Species losses, gains, and changes in persistent species are associated with distinct effects on ecosystem functioning in global grasslands

Authors: Emma Ladouceur[1,2,3,*], Shane A. Blowes[1,4], Jonathan M. Chase[1,4], Adam T. Clark[1,2,5], Magda Garbowski[1,2], Juan Alberti[6], Carlos Alberto Arnillas[7], Jonathan D. Bakker[8], Isabel C. Barrio[9], Siddharth Bharath[10], Elizabeth T. Borer[11], Lars A. Brudvig[12], Marc W. Cadotte[13], Qingqing Chen[14], Scott L. Collins[15], Christopher R. Dickman[16], Ian Donohue[17], Guozhen Du[18], Anne Ebeling[19], Nico Eisenhauer[1,20], Philip A. Fay[21], Nicole Hagenah[22], Yann Hautier[23], Anke Jentsch[24], Ingibjörg S. Jónsdóttir[25], Kimberly Komatsu[26], Andrew MacDougall[27], Jason P. Martina[28], Joslin L. Moore [29,30], John W. Morgan[31], Pablo L. Peri[32], Sally A. Power[33], Zhengwei Ren[18], Anita C. Risch[34], Christiane Roscher[1,2], Max A. Schuchardt[24], Eric W. Seabloom[11], Carly J. Stevens[35], G.F. (Ciska) Veen[36], Risto Virtanen[37], Glenda M. Wardle[16], Peter A. Wilfahrt[11], W. Stanley Harpole[1,2,20]

[1] German Centre for Integrative Biodiversity Research (iDiv) Leipzig-Halle-Jena, Puschstraße 4, 04103 Leipzig, Germany
[2] Department of Physiological Diversity, Helmholtz Centre for Environmental Research -UFZ, Permoserstrasse 15, 04318 Leipzig, Germany.
[3] University of Leipzig,
[4] Institute of Computer Science, Martin Luther University Halle-Wittenberg, 06120 Halle (Saale), Germany.
[5] Institute of Biology, Karl-Franzens University of Graz, Styria, Austria
[6] Laboratorio de Ecología, Instituto de Investigaciones Marinas y Costeras (IIMyC), Universidad Nacional de Mar del Plata, Consejo Nacional de Investigaciones Científicas y Técnicas (CONICET), CC 1260 Correo Central, B7600WAG, Mar del Plata, Argentina.
[7] Department of Physical and Environmental Sciences, University of Toronto Scarborough, Toronto, ON, M1C 1A4, Canada
[8] School of Environmental and Forest Sciences, University of Washington, Seattle, WA 98195
[9] Faculty of Environmental and Forest Sciences, Agricultural University of Iceland, Árleyni 22, 112 Reykjavík, Iceland
[10] Atria University, Hebbal, Bengaluru - 560024, Karnataka, India
[11] Department of Ecology, Evolution, and Behavior, University of Minnesota, St. Paul, MN 55108 USA
[12] Department of Plant Biology and Program in Ecology, Evolution, and Behavior, Michigan State University, East Lansing, MI 48824
[13] Department of Biological Sciences, University of Toronto Scarborough, Toronto, ON, M1C 1A4, Canada
[14] Institute of Ecology, College of Urban and Environmental Science, Peking University, 100871, Beijing, China.
[15] Department of Biology, University of New Mexico, Albuquerque, NM 87131, USA
[16] School of Life and Environmental Sciences, The University of Sydney, Sydney 2006, New South Wales, Australia
[17] Department of Zoology, Trinity College Dublin, Dublin, Ireland
[18] School of Life Sciences, Lanzhou University, No.222, Tianshui South Road, Gansu, China
[19] Institute of Ecology and Evolution, Friedrich-Schiller University Jena, Dornburger Str. 159, 07743 Jena, Germany
[20] Institute of Biology, Martin Luther University Halle- Wittenberg, Am Kirchtor 1, Halle (Saale) 06108, Germany
[21] USDA-ARS Grassland Soil and Water Research Lab, 808 E. Blackland Road, Temple, TX 76502 USA
[22] Mammal Research Institute, Department of Zoology & Entomology, University of Pretoria, Pretoria, South Africa

[23] Ecology and Biodiversity Group, Department of Biology, Utrecht University, Padualaan 8, 3584 CH Utrecht, The Netherlands.
[24] Disturbance Ecology, Bayreuth Center of Ecology and Environmental Research, University of Bayreuth, Universitätsstr. 30, 95447 Bayreuth, Germany
[25] Institute of Life and Environmental Sciences, University of Iceland, Sturlugara 7, 102 Reykjavík, Iceland
[26] Smithsonian Environmental Research Center, 647 Contees Wharf Road, Edgewater, MD 21037 USA
[27] Dept of Integrative Biology, University of Guelph, Guelph, Ontario, Canada N1G2W1
[28] Department of Biology, Texas State University, San Marcos, TX 78666, USA
[29] Arthur Rylah Institute for Environmental Research, 123 Brown Street, Heidelberg, Victoria 3084, Australia
[30] School of Biological Sciences, Monash University, 25 Rainforest Walk, Clayton, Victoria 3800, Australia
[31] Department of Ecology, Environment and Evolution, La Trobe University, Bundoora 3086, Victoria, Australia
[32] National Institute of Agricultural Research (INTA), Southern Patagonia National University (UNPA), CONICET, Río Gallegos, (CP 9400), Santa Cruz, Argentina
[33] Hawkesbury Institute for the Environment, Western Sydney University, Locked Bag 1797, Penrith, NSW, 2751, Australia
[34] Swiss Federal Institute for Forest, Snow and Landscape Research WSL, Community Ecology, Zuercherstrasse 111, 8903 Birmensdorf, Switzerland
[35] Lancaster Environment Centre, Lancaster University, Lancaster, LA1 4YQ
[36] Department of Terrestrial Ecology, Netherlands Institute of Ecology, Droevendaalsesteeg 10, 6708 PB, Wageningen, the Netherlands
[37] Ecology and Genetics, University of Oulu, Finland

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***Corresponding author:** Dr. Emma Ladouceur, Biodiversity Synthesis & Physiological Diversity, The German Centre for Integrative Biodiversity Research (iDiv) Leipzig-Halle-Jena, Puschstraße 4, 04103 Leipzig, Germany, +49 1520 7210 282, emma.ladouceur@idiv.de

Author Contributions

E.L., W. S.H., & J.M.C. conceived the idea. E.L., W.S.H., J.M.C., S.A.B. & A.T.C., conceptually framed the paper and discussed and shaped approaches to analyses. E.L. &

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 writing 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.

Data Accessibility Statement: Plot level data (species richness, aboveground biomass, and pairwise price equation partition responses) used to produce results will be made open access in a data repository such as Dryad or FigShare. Model objects, and data extracted from models to reproduce results will also be made open access. Code to produce results will be made freely available on Github and archived through Zenodo. Some data associated with the Nutrient Network are already open access (https://nutnet.org/index.php/datadois), but this dataset used here is unique in the number of sites, the temporal grain, and the metrics used.

Novelty Statement: We develop a synthesis approach to partition temporal changes in species richness and aboveground biomass under ambient conditions (control) and fertilization (NPK) into species losses, species gains, and species change in 59 grasslands on six continents. This approach elucidates the rates of change in these components of community composition and the change in ecosystem functioning associated with each.

Abstract

Global change drivers such as anthropogenic nutrient inputs simultaneously alter biodiversity, species composition, and ecosystem functions such as aboveground biomass. These changes are interconnected by complex feedbacks among extinction, invasion, and shifting relative abundance. Here, we use a novel temporal application of the Price equation to quantify the functional contributions of species that are lost, gained, and persist under ambient and experimental nutrient addition in 59 global grasslands. Under ambient conditions, compositional and biomass turnover was high, but species losses (i.e., local extinctions) were balanced by gains (i.e. colonization). There was biomass loss associated with species loss under fertilization. Few species were gained in fertilized conditions over time but those that were, and species that persisted, contributed to net biomass gains, outweighing biomass loss. These components of community change are key to understanding the relationship between diversity change and functioning.

Introduction

Human pressures are fundamentally changing the global environment in terms of species diversity and the functioning of ecosystems (Moreno-Mateos *et al.* 2017; Chaplin-Kramer *et al.* 2019). There are elevated extinction rates globally, but this is often not reflected in measures of species richness and diversity at local scales (Dornelas *et al.* 2014; Blowes *et al.* 2019). Instead, compositional change in species is predominant (Hillebrand *et al.* 2018; Blowes *et al.* 2019), as there is a mixture of winners and losers in ecological communities under anthropogenic pressures (Dornelas *et al.* 2019). Biodiversity is known to positively influence ecosystems in terms of important functions such as biomass production, nutrient absorption, and carbon sequestration (Cardinale *et al.* 2013; Hooper *et al.* 2016), and species loss is known to negatively affect these measures of ecosystem function (Smith & Knapp 2003; Isbell *et al.* 2013; Genung *et al.* 2020). However, aggregate community measures of biodiversity and functioning, while 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 measures of ecosystem function.

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, alterations in nutrient supplies change the conditions of species coexistence via tradeoffs in competition for limiting resources, 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). Resulting changes in biodiversity might further alter key ecosystem functions and services such as the production of biomass, carbon sequestration, and nutrient cycling (Hooper *et al.* 2005). Live aboveground biomass is a particularly important measure of ecosystem function, as plant biomass is an important source of energy for most life on land (Yang *et al.* 2020). However, the relationship between biodiversity and aboveground biomass under global change pressures such as nutrient enrichment varies in direction and strength across contexts, systems, and sites (Harpole *et al.* 2016). Understanding how biodiversity, composition, and aboveground biomass change are interrelated is essential for anticipating the impacts of global change pressures such as nutrient deposition on ecosystems and their functions.

Global change drivers such as nutrient addition can alter community assembly processes, community composition, and ecosystem functioning concurrently (Bannar-Martin *et al.* 2017; Leibold & Chase 2017; Leibold *et al.* 2017). In some cases, small changes in species richness mask large compositional changes (Spaak *et al.* 2017; Hillebrand *et al.* 2018). Changes in competition and coexistence resulting from nutrient inputs can affect compositional turnover, or community change, including gains of novel species, losses of existing species, and changes in abundance of species that persist. Because the functional contributions of novel species may not offset the functional contributions of species that are lost, the processes controlling species diversity and those controlling ecosystem functions may be decoupled. Differences in community change following fertilization could also help explain findings of little change in overall community function despite substantial loss of diversity (Fay *et al.* 2015; Harpole *et al.* 2016).

Here, we apply an adaptation of the Price equation (Price 1970, 1972; Fox & Kerr 2012) to quantify the functional contributions of individual species that are lost, gained, or persist under ambient and fertilized conditions to better understand the role of these community assembly processes on the functioning of ecosystems (Bannar-Martin *et al.* 2017). The Price equation was originally developed for use in evolutionary biology (Price 1970, 1972), but has potential to be 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 can help elucidate the biological relationships that underpin the variation between aggregate changes in species richness, composition, and additive measures of ecosystem functioning, and has been adapted for this use in many ways (Winfree *et al.* 2015; Genung *et al.* 2020; Lefcheck *et al.* 2021; Ulrich *et* *al.* 2021). We use a novel application of this approach based on previous developments (Fox & Kerr 2012; Bannar-Martin *et al.* 2017), to link temporal changes in biodiversity to an additive measure of ecosystem functioning (i.e., aboveground biomass) using a long-term dataset with global coverage. By following compositional changes in experimental plots through time, we separate species richness change to quantify the cumulative number of species lost, gained, and persisting, as well as the associated change in aboveground biomass attributed to each (Fig. 1).

We quantify how community compositional change induced by nutrient addition contributes to altered ecosystem function (aboveground biomass) using data from sites within the Nutrient Network, a globally distributed nutrient addition experiment, replicated across grassland sites (NutNet; http://www.nutnet.org) (Borer *et al.* 2014a). Specifically, we synthesize results from 59 experimental sites across six continents comparing control plots and plots that were fertilized with a combination of nitrogen (N), phosphorus (P), potassium (K) and micronutrients (hereafter the NPK treatment). We leverage long-term data to determine rates of change over time for each component.

Previous work has that documented that grassland communities experience reduced richness and increased aboveground biomass with fertilization (Borer *et al.* 2014b; Harpole *et al.* 2016) (Box 1). We expect that how a loss in richness will be associated with change in function likely depends on the functional contributions of species lost, gained, or persisting in the community. On one hand, a weak response of persistent species or the loss of relatively high-functioning 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 functional 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 which components of community change are associated with changes in function would advance understanding of how global change affects interdependent dimensions of natural 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 *et al.* 2014a) (Table S1, Fig. S1). At each site, a factorial combination of nitrogen (N), phosphorus (P), and potassium (K with a one-time addition of micronutrients) are applied annually, alongside an unmanipulated control treatment with no added nutrients. Plots are 5 m x 5 m and 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 treatments: unfenced control (ambient conditions) and full fertilization (NPK) treatments. Sites with measurements the year prior to fertilization (year 0) and for at least three years with fertilization were included in this analysis. The mean length of experiments across all sites included in this analysis is eight years. This resulted in 59 sites meeting all criteria, situated on every continent except Antarctica (Supplementary Table S1, Fig. S1, Fig. S2).

Sampling

Aboveground plant biomass and plant community composition were sampled annually during the peak of the local growing season. All aboveground biomass was clipped in two 0.1 m x 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, 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 percentage cover in a permanent 1 m x 1 m subplot close to biomass strips. Absolute cover was estimated 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 species relative cover and aboveground biomass to estimate per species 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 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 (Fig. 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 to functional groups, or in plots where samples of functional groups were not matched between 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, 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) (Fig. 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 percent 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 (Fig. S3c). In addition, we examined whether using species' percent cover instead of biomass as a response altered our inferences (Fig. S4). Changes in percent cover through time were broadly qualitatively consistent with those estimated using biomass. However, 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 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 cover and likely underestimated due to these differences (Fig. S4).

Data Analysis

After data were prepared and cleaned, species richness and total live biomass was 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; Fig. 1).

Quantifying components of change

We used two approaches to quantify community change under nutrient addition. First, we used an ecological adaptation of the Price equation (Fox & Kerr 2012; Bannar-Martin *et al.* 2017) to partition overall richness and biomass changes into those associated with species losses, species gains, and persistent species between two samples in time in every plot (Fig. 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. Specifically, we use the 'Community Assembly' 3-part partition approach suggested by Bannar-Martin *et al.* 2017 (Fig. 1, Box 1). We used a complementary, but separate approach to quantify absolute species losses and gains (Figure 1). 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 (comparison, year n, tn) using the R package priceTools (Bannar-Martin *et al.* 2017) (Fig. 1). Importantly, there are different options to arrange the pairwise comparisons for the Price equation, which depend on the questions being asked. There has been other work that looks at temporal variance or change through approaches different to that presented here (Winfree *et al.* 2015; Genung *et al.* 2017). The approach we take here is rooted in the original temporal approach taken by Price (Price 1970, 1972) to quantify change by comparing the same unit to itself through multiple temporal samples. In the context of the Nutrient Network, this quantifies the cumulative change in each plot across time, relative to the starting point of the plot before experimental fertilization began. These species and biomass partitions sum up to the exact change quantified between two plots in time (Fig. 1).

We partitioned changes in species composition and biomass in each plot into five continuous components: 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)), and using the Price equation: 3) biomass change associated with species loss (SL, biomass change associated with species loss, year 0), 4) biomass change associated with species gains (SG, biomass associated with species unique in comparison, year tn), and 5) the change in biomass associated with persistent species (PS, species shared between comparisons year t0 and year tn) (Fig. 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 fertilization. These pairwise comparisons resulted in continuous response metrics for every year after year 0 (t0) that we hierarchically modelled as a function of time. This estimates a rate of change over time (i.e., slope) for each metric, allowing us to examine general temporal trends and make direct comparisons of site-level variability within and among treatments and sites. We use this approach to estimate 1) absolute average total change in each component and experimental treatment and, 2) the estimated overall rates of change (slope parameters) for each metric component in our results and discussion.

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 multilevel regression models. We fitted five separate univariate multilevel regression models, one to each metric to quantify the effect of NPK treatments on local communities across time compared to community change across time in control plots. We also examined species richness and plot level biomass across time using this unique dataset containing more sites and time points than in previous analyses (Box 1. Supplementary Fig. S5).

Each univariate model included treatment (NPK or Control) as a categorical fixed effect, time since experimental start as a 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).

To quantify the joint response of these metrics to NPK treatments across time, we also fitted two multivariate multilevel 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; the second examined the joint response of all five components of the partition (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. 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 (Supplementary Information Fig. S6 a-n). Our results did not qualitatively change when only sites with experiments running for varying numbers of years (all years, ≥ 3, ≥ 6, or ≥ 10 years) were included (Fig. 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 4 chains, and varying iterations (Supplementary Information). We report the 95% Credible Intervals (hereafter CI) around the absolute average total change and the 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.

Results

Average total change

On average, in controls, a similar number of total species were lost (-5.74, 95% CI: -7.02 to -4.48) and gained (4.46, 95% CI: 3.40 to 5.54) (Fig.2 a, b). Biomass loss in control plots associated with species loss (-37.9, 95% CI: -48.7 to 27.4) was slightly less than biomass gained associated with species gain (61.8, 95% CI: 41.6 to 84.9) (Fig. 2 c, d). 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) (Fig. 2 e).

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

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 to 0.21, species gained (s.gain)/ year) (Fig. 3 a, 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 slightly 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) (Fig. 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) (Fig. 3e).

Compared to controls, NPK treatments increased the rate of species loss over time (-0.38, 95% CI: -0.51 to -0.26 species/year Fig. 3a), whereas the rate of species gain did not differ from zero (-0.01, 95% CI: -0.08 to 0.06 species/year, Fig. 3b). That is, species were gained in NPK (average total ~3, Fig. 2b), but this gain stayed relatively constant overtime (Fig. 3b). In NPK plots, biomass loss was associated with species loss per year (-7.44, 95% CI: -10.18 to -4.92 g/m^2/year, Fig. 3c). Species that were gained in NPK plots were associated with positive biomass change per year (7.36, 95% CI: 5.27 to 9.77 g/m^2/ year, Fig. 3d), similar to that of biomass lost associated with species loss. Finally, change in biomass over time associated with persistent species exhibited considerable variation in NPK treatments (3.05, 95% CI: -6.14 to 11.88 g/m^2/year, Fig. 3e). Combined, biomass gains associated with species gained, and biomass increases associated with persistent species over time contributed to overall biomass gained in NPK plots.

The components of species and associated biomass change relative to the starting community before experimental treatments began can be considered together as an absolute average total change (Fig 4 a) and as a slope or rate of change through time (Fig 4b). This helps to understand the change in each component relative to the starting community and as a contribution to total community change to better understand different treatment conditions. In control plots, the average total change indicates there is species and biomass turnover that balance each other out (Fig. 4a) and that while this turnover continues over time (Fig b), there is no effect on community change overall. Under fertilization, we learn that average total species loss and associated biomass loss is pronounced compared to controls (Fig. 4a), and that this increasing loss increases over time (Figure 4b). We learn that the average total species gains and associated biomass gain is less than the loss (Fig. 4a), and that these reduced gains stay relatively constant over time, even a slightly negative slope, indicating species gains slightly decline over time relative to species gains between year 0 and year 1 of experimental treatments (Fig 4b). However, the species that are gained contribute to associated increasing biomass gains through time (Fig. 4b). Lastly, the average total biomass change associated with persistent species contributes the biomass gained under nutrient addition in grasslands globally, relative to the starting point before experimental treatments, and relative to control plots Across time, biomass change associated with persistent species shows much variation at the site level (Fig. 3e), and does not indicate large increases through time relative to the starting point, but still an overall positive trend.

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

We used an ecological adaptation of the Price equation to partition components of compositional change across time into species and functional change associated with gains, losses, and persistent species. Using data from 59 global grasslands we show that high compositional turnover under ambient conditions also affects turnover in community aboveground biomass, while aggregate plot-level biomass remains stable over time. In contrast, the addition of multiple limiting nutrients resulted in greater species loss and reduced gains over time compared to controls, which both contribute to a net decline in richness. Under fertilization, species loss was associated with a decline in biomass over time and the species that were gained were associated with overall biomass gains. Species that persisted over time were also associated with biomass gained, jointly leading to overall biomass increases with nutrient addition, on average.

Some of the most important components of biodiversity change are not obvious when considering just changes in species numbers (i.e. species richness) because these aggregate measures often obscure functional contributions resulting from change in species composition (Jones *et al.* 2017; Hillebrand *et al.* 2018). In addition, compositional change (i.e. species turnover) can be uncoupled from changes in species richness (Hillebrand *et al.* 2018; Blowes *et al.* 2019), whether richness is changing or not (Harpole *et al.* 2016; Hautier *et al.* 2018; Seabloom *et al.* 2020) in global grasslands. In this study, we observed substantial turnover of species and biomass over time but no change in overall richness and biomass in ambient conditions (Fig. S5, Fig. 2, Fig. 3). In contrast, in fertilised conditions, there is more average total species loss and biomass loss associated with species loss under NPK (Fig. 2a, c), and importantly, species continue to be lost through time (Fig. 3a) and this loss leads to increasing loss of biomass (Fig. 3c). The consequences of biodiversity loss for aboveground biomass are magnified through time relative to the community before experimental nutrient addition began.

Species gain and species that persist were also found to contribute to compositional and functional change over time. Additionally, we found that species gains were reduced under fertilized conditions relative to the control (Fig. 2b), and that these reduced gains stayed relatively constant through time (Fig. 3b), so these reduced species gains can be interpreted to also contribute to declining richness through time. Despite consistent species, biomass associated with species gained and persistent species outweighed the biomass lost by species losses (Fig. 3, Fig. 4a, b). Species that are gained under nutrient addition grow substantially and contribute to overall, total biomass gain on average (Fig. 2d), as well as increasing biomass gain through time (Fig. 3d). Under fertilized conditions, the average total contribution of persistent species to biomass change relative to control plots was very large, but demonstrated much variation in the trends across time resulting in little change in this biomass component over time overall (Fig. 3). Species gains and persistent species were both found to contribute to biomass gain under nutrient addition, on average, through time, and relative to controls (Fig. 4a, b). Our findings help elucidate how the components of community change contribute to biomass production under fertilization over time, but we cannot explicitly comment on whether species change in their dominance or the mechanisms that cause these changes. We can comment that our findings support the previous findings that 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 changes in ecosystem functioning. Focusing on aggregate measures of biodiversity change alone can lead to underestimation of change and its impacts on the functioning of ecosystems.

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 function (Helsen *et al.* 2014). This indicates that increasing biomass associated with fertilization may contribute to diversity loss, and changes in composition can in turn have varying effects associated with biomass (Harpole *et al.* 2016; Leibold *et al.* 2017). Our results support the idea that diversity and functioning changes need to be considered independently, but concomitantly (Ladouceur *et al.* 2020) to better understand how these relationships shift under global change processes and pressures. We've found that the effect of compositional change on ecosystem functioning is dependent on the magnitude and functional contribution of species entering, persisting, and exiting communities. Which species thrive under nutrient addition and which are excluded from fertilized communities, is in part determined by species identities, their traits, and the matching of traits to the environment (Lind *et al.* 2013; Seabloom *et al.* 2015; Morgan *et al.* 2016). Because species contribute to ecosystem function to different extents (Isbell *et al.* 2013; Hautier *et al.* 2018), considering various compositional changes simultaneously and in relation to their individual contributions to function provides a more comprehensive understanding of the effects of global change pressures on ecological communities and ecosystems.

Grassland productivity is often limited by multiple nutrients (Fay *et al.* 2015; Harpole *et al.* 2016), and species richness and productivity are controlled by a complex network of processes (Grace *et al.* 2016). Changes in components of compositional change contributes to variation in site-level responses to fertilization in terms of both richness and biomass (Fig. S8, S9). This work presented here points to many interesting avenues surrounding species compositional change and ecosystem functioning for further development and investigation. For example, because the plots used in this analyses were unfenced, we expect that herbivory reduced biomass (Borer *et al.* 2014b, 2020; Hodapp *et al.* 2018; Ebeling *et al.* 2021), possibly explaining some variation in the effect of NPK on aboveground biomass in many sites. Further work could investigate composition and biomass relationships under fertilization and with herbivory ex-closures. Additionally, some variation in site-level responses may be due to water limitation, and may account for some cases where nutrient induced species-loss does not affect biomass (Fig. S10). Opportunities also exist for future work to explore additional mechanisms driving patterns within and across sites (Fig. S10) (Avolio *et al.* 2021), spatial scales (Chase *et al.* 2019; Barry *et al.* 2021; Seabloom *et al.* 2021), and according to species' identities and characteristics (Crawford *et al.* 2021). We now know that the risk of a species being lost from a plot decreases with its abundance in both space and time, and varies across lifespans and functional forms (Wilfahrt *et al.* 2021). The degree to which these species' characteristics (e.g., traits, dominance) influence the magnitude of community level species loss and gains and change associated with functioning are beyond the scope of this investigation, but present nice opportunities for adaptations to the approach taken here to ask these questions explicitly. However, because our temporal approach provides estimates of rates of functional change over time, a similar approach could possibly be adapted to functions that are not additive, such as stability (e.g., estimates of temporal variability within an assemblage), with some substantial adaptations.

In sum, we partition measures of species richness and a measure of ecosystem functioning (live 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 ecosystem functioning, particularly in ecological systems that are experiencing ongoing anthropogenic change. By partitioning the roles of individual species, this work provides a more detailed understanding of the relationships between biodiversity change and ecosystem function in natural systems and how global change drivers can affect them.

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Supplementary Information

To explore site-level model estimates see: https://emma-ladouceur.shinyapps.io/nn-cafe-app/ See Supplementary Information document for site information, supplementary Fig. s that provide extra relevant information to complement results and statistical model details.

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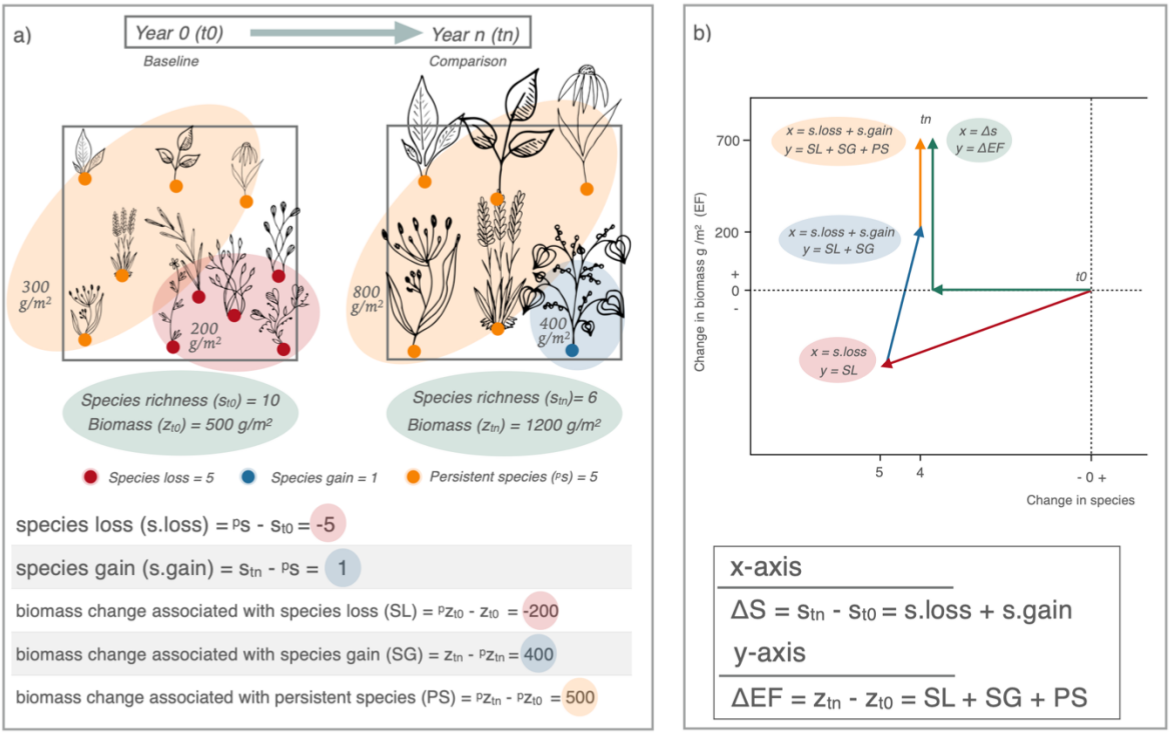

z = ecosystem function

^{p}z = ecosystem function of persistent species

z_{tn} = ecosystem function at time(t) = n

z_{t0} = ecosystem function 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 functioning based on the ecological version of the Price equation as suggested by Fox and Kerr (2012). And Banner-Martin et al. 2018) A) Represents 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 this composition-functioning relationship 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 together to understand the joint response. This represents our expectations for the overall effect of NPK addition on change in species and biomass as a rate over time, and our expectations for partitioning this effect into biomass lost associated with species loss, biomass gained associated with species gain and the biomass change associated with persistent species. Plant images by Alex Muravev, The Noun Project.

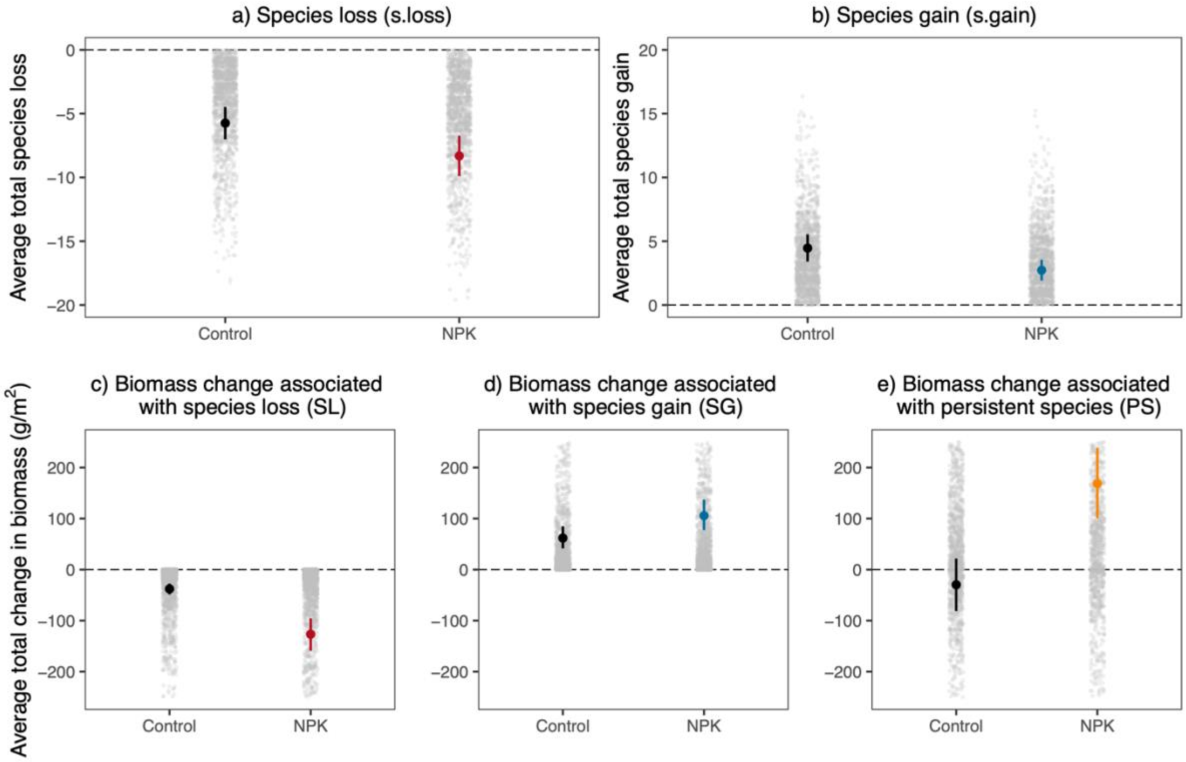

Figure 2. The absolute average total change in species (a, b) and biomass (c, d, e) across time. Small grey jittered points show the data models were fit to at every site's most recently recorded experimental year (maximum); large colored points are the fitted overall effects of treatment at 13 years (maximum year of experimental measurements across all sites) and colored lines show the 95% credible intervals.

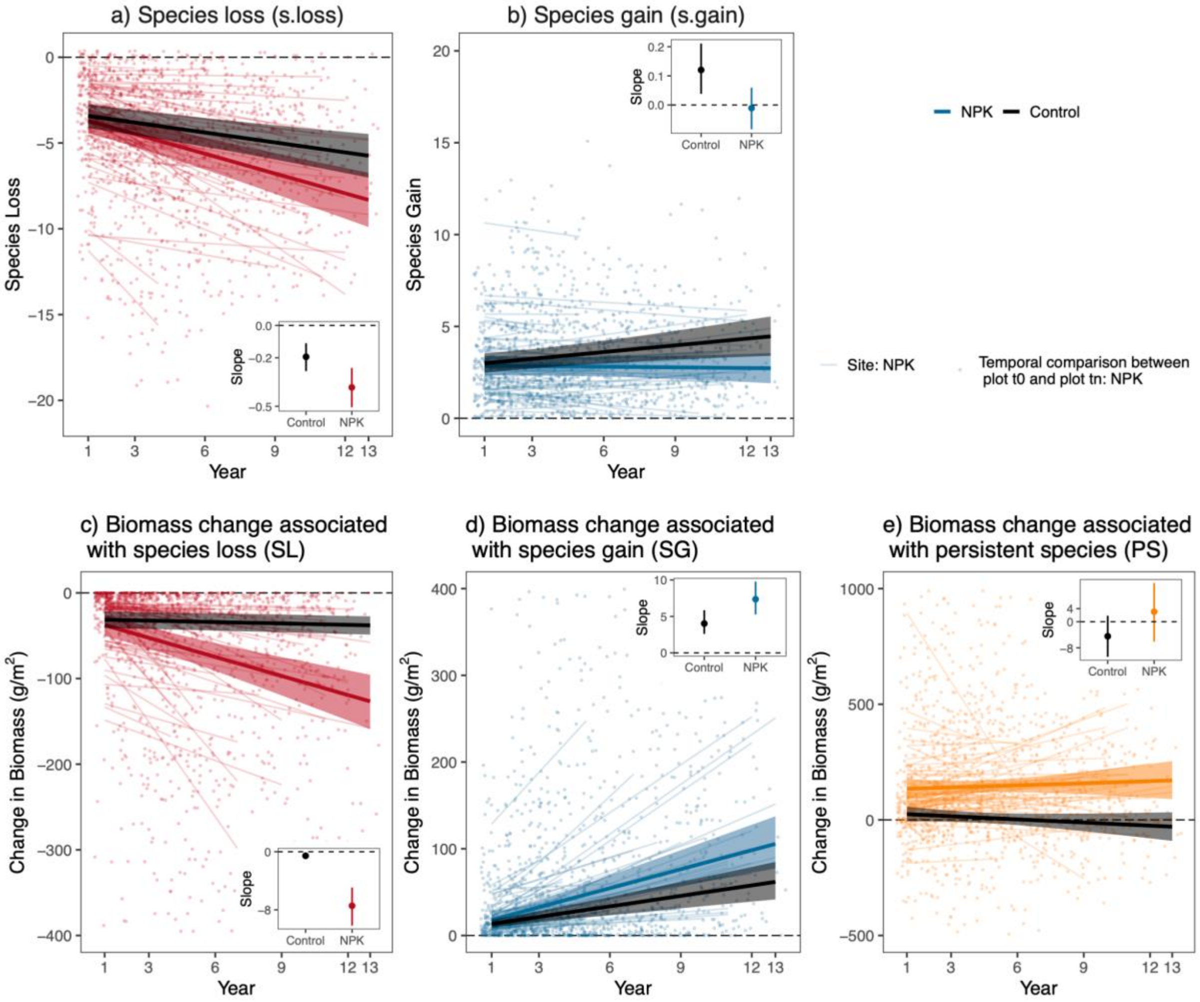

Figure 3: Changes in the components of species richness and aboveground biomass through time for control and NPK treatment. In regressions represented in a)-e), the solid thick lines represent the overall effect estimate for NPK (solid) and Control (dashed) treatments, and the shading around these black lines shows the 95% credible interval. Each jittered grey point represents a pairwise comparison of a single plot before NPK nutrient addition (year 0) and for each year after treatment respectively. 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 (colored) treatments, error bars represent 95% credible intervals, and the dashed reference line at 0 represents a slope of 0 for each metric.

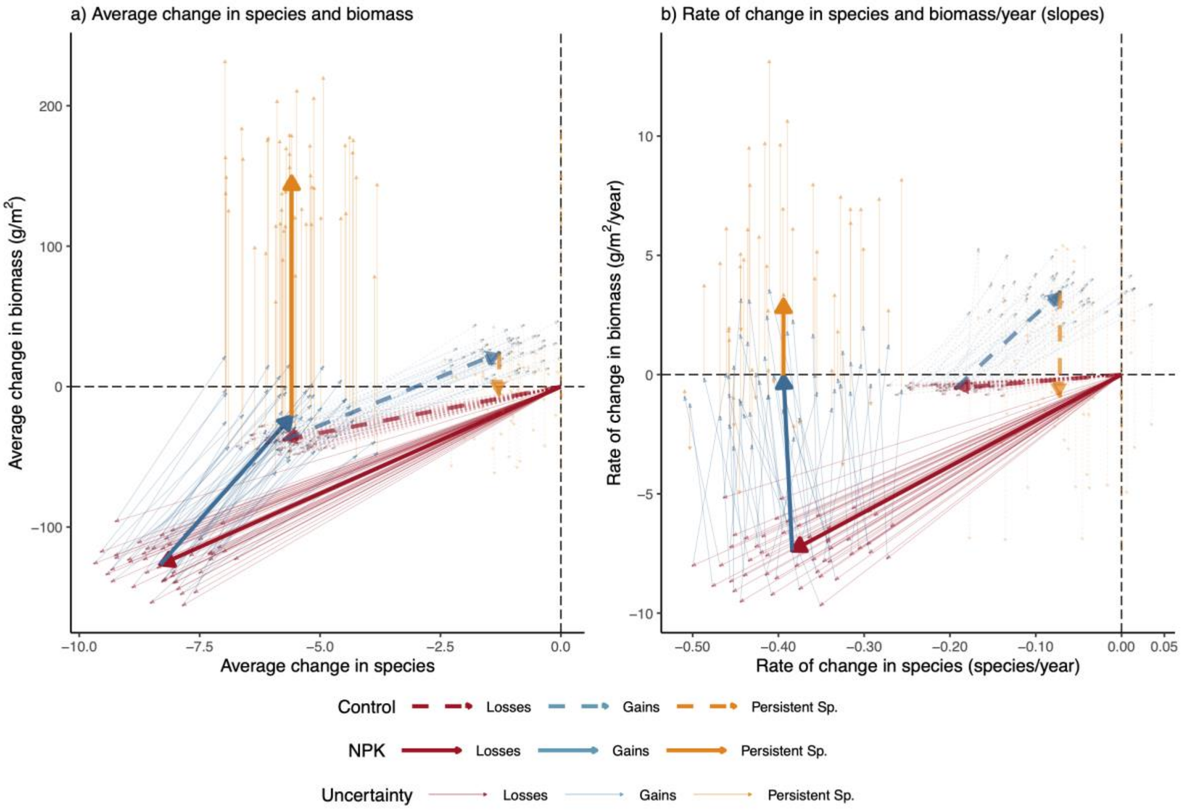

Figure 4: Change in species and biomass. Change in control (dashed lines) and fertilized plots (solid lines) on species (x-axis) and biomass change (y-axis) as a) an Average overall change after 13 years and b) a rate of change across time (slope). Thick lines show the overall effect estimate (mean overall change in Control and NPK plots) of each response (a) effect sizes from Fig. 2 and b) slopes from Fig. 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.

Box 1

After over a decade of the Nutrient Network (Borer *et al.* 2014a) we know that the more resources (Nitrogen, Phosphorus, 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 dataset 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, Potassium - NPK hereafter) on species richness over time and biomass over time simply as a reference point with this updated dataset (Fig S5, Table S2, S3, S4, S5)

The ecological adaptation of the Price equation enables the partitioning of community change into 5 components, named the ‘5-part Price partition’ or alternatively into 3 components (Fox & Kerr 2012; Bannar-Martin *et al.* 2017). Here, we use the 3-part ‘Community assembly’ partition proposed by (Bannar-Martin *et al.* 2017) to understand the effects on biomass change of all lost species unique in the baseline sample (SL), all gained species in the comparison sample (SG), and changes in the function of shared species called the ‘Context Dependent Effect’ or CDE, but here called persistent species (PS) (Figure 1, Table below). This partition requires two comparable units to quantify pairwise differences between the two. Here, we compare every plot at the year before experimental treatments began as a baseline (year 0 = s_{t0}) to itself at every point in time as a comparison (year n = s_{tn}) measured since experimental treatments began to quantify cumulative temporal changes in each and every plot.

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 function in each community (z_{t0}, z_{tn}) and the function of species shared by the baseline ($^{p}z_{t0}$) and comparison communities ($^{p}z_{tn}$) (Bannar-Martin *et al.* 2017). Here, we additionally use the number of species shared between two samples in time (^{p}s), those unique in the baseline community (s_{t0}) to quantify species loss (s.loss), and those unique in the comparison community (s_{tn}) to quantify species gains (s.gain) (Figure 1). These are the same number of species used to calculate the impacts of these gains and losses on ecosystem function the Price equation. Next, we use an ecological version of the Price partition to quantify total ecosystem function change associated with species loss (SL), gains (SG) and persistent species (PS). Slightly different language has been used to describe the components of this 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 each component has been given in previous literature to address various contexts, and their acronyms compared against the components used in this work. Acronyms for each component are in bold italic. Initials 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.

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

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)	species loss associated with ecosystem function loss Equal to the sum of a) and b) in 5-part partition. ***SL*** (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 ecosystem function. Equal to the sum of c) and d) in 5-part partition. ***SG*** (BM)
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 ***CDE*** (FK, BM) ***ABUN*** (W)	c) Biomass change associated with persistent species. Equal to e) in the 5-part partition. **PS** (this work)