examine the joint response of species richness and biomass to NPK treatments (Supplementary Information); the second examined the joint response of all five components of species and biomass change (species loss, species gain and biomass change associated with species loss, gain and persistent species) in control and NPK plots. This multivariate approach allows for correlations between responses to be quantified. For the multivariate models assessing the joint responses between variables, we could only allow treatment, year and their interaction to vary among sites, as models did not converge when finer grouping variables were included. The parameter estimates between univariate and multivariate models did not qualitatively differ. We report results from the univariate models for our main results and report the strength of the correlation between different responses estimated with the multivariate models. We visually examined plots of residuals for all models to assess whether model assumptions (e.g. homogeneity of variance) were met. Posterior predictive plots were used to visually determine how well models reproduced the data (Figure S6a–n). Our results did not qualitatively change when only sites with experiments running for a minimum number of years (i.e. all years, ≥3, ≥6 or ≥ 10 years) were included (Figure S7), and we present results using a minimum of 3 years in the main text.

For Bayesian inferences and estimates of uncertainty, all models described above were fitted using the Hamiltonian Monte Carlo (HMC) sampler Stan (Carpenter et al., 2017) and coded using the 'brms' package (Bürkner, 2018) in the R for Statistical Computing and Graphics environment (v.4.0.2; (R Core Development Team, 2019)). All models were fitted with four chains and varying iterations (Supplementary Information). We report the 95% Credible Intervals (hereafter CI) around the absolute average total change after 13 years, and the

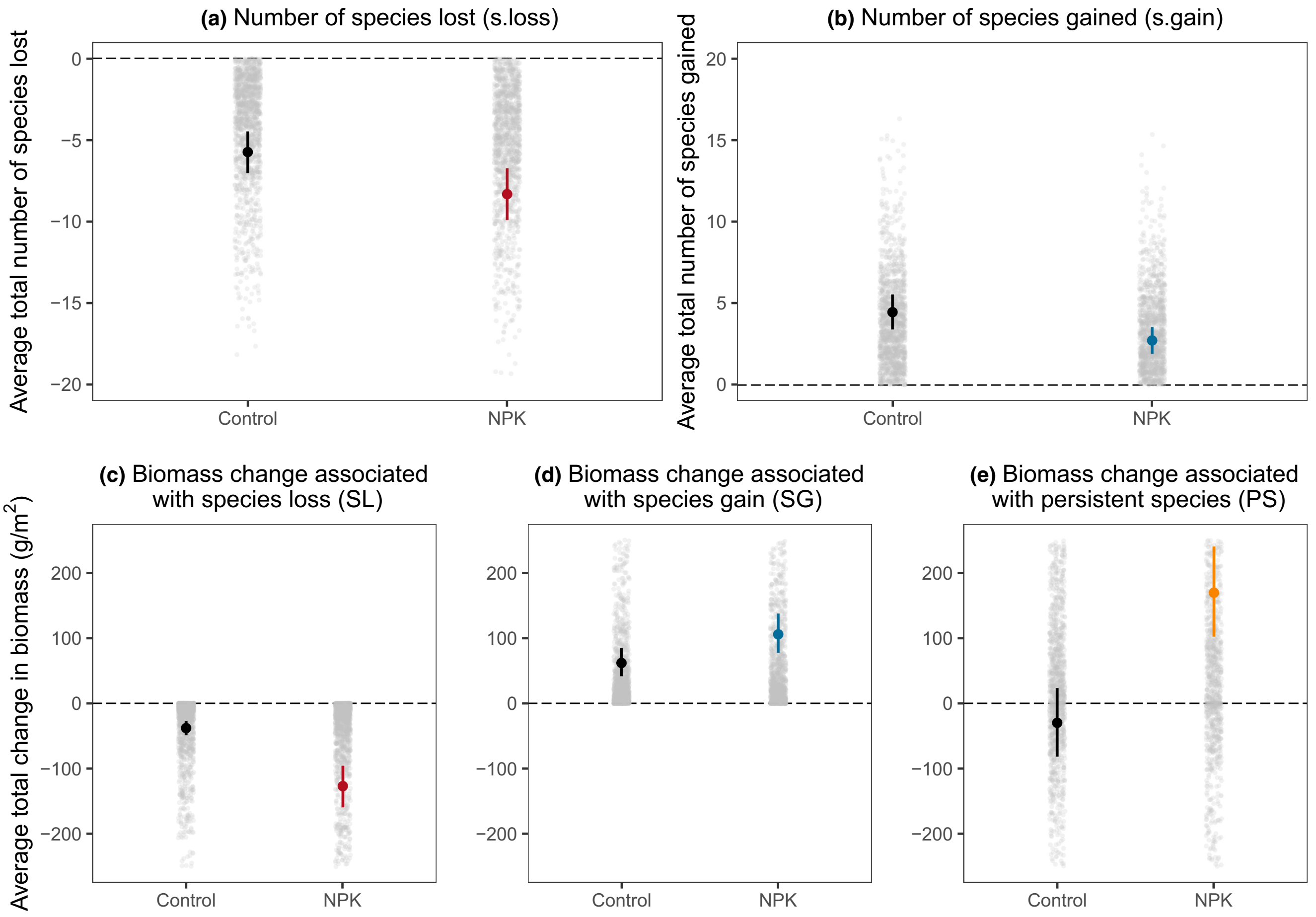


FIGURE 2 The absolute average total change in the number of species (a, b) and live aboveground biomass (c–e). Each small jittered grey point represents a pairwise comparison before experimental treatments began (year 0) and the last recorded temporal measurement of a plot for each treatment and metric respectively (~3–6 plots per treatment per site). Large coloured points are the predicted overall effects (average total) of treatment at 13 years (maximum year of experimental measurements across all sites) and coloured lines show the 95% credible intervals.

mean overall slope for each metric in the main results (Table S2). We used weakly regularizing priors and visual inspection of HMC chains showed excellent convergence for selected models.

RESULTS

Average total change

On average, in controls, a similar total number of species were lost (−5.74, 95% CI: −7.02 to −4.48, number of species) and gained (4.46, 95% CI: 3.40 to 5.54, number of species) (Figure 2a,b). Total biomass loss in control plots associated with species loss (−37.9, 95% CI: −48.7 to 27.4, g/m^2) was slightly less than biomass increases associated with species gain (61.8, 95% CI: 41.6–84.9, g/m^2) (Figure 2c,d). Total biomass change associated with persistent species was negative but was not found to differ from zero (−30.9, 95% CI: −81.2 to 19.8, g/m^2) (Figure 2e).

On average, in NPK plots, a much greater number of species were lost in total (−8.32, 95% CI: −9.90 to −6.73, number of species) than gained (2.73, 95% CI: 1.91 to 3.55, number of species) (Figure 2a,b). NPK treatments resulted in greater total biomass loss associated with species loss (−127, 95% CI: −159 to −95.6, g/m^2) than total biomass gain associated with species gain (106, 95% CI: 77.3 to 137, g/m^2) (Figure 2c,d). Total biomass change associated with persistent species greatly increased on average (171, 95% CI: 104–241, g/m^2) (Figure 2e).

Rates of change

In controls, similar numbers of species were lost per year (−0.19, 95% CI: −0.28 to −0.11, species loss (s.loss)/year) and gained per year (0.12, 95% CI: 0.04–0.21, species gained (s.gain)/year) (Figure 3a,b). Biomass loss in controls associated with species losses each year (−0.56, 95% CI: −0.97 to −0.26, SL g/m^2 associated with species loss/year) was less than the biomass gain associated with species gains each year (4.02, 95% CI: 2.6 to 5.86, SG g/m^2 associated with species gain/year) (Figure 3c,d). Biomass change associated with persistent species showed considerable variation, but no directional change (−4.47, 95% CI: −10.76 to 1.84, PS g/m^2 associated with persistent species/year) (Figure 3e).

NPK treatments had higher rates of species loss over time (−0.38, 95% CI: −0.51 to −0.26 species/year Figure 3a) than controls. In contrast, the rate of species gain in NPK treatments was less than controls and did not differ from zero (−0.01, 95% CI: −0.08 to 0.06 species/year, Figure 3b). That is, species were gained in NPK (on average, approximately 3 in total, Figure 2b), but this gain was relatively constant over time (Figure 3b). In NPK plots, the rate of biomass loss associated with species loss was greater than in controls (−7.44, 95% CI: −10.18 to −4.92 g/m^2/year, Figure 3c). Species that were gained in NPK plots were also associated with more biomass change per year than control plots (7.36, 95% CI: 5.27–9.77 g/m^2/ year, Figure 3d).

Finally, change in biomass over time associated with persistent species exhibited considerable variation in NPK treatments that overlapped zero (3.05, 95% CI: −6.14 to 11.88 g/m^2/year, Figure 3e). Notably, much of the biomass gains due to persistent species was apparent after the first year of experimental treatments (Figure S8e), and this gain stayed relatively constant through time.

To visualise how these component changes combine additively as total community change, we plotted them as vectors (Figure 4). In control plots, these vectors show that biomass turnover was approximately balanced as losses due to species losses and reduced contributions of persistent species were countered by biomass gains due to species gains and that total average species losses were slightly larger than the species gains (~ total average loss of 1 species) (Figure 4a,b). Under fertilisation, we see that species losses outweigh species gains, though the rate of species gain is very close to zero (i.e. the solid blue vector is approximately vertical on Figure 4b) and that biomass gains due to species gains approximately balances biomass losses due to species losses, with biomass increases due to persistent species making for increased biomass (Figure 4a,b). Indeed, persistent species contribute to the majority of biomass gained through time for the NPK plots (Figure 4a,b) newly gained species contribute 39% of total biomass gained on average (CI: 29.5–53.4%) and persistent species contribute 60% (CI: 46.6 to 70.5).

Species losses and gains due to nutrient addition were largely uncorrelated (0.29, 95% CI: −0.03 to 0.58, Table S5), as was the net change in biomass from losses and gains (−0.07, 95% CI: −0.38 to 0.23). Biomass change associated with species losses and biomass change in persistent species responses to NPK were also uncorrelated (−0.24, 95% CI: −0.55 to 0.09), as was the relationship between biomass changes from species gains and persistent species (−0.06, 95% CI: −0.39 to 0.29).

DISCUSSION

Turnover in species composition is a dominant form of biodiversity change (Blowes et al., 2019; Dornelas et al., 2014), though how turnover contributes to changes in other ecosystem properties or services is less well known. By quantifying biomass change associated with species entering, leaving or persisting in communities, we provide new insights into the relationship between compositional change and an important ecosystem function for grasslands. Using data from 59 grassland sites, we show that under ambient conditions, compositional and biomass turnover were approximately balanced, resulting in roughly constant aggregate plot-level species richness and biomass. In

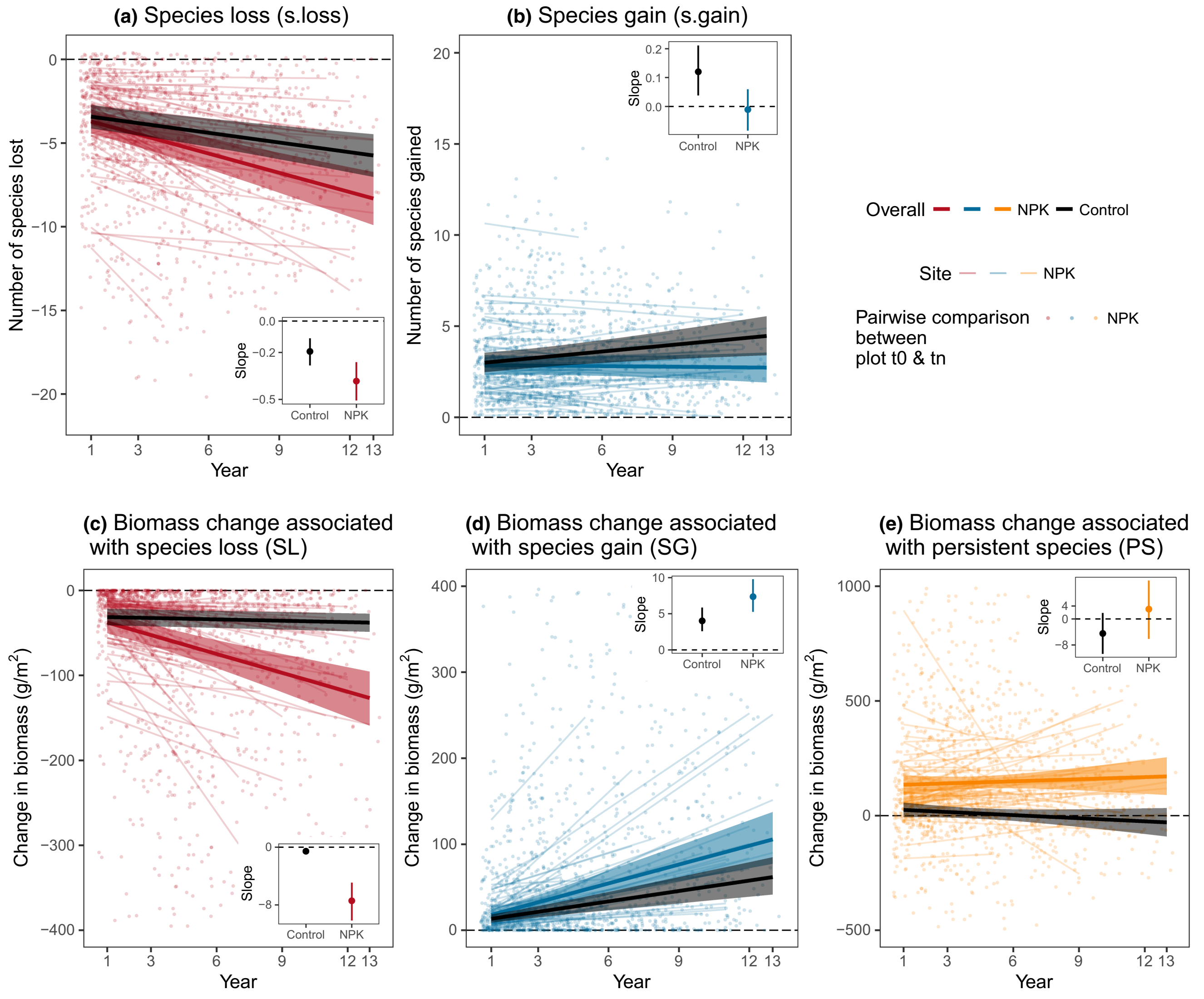


FIGURE 3 Changes in the components of species and aboveground biomass through time for control and NPK treatment. In regressions represented in (a–e), the solid thick lines represent the overall effect estimate for NPK (solid) and Control (dashed) treatments, and the shading around these black lines shows the 95% credible interval. Each jittered point represents a pairwise comparison of a single plot before NPK nutrient addition (year 0) and for each year after treatment respectively (~3–6 plots per treatment per site measured every year). Each thin line represents the slope of NPK plots for a site ($n = 59$), estimated as a random effect. The inset plots represent the overall effect (i.e. slope) estimate of control (black) and NPK (coloured) treatments, error bars represent 95% credible intervals, and the dashed reference line at 0 represents a slope of 0 for each metric.

contrast, the addition of multiple limiting nutrients resulted in greater species loss and reduced gains compared with controls, which both contributed to a net decline in richness. Under fertilisation, biomass turnover is much higher on average and increases through time compared to under ambient conditions. Despite a relatively constant number of species gained through time on average, species gained were associated with substantial biomass gains that increased through time. Interestingly, persistent species contributed the most to biomass gained on average, and the majority of these gains were apparent soon after fertilisation but did not grow with time. In contrast, biomass associated with extinctions and colonisations did not vary much between controls and the NPK treatment within the first year of treatment, however, biomass losses and gains continued to accumulate in magnitude through time.

Compositional change (i.e. species turnover) can be uncoupled from changes in species richness (Blowes et al., 2019; Hautier et al., 2018; Hillebrand et al., 2018). Our findings support the previous findings that the strength and direction of biodiversity change depends on the balance of species losses, species gains and species that persist over time (Dornelas et al., 2019), and as we show here, so do associated changes in aboveground biomass. Which species thrive under nutrient addition and which are excluded from fertilized communities is in part determined by species identities, their traits

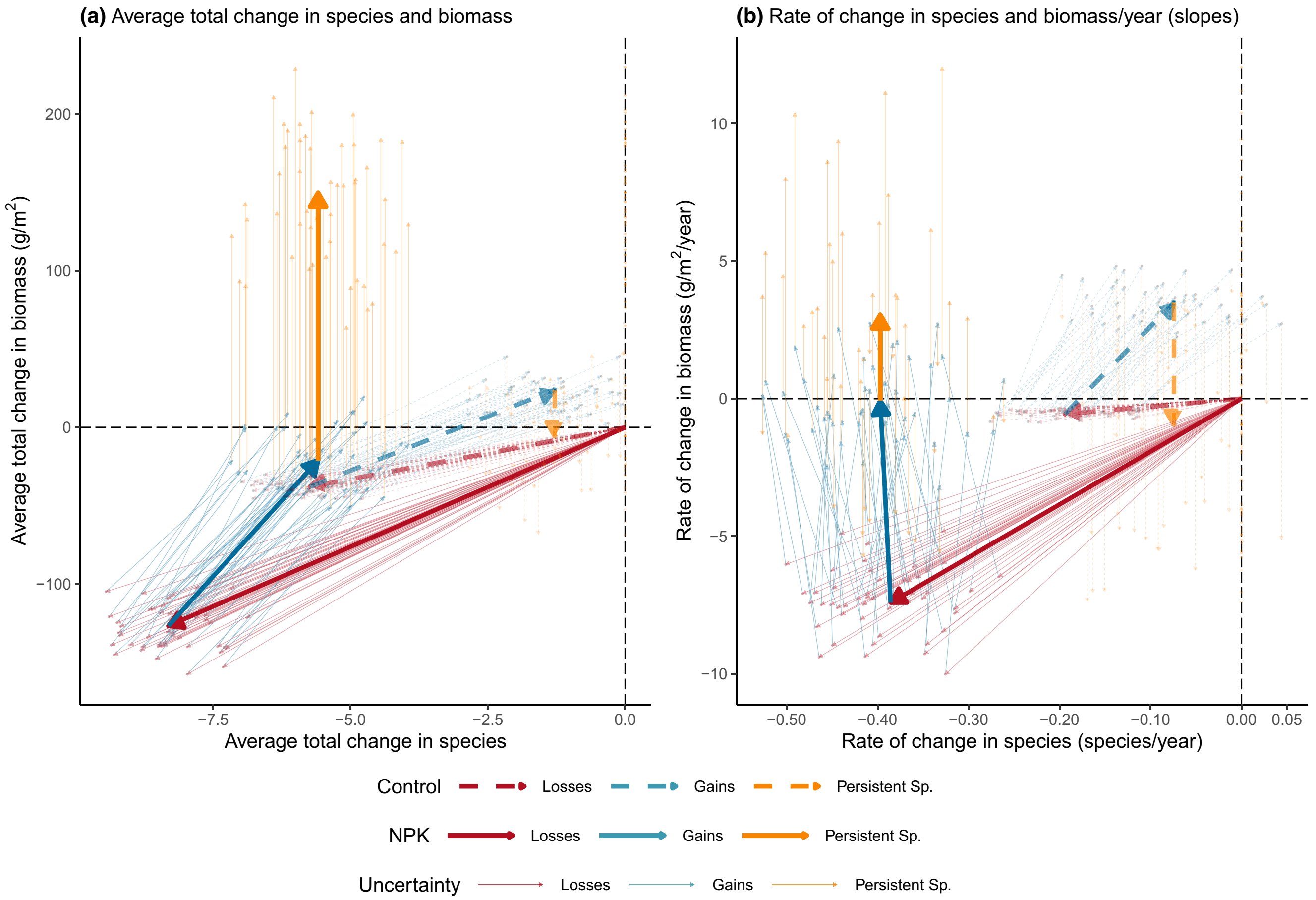


FIGURE 4 Change in species and biomass. Change in control (dashed lines) and fertilised plots (solid lines) on species (x-axis) and aboveground biomass change (y-axis) as (a) an average overall change after 13 years and (b) a rate of change across time (slope). Thick lines show the overall effect estimate (mean overall change in control and NPK plots) of each response (a) effect sizes from Figure 2 and b) slopes from Figure 3), and thin lines represent the variation in the posterior distribution (uncertainty) sampled from each overall effect estimate within the 95% credible intervals ($n = 50$ samples). Effects can be plotted in any order but here we start with losses for visual clarity. Both x and y axes vary for clarity.

and the matching of traits to the environment (Lind et al., 2013; Morgan et al., 2016; Seabloom et al., 2015). Species that are lost might be poor competitors or species gained might be competitive dominants under nutrient addition, combining to result in different outcomes for local ecosystem processes and functions (Leibold et al., 2017). Because species contribute to aboveground biomass to different extents (Hautier et al., 2018; Isbell et al., 2013), considering compositional changes in relation to their individual contributions to biomass provides a more comprehensive understanding of the effects of global change pressures on ecological communities and ecosystems.

Global change factors can affect species extinctions, colonisations and relative abundance of species that persist in different ways and additionally, at different times. Rates of change in the metrics investigated here were uncorrelated, supporting the idea that drivers of change can act relatively independently on diversity, composition and ecosystem processes and functions such as aboveground biomass (Helsen et al., 2014). Here, biomass of persistent species initially increased soon after fertilisation and accounts for the majority of biomass gained so far. In contrast, biomass change coming from extinctions and colonisations change more through time. Whether associated changes in biomass from one of these components will outpace another through time remains an open question. Increasing biomass associated with fertilisation may contribute to processes involved in diversity loss and changes in composition can in turn have varying effects associated with biomass (Harpole et al., 2016; Leibold et al., 2017). Resource addition can affect ecological communities by decreasing the number, stoichiometry, identity or heterogeneity of limiting resources (Harpole et al., 2017). Here we better understand how processes of community assembly are linked with these multifaceted changes by considering them independently, yet concomitantly (Ladouceur et al., 2020). We've found that the effect of compositional change on aboveground biomass is dependent on the magnitude and contribution of species entering, persisting in and exiting communities.

The clarity and consistency of our results on average are despite heterogeneity among sites in terms of herbivory, soils and climate (Borer et al., 2020; Harpole et al., 2016). The majority of sites investigated here demonstrate the expected overall response of a gain in biomass and loss in richness through time (41 sites). However, there is also variation among sites that demonstrate a loss in biomass and a loss in richness (9 sites), a gain in biomass and a gain in richness (6), and a loss in biomass and a loss in richness (3) (Figure S9). Components of change in composition contribute to this observed variation in aggregate measures at the site level (Figure S10). For example, in sites where biomass was lost, we observe a greater loss of biomass associated with species loss, and the sign of changes in biomass associated with persistent species was negative (Figure S10c,e,i,j). Tracking species-level components provides a new approach for examining processes that moderate grassland richness and productivity.

The work presented here points to many interesting avenues for further development and investigation. For example, we expect that herbivory reduced biomass in NPK plots, as nutrient addition attracts grazing (Borer et al., 2020; Borer, Seabloom, et al., 2014; Ebeling et al., 2021; Hodapp et al., 2018), possibly explaining some site-level variation. How these relationships change with grazing exclusion is currently an open question. Additionally, some variation in site-level responses may be due to water limitation, and may account for some cases where nutrients do not affect biomass in very high and very low ends of the precipitation gradient represented here (Figure S11). Additional mechanisms driving patterns within and across sites (Figure S11) (Avolio et al., 2021), spatial scales (Barry et al., 2021; Chase et al., 2019; Seabloom et al., 2021) and according to species' functional identities and characteristics (Crawford et al., 2021) could also be further investigated. We now know that the risk of a species being lost from a plot decreases with its abundance and varies across functional forms (Wilfahrt et al., 2021). The degree to which these species' characteristics (e.g. traits, dominance) influence the magnitude of change associated with biomass are beyond the scope of this investigation, but our approach could be adapted to ask these questions. A substantially adapted approach within a similar temporal framework could possibly also be applied to measures that are not additive, such as stability (e.g. estimates of temporal variability within an assemblage).

In sum, we partition measures of species richness and aboveground live plant biomass to better understand the underlying mechanisms of community change under pressure from a key driver of global environmental change, nutrient enrichment. Our results demonstrate that the components of compositional change are key to understanding the relationship between diversity and aboveground biomass, particularly in ecological systems that are experiencing ongoing anthropogenic pressures. By partitioning the roles of individual species, this work provides a more detailed understanding of the relationships between biodiversity change and aboveground biomass in natural systems and how global change drivers can affect them.

AUTHOR CONTRIBUTIONS

E.L., W. S.H. and J.M.C. conceived the idea; E.L., W.S.H., J.M.C., S.A.B. and A.T.C. conceptually framed the paper and discussed and shaped approaches to analyses; E.L. and S.A.B. led and conducted analysis; Authors listed as site coordinators listed in Table S1 set up experiments, collected data annually and contributed data. E.L. led the writing of the paper. All authors contributed to at least two items listed in the co-authorship details in the co-authorship table attached. All authors contributed to paper writing.

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PEER REVIEW

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OPEN RESEARCH BADGES

This article has earned Open Data and Open Materials badges. Data and materials are available at: https://doi.org/10.6073/pasta/293faff7ed2e287b56e85796c87c3e4b.

DATA AVAILABILITY STATEMENT

Data are publicly available on the Environmental Data Initiative (EDI) (https://doi.org/10.6073/pasta/293faff7ed2e287b56e85796c87c3e4b). Code to produce results is freely available on GitHub (https://github.com/emma-ladouceur/NutNet-CAFE) and archived through Zenodo (https://doi.org/10.5281/zenodo.7108504). Some data associated with the Nutrient Network are already open access (https://nutnet.org/index.php/datadois), but this data set used here is unique in the number of sites, the temporal grain and the metrics used.

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SUPPORTING INFORMATION

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

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