1 **Species losses, gains, and changes in persistent species are associated with distinct**
2 **effects on ecosystem functioning in global grasslands**
3

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99 **Author Contributions**
100 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.,
101 conceptually framed the paper and discussed and shaped approaches to analyses. E.L. &

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102   S.A.B. led and conducted analysis. Authors listed as site coordinators listed in Table S1 set
103   up experiments, collected data annually and contributed data. E.L. led writing the paper. All
104   authors contributed to at least two items listed in the co-authorship details in the co-
105   authorship table attached. All authors contributed to paper writing.
106
107   **Data Accessibility Statement:** Plot level data (species richness, aboveground biomass,
108   and pairwise price equation partition responses, absolute species gains and losses) used to
109   produce results will be made open access on the Environmental Data Initiative (EDI). Model
110   objects, and data extracted from models to reproduce results will also be made open access.
111   Code to produce results will be made freely available on Github and archived through
112   Zenodo. Some data associated with the Nutrient Network are already open access
113   (https://nutnet.org/index.php/datadois), but this dataset used here is unique in the number of
114   sites, the temporal grain, and the metrics used.
115
116   **Novelty Statement:** We develop a synthesis approach to partition temporal changes in
117   species richness and aboveground biomass under ambient conditions (control) and
118   fertilization (NPK) into that associated with species losses, species gains, and persistent
119   species in 59 grasslands on six continents. This approach elucidates the absolute average
120   change over time and the rates of change in these components of community composition
121   and the change in ecosystem functioning associated with each.
122
123
124   **Abstract**

125   Global change drivers such as anthropogenic nutrient inputs simultaneously alter
126   biodiversity, species composition, and ecosystem functions such as aboveground biomass.
127   These changes are interconnected by complex feedbacks among extinction, colonization,
128   and shifting relative abundance. Here, we use a novel temporal application of the Price
129   equation to quantify the functional contributions of species that are lost, gained, and persist
130   under ambient and experimental nutrient addition in 59 global grasslands. Under ambient
131   conditions, compositional and biomass turnover was high, but species losses (i.e., local
132   extinctions) were balanced by gains (i.e. colonization). There was biomass loss associated
133   with species loss under fertilization. Few species were gained in fertilized conditions over
134   time but those that were, and species that persisted, contributed to net biomass gains,
135   outweighing biomass loss. These components of community change are key to
136   understanding the relationship between change in composition, diversity and functioning.
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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 (Hooper *et al.* 2005; Cardinale *et al.* 2013), 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 trade-offs 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 interact with changes in 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.* 2021) and is well-known to increase under nutrient

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167   deposition. However, the relationship between biodiversity and aboveground biomass under

168   global change pressures such as nutrient enrichment varies in direction and strength across

169   contexts, systems, and sites (Harpole *et al.* 2016). Understanding how biodiversity,

170   composition, and aboveground biomass change are interrelated is essential for anticipating

171   the impacts of global change pressures such as nutrient deposition on ecosystems and their

172   functions.

173   Global change drivers such as nutrient addition can alter community assembly

174   processes, community composition, and ecosystem functioning concurrently (Bannar-Martin

175   *et al.* 2017; Leibold & Chase 2017; Leibold *et al.* 2017). In some cases, small changes in

176   species richness can be associated with large compositional changes, or not (Spaak *et al.*

177   2017; Hillebrand *et al.* 2018). Changes in competition and coexistence resulting from

178   changes such as nutrient inputs can affect losses of existing species, gains of novel species,

179   and changes in abundance of species that persist. Because the functional contributions of

180   colonizing species may or may not offset the functional contributions of species that go

181   locally extinct, the processes controlling species diversity and those controlling ecosystem

182   functions may be decoupled. Differences in compositional change following fertilization could

183   also help explain variability in community responses to nutrient addition (Fay *et al.* 2015;

184   Harpole *et al.* 2016).

185   Here, we apply an adaptation of the Price equation (Price 1970, 1972; Fox & Kerr

186   2012) to quantify the functional contributions of individual species that are lost, gained, or

187   persist through time. We examine these dynamics under ambient and fertilized conditions to

188   better understand the role of these community assembly processes on the functioning of

189   ecosystems (Bannar-Martin *et al.* 2017). The Price equation was originally developed for use

190   in evolutionary biology (Price 1970, 1972), but has potential to be widely adapted and

191   applied in many contexts to compare two samples and quantify what is unique in each,

192   versus shared between the two (Lehtonen *et al.* 2020). In ecology, this approach can help

193   elucidate the biological relationships that underpin the variation between aggregate changes

194   in species richness, composition, and additive measures of ecosystem functioning, and has

195   been adapted for this use in many ways (Winfree *et al.* 2015; Genung *et al.* 2020; Lefcheck

196   *et al.* 2021; Ulrich *et al.* 2021). We use the 3- part 'Community Assembly' Price partition

197   proposed by (Bannar-Martin *et al.* 2017), to link temporal changes in biodiversity to an

198   additive measure of ecosystem functioning (i.e., aboveground biomass). Additionally, we

199   quantify absolute species losses and gains to better understand how species changes and

200   changes in biomass associated with species changes are related. By following compositional

201   changes in experimental plots through time, we separate cumulative species change, as well

202   as the associated change in aboveground biomass into that of species losses, gains and

203   that which persist through time (Fig. 1).

204   We quantify how community compositional change induced by nutrient addition

205   contributes to altered ecosystem functioning (aboveground biomass) using data from sites

206   within the Nutrient Network, a globally distributed nutrient addition experiment, replicated

207   across grassland sites (NutNet; http://www.nutnet.org) (Borer *et al.* 2014a). Specifically, we

208   synthesize results from 59 experimental sites across six continents comparing control plots

209   and plots that were fertilized with a combination of nitrogen (N), phosphorus (P), potassium

210   (K) and micronutrients (hereafter the NPK treatment). We leverage time series data to

211   determine rates of change over time for each component.

212   Previous work has documented that grassland communities experience reduced

213   richness and increased aboveground biomass with fertilization generally, but that there is

214   much site-level variation in this response (Borer *et al.* 2014b; Harpole *et al.* 2016) (Box 1).

215   We expect that how a loss in richness will be associated with change in function likely

216   depends on the functional contributions of species lost, gained, or persisting in the

217   community. On one hand, a weak response of persistent species or the loss of relatively

218   abundant species could be associated with minimal changes or even reductions in biomass

219   (Fay *et al.* 2015; Harpole *et al.* 2016). On the other hand, if functional change associated

220   with persisting and gained species exceeds that of lost species in response to nutrient

221   addition, biomass may increase even if more species are lost than gained. Determining how

222 components of community change are associated with changes in function would advance

223 understanding of how global change affects interdependent dimensions of natural systems.

224

225

226 **Methods**

227 **Experimental Design**

228 The Nutrient Network (NutNet) is a distributed experiment replicated in herbaceous

229 terrestrial systems across six continents, representing a range of grassland habitats (Borer

230 *et al.* 2014a) (Table S1, Fig. S1). At each site, a factorial combination of nitrogen (N),

231 phosphorus (P), and potassium (K with a one-time addition of micronutrients) are applied

232 annually, alongside an unmanipulated control treatment with no added nutrients. Plots are 5

233 x 5 m and treatments are applied in a randomized block design, usually with three blocks

234 (range 3 - 6 among sites). All sites have the same experimental design and sampling

235 protocols.

236 For this study, we used data from two treatments: unmanipulated control (ambient

237 conditions) and full fertilization (NPK) treatments. Sites with measurements the year prior to

238 fertilization (year 0) and for at least three years with fertilization were included in this

239 analysis. The mean length of experiments across all sites included in this analysis is eight

240 years. This resulted in 59 sites meeting all criteria, situated on every continent except

241 Antarctica (Supplementary Table S1, Fig. S1, Fig. S2).

242

243 **Sampling**

244 Aboveground plant biomass and plant community composition were sampled

245 annually during the peak of the local growing season. All aboveground biomass was clipped

246 in two 0.1 m x 1 m strips. Live (current year's growth) and dead (previous year's growth)

247 biomass were separated, and live biomass was typically sorted into functional group

248 categories (e.g., graminoid, forb, legume, fern). All sites recorded total live biomass.

249 Biomass was dried at 60°C and weighed to the nearest 0.01 g. The location of the biomass

250   clip plot was moved every year within a subplot designated for biomass sampling.

251   Community composition was sampled as percentage cover in a permanent 1 m x 1 m

252   subplot close to biomass strips. Absolute cover was estimated visually for each species, so

253   that the summed cover of all species could exceed 100% to most accurately represent multi-

254   layered grasslands. We excluded non-living litter and debris, woody species, and non-

255   vascular species such as bryophytes from the data for this analysis, as these categories

256   were not consistently accounted for in living herbaceous biomass samples across sites.

257

258   **Data Preparation**

259   We used species relative cover and aboveground biomass to estimate per species

260   biomass in two ways. In sites and years when biomass was sorted into functional groups,

261   the species percentage cover was summed within those same functional groups and the

262   relative cover of each species within a functional group was multiplied by the sorted biomass

263   of that functional group to estimate per-species biomass (Axmanová *et al.* 2012). This

264   relates the species cover to biomass for different functional groups (Fig. S3a), and accounts

265   for differences in the mass to cover relationships among different life forms. For example,

266   broadleaf forbs will likely have a higher cover to mass relationship as their leaves are more

267   horizontal.

268   In sites and years where biomass was not sorted to functional groups, or in plots

269   where samples of functional groups were not matched between cover and biomass data

270   (e.g., a legume recorded in cover measurements but not in biomass samples), total live

271   biomass values were used to estimate per species biomass. In these cases, cover of each

272   species relative to the whole plot was multiplied by the total live biomass for the plot

273   (Axmanová *et al.* 2012; Hautier *et al.* 2014; Isbell *et al.* 2015) (Fig. S3b). We expect that the

274   first method provides more accurate species-level estimates, so this method was used

275   wherever possible. These approaches use the best available data from destructively

276   sampled biomass strips to estimate species-level biomass from percent cover data. We

277   acknowledge that this is not an exact measure of per species biomass, and introduces some

278 uncertainty in our analyses. However, we compared both methods and found no major

279 differences in estimates of overall biomass change associated with components of diversity

280 change between major functional groups (Fig. S3c). In addition, we examined whether using

281 species' percent cover instead of biomass as a response altered our inferences (Fig. S4).

282 Changes in species' percent cover through time were broadly qualitatively consistent with

283 those estimated using biomass. However, cover is a constrained and two-dimensional

284 measure that does not fully describe growth in a plant community. We find that the rate of

285 change in cover does not change as much as biomass in response to NPK, but still

286 demonstrates turnover within communities, so when we relate biomass measures to cover to

287 estimate per species biomass, biomass estimates are moderated by cover and likely

288 underestimated due to these differences (Fig. S4).

289

290 **Data Analysis**

291 After data were prepared and cleaned, species richness and total live biomass was

292 quantified for every 1 m^2 subplot each year. To partition plot level measures into changes

293 associated with species losses, gains, and species persistence, we made pairwise

294 comparisons between each plot pre-treatment (t0) to itself at every subsequent time point

295 after nutrient addition treatments were applied (tn; Fig. 1).

296

297 **Quantifying components of change**

298 To quantify changes in species and biomass through time, we compared the

299 composition of each plot in the year before fertilization (year 0, t0) to itself at every

300 subsequent time-step measured annully (comparison, year n, tn) using the R package

301 priceTools (Bannar-Martin *et al.* 2017) (Fig. 1). We used two approaches to quantify

302 community change under nutrient addition. First, we used an ecological adaptation of the

303 Price equation (Fox & Kerr 2012; Bannar-Martin *et al.* 2017) to partition overall biomass

304 changes into those associated with species losses, species gains, and persistent species

305 between two samples in time in every plot (Fig. 1). Specifically, we use the 'Community

306   Assembly' 3-part partition approach suggested by Bannar-Martin *et al.* 2017 (Fig. 1, Box 1).

307   This equation quantifies additive differences between comparable units (e.g., plots). Here,

308   this equates to additive species-level changes in aboveground biomass through time

309   associated with specific changes in species composition, relative to the plot before

310   experimental treatments began. Second, we used a complementary, but separate approach

311   to quantify absolute species losses and gains (Fig. 1).

312   To quantify the absolute number of species lost (s.loss), the species richness of the

313   plot at year 0 (s_{t0}) is subtracted from the shared species (^ps) between two samples. That is,

314   species lost are the species that are unique in the first sample at year 0, but are not present

315   in the sample at year n. For species gains (s.gain), the shared species (^ps) between two

316   samples is subtracted from the species richness of the plot at year n (s_{tn}). Simply put,

317   species gained are the species that are unique in the sample at year n but are not present at

318   year 0.

319   For the 3-part Price equation partition, components associated with biomass change

320   can be simplified to a similar explanation, as the same species terms are used to quantify

321   components of biomass change (Bannar-Martin *et al.* 2017). Biomass change associated

322   with species loss (SL), equates to the sum of the biomass of shared species ($^pz_{t0}$) between

323   two samples at year 0 is subtracted from the total biomass of the plot at year 0 (z_{t0}). Biomass

324   change associated with species gains (SG) is equal to the sum of the biomass of shared

325   species ($^pz_{tn}$) between two samples at year n, is subtracted from the total biomass of the plot

326   year n (z_{tn}). Biomass change in persistent species (PS), is the sum of the biomass of shared

327   species at year 0 ($^pz_{tn}$) is subtracted from the sum of the biomass of shared species at year

328   tn ($^pz_{t0}$). The full details of the 5-part and 3-part Price equation partition can be found in

329   (Bannar-Martin *et al.* 2017) and are summarised as relevant for this study in Fig.1.

330   Importantly, there are different options to arrange the pairwise comparisons for the

331   Price equation, which depend on the questions being asked. There has been other work that

332   looks at temporal changes including temporal variance as a metric of change between two

333   samples or temporal change in space-for-time contexts different to that presented here

334 (Winfree *et al.* 2015; Genung *et al.* 2017). The approach we take here is rooted in the

335 original temporal approach taken by Price (Price 1970, 1972) to quantify change by

336 comparing the same unit to itself through multiple temporal samples. In the context of the

337 Nutrient Network, this quantifies the cumulative change in each plot across time, relative to

338 the starting point of the plot before experimental fertilization began. These species and

339 biomass partitions sum up to the exact change quantified between two plots in time (Fig. 1).

340   We partitioned changes in species composition and biomass in each plot into five

341 continuous components: 1) number of species lost (s.loss, species unique in baseline (t0)

342 compared to same plot at another point in time (tn)), 2) number of species gained (s.gain,

343 species unique in comparison plot (tn) compared to species in baseline (t0)), and using the

344 3-part Price equation: 3) biomass change associated with species loss (SL, biomass change

345 associated with species loss, year 0), 4) biomass change associated with species gains (SG,

346 biomass associated with species unique in comparison, year tn), and 5) the change in

347 biomass associated with persistent species (PS, species shared between comparisons year

348 t0 and year tn) (Fig. 1, Box 1). We compare control plots to themselves through time, and

349 NPK plots to themselves through time to examine component changes under ambient

350 conditions and under fertilization. These pairwise comparisons resulted in continuous

351 response metrics for every year after year 0 (t0) that we modelled as a function of time. This

352 approach estimates change over time (i.e., slope) for each metric, allowing us to examine

353 general temporal trends and make direct comparisons of site-level variability within and

354 among treatments and sites. We use this approach to estimate 1) absolute average total

355 change in each component and experimental treatment (Intercept of the slope at year 13)

356 and, 2) the estimated overall rates of change (slope parameters) for each metric component

357 in our results and discussion.

358

359 **Statistical Models**

360   We examined how nutrient addition (NPK treatment) influenced species losses and

361 gains, and the three components associated with the Price equation partition, using

362 multilevel regression models. We fitted five separate univariate multilevel regression models,

363 one to each metric to quantify the effect of NPK treatments on local communities across time

364 compared to community change across time in control plots. We also examined species

365 richness and plot level biomass across time using the largest dataset coming from the

366 Nutrient Network to date (Box 1. Supplementary Fig. S5).

367 Each univariate model included treatment (NPK or Control) as a categorical fixed

368 effect, time since experimental start as a centred continuous fixed effect (in years), and their

369 interaction. These same covariates were also allowed to vary as random intercepts and

370 slopes among sites, blocks (nested within sites), and plots (nested within blocks).

371 To quantify the joint response of these metrics to NPK treatments across time, we

372 also fitted two multivariate multilevel regression models that included multiple response

373 variables in the same model. The first multivariate model was fitted to examine the joint

374 response of species richness and biomass to NPK treatments; the second examined the

375 joint response of all five components of species and biomass change (species loss, species

376 gain, and biomass change associated with species loss, gain and persistent species) in

377 control and NPK plots. This multivariate approach allows for correlations between responses

378 to be quantified. For the multivariate models assessing the joint responses between

379 variables, we could only allow treatment, year, and their interaction to vary among sites, as

380 models did not converge when finer grouping variables were included. The parameter

381 estimates between univariate and multivariate models did not qualitatively differ. We report

382 results from the univariate models for our main results, and report the strength of the

383 correlation between different responses estimated with the multivariate models. We visually

384 examined plots of residuals for all models to assess whether model assumptions (e.g.,

385 homogeneity of variance) were met. Posterior predictive plots were used to visually

386 determine how well models reproduced the data (Supplementary Information Fig. S6 a-n).

387 Our results did not qualitatively change when only sites with experiments running for varying

388 numbers of years (all years, ≥ 3, ≥ 6, or ≥ 10 years) were included (Fig. S7), and we present

389 results using a minimum of 3 years in the main text.

390   For Bayesian inferences and estimates of uncertainty, all models described above

391   were fitted using the Hamiltonian Monte Carlo (HMC) sampler Stan (Carpenter *et al.* 2017),

392   and coded using the 'brms' package (Bürkner 2018) in the R for Statistical Computing and

393   Graphics environment (v.4.0.2; (R Core Development Team 2019). All models were fitted

394   with 4 chains, and varying iterations (Supplementary Information). We report the 95%

395   Credible Intervals (hereafter CI) around the absolute average total change after 13 years

396   and the mean overall slope for each metric in the main results (Table S2). We used weakly

397   regularizing priors and visual inspection of HMC chains showed excellent convergence.

398

399   **Results**

400   **Average total change**

401   On average, in controls, a similar total number of species were lost (-5.74, 95% CI: -

402   7.02 to -4.48, number of species) and gained (4.46, 95% CI: 3.40 to 5.54, number of

403   species) (Fig.2 a, b). Total biomass loss in control plots associated with species loss (-37.9,

404   95% CI: -48.7 to 27.4, g/m^2) was slightly less than biomass gained associated with species

405   gain (61.8, 95% CI: 41.6 to 84.9, g/m^2) (Fig. 2 c, d). Total biomass change associated with

406   persistent species was negative, but was not found to differ from zero (-30.9 95% CI: -81.2

407   to 19.8, g/m^2) (Fig. 2 e).

408   On average, in NPK plots, a much greater number of total species were lost (-8.32,

409   95% CI: -9.90 to -6.73, number of species) than gained (2.73, 95% CI: 1.91 to 3.55, number

410   of species) (Fig. 2 a b). NPK treatments resulted in greater total biomass loss associated

411   with species loss (-127, 95% CI: -159 to -95.6, g/m^2) than total biomass gain associated with

412   species gain (106, 95% CI: 77.3 to 137, g/m^2) (Fig. 2 c, d). Total biomass change associated

413   with persistent species greatly increased on average (171, 95% CI: 104 to 241, g/m^2) (Fig. 2

414   e).

415   **Rates of change**

416   In controls, similar numbers of species were lost per year (-0.19, 95% CI: -0.28 to -

417   0.11, species loss (s.loss)/year) and gained per year (0.12, 95% CI: 0.04 to 0.21, species

418 gained (s.gain)/ year) (Fig. 3 a, b). Biomass loss in controls associated with species losses

419 each year (-0.56, 95% CI: -0.97 to -0.26, SL g/m^2 associated with species loss/year) was

420 slightly less than the biomass gain associated with species gains each year (4.02, 95% CI:

421 2.6 to 5.86, SG g/m^2 associated with species gain/year) (Fig. 3c, d). Biomass change

422 associated with persistent species showed considerable variation, but no directional change

423 (-4.47, 95% CI: -10.76 to 1.84, PS g/m^2 associated with persistent species/year) (Fig. 3e).

424   Compared to controls, NPK treatments increased the rate of species loss over time (-

425 0.38, 95% CI: -0.51 to -0.26 species/year Fig. 3a), whereas the rate of species gain did not

426 differ from zero (-0.01, 95% CI: -0.08 to 0.06 species/year, Fig. 3b). That is, species were

427 gained in NPK (average total ~3, Fig. 2b), but this gain stayed relatively constant overtime

428 (Fig. 3b). In NPK plots, biomass loss was associated with species loss per year (-7.44, 95%

429 CI: -10.18 to -4.92 g/m^2/year, Fig. 3c). Species that were gained in NPK plots were

430 associated with positive biomass change per year (7.36, 95% CI: 5.27 to 9.77 g/m^2/ year,

431 Fig. 3d), similar to that of biomass lost associated with species loss. Finally, change in

432 biomass over time associated with persistent species exhibited considerable variation in

433 NPK treatments (3.05, 95% CI: -6.14 to 11.88 g/m^2/year, Fig. 3e). Combined, biomass gains

434 associated with species gained, and biomass increases associated with persistent species

435 over time contributed to overall biomass gained in NPK plots.

436   In control plots, the average total change indicates there is species and biomass

437 turnover that balance each other out (Fig. 4a) and that while this turnover continues over

438 time (Fig. 4b), there is no effect on community change overall. Under fertilization, we learn

439 that average total species loss and associated biomass loss is pronounced compared to

440 controls (Fig. 4a), and that this increasing loss increases over time (Figure 4b). We learn that

441 the average total species gains and associated biomass gain is less than the loss (Fig. 4a),

442 and that these reduced gains stay relatively constant over time, even a slightly negative

443 slope, indicating species gains slightly decline over time relative to species gains between

444 year 0 and year 1 of experimental treatments (Fig 4b). However, the species that are gained

445 contribute to associated increasing biomass gains through time (Fig. 4b). Lastly, the average

446   total biomass change associated with persistent species contributes the biomass gained

447   under nutrient addition in grasslands globally, relative to the starting point before

448   experimental treatments, and relative to control plots. Across time, biomass change

449   associated with persistent species shows much variation at the site level (Fig. 3e), and does

450   not indicate large increases through time relative to the starting point (Fig. 3e). However,

451   persistent species increase in biomass notably between the year before experimental

452   treatments began and the first year of experimental treatments (Fig. 3e), and this initial

453   biomass increase maintains itself through time (Fig. 4a, b) contributing to the majority of

454   biomass gained in the Nutrient Network overall (Fig S8).

455   Species losses and gains due to nutrient addition were largely uncorrelated (0.29,

456   95% CI: -0.03 to 0.58, Table S5), as was the net change in biomass from losses and gains (-

457   0.07, 95% CI: -0.38 to 0.23). Biomass change associated with species losses and biomass

458   change in persistent species responses to NPK were also uncorrelated (-0.24, 95% CI: -0.55

459   to 0.09), as was the relationship between biomass changes from species gains and

460   persistent species (-0.06, 95% CI: -0.39 to 0.29).

461

462   **Discussion**

463   We quantify components of compositional change across time into species and

464   functional change associated with gains, losses, and persistent species. Using data from 59

465   global grasslands we show that high compositional turnover under ambient conditions also

466   affects turnover in community aboveground biomass, while aggregate plot-level biomass

467   remains stable over time. In contrast, the addition of multiple limiting nutrients resulted in

468   greater species loss and reduced gains over time compared to controls, which both

469   contribute to a net decline in richness. Under fertilization, species loss was associated with a

470   decline in biomass over time and the species that were gained were associated with overall

471   biomass gains, compensating for much of the biomass lost. Species that persisted over time

472   were also associated with biomass gained, jointly leading to overall biomass increases with

473   nutrient addition, on average.

474   Quantifying aggregate change in species numbers (i.e. species richness) is not

475   enough to understand the relationship between biodiversity change and functional change

476   (Jones *et al.* 2017; Hillebrand *et al.* 2018). In addition, compositional change (i.e. species

477   turnover) can be uncoupled from changes in species richness (Hillebrand *et al.* 2018;

478   Blowes *et al.* 2019), whether richness is changing or not (Harpole *et al.* 2016; Hautier *et al.*

479   2018; Seabloom *et al.* 2020). In this study, we observed substantial turnover of species and

480   biomass over time but no change in overall richness and biomass in ambient conditions (Fig.

481   S5, Fig. 2, Fig. 3). In contrast, in fertilised conditions, there were more average total species

482   loss and biomass loss associated with species loss under NPK (Fig. 2a, c). Importantly,

483   species continued to be lost through time (Fig. 3a) and this loss leads to increasing loss of

484   biomass (Fig. 3c). The consequences of biodiversity loss for aboveground biomass are

485   magnified through time relative to the community before experimental nutrient addition

486   began.

487   Species gain and species that persist were also found to contribute to compositional

488   and functional change over time. Additionally, we found that species gains were reduced

489   under fertilized conditions relative to the control (Fig. 2b), and that these reduced gains

490   stayed relatively constant through time (Fig. 3b), so these reduced species gains can be

491   interpreted to also contribute to declining richness through time. Despite consistent species

492   gains through time, biomass associated with species gained and persistent species

493   outweighed the biomass lost by species losses (Fig. 3, Fig. 4a, b). Species that are gained

494   under nutrient addition grow substantially and contribute to overall, total biomass gain on

495   average (Fig. 2d), as well as increasing biomass gain through time (Fig. 3d). Under fertilized

496   conditions, the average total contribution of persistent species to biomass change relative to

497   control plots was very large, but demonstrated much variation in the trends across time

498   resulting in little change in this biomass component over time overall (Fig. 3). Species gains

499   and persistent species were both found to contribute to biomass gain under nutrient addition,

500   on average, through time, and relative to controls (Fig. 4a, b). Our findings help elucidate

501   how the components of community change contribute to biomass production under

502 fertilization over time, but we cannot explicitly comment on whether species change in their

503 dominance or the mechanisms that cause these changes. Our findings support the previous

504 findings that strength and direction of biodiversity change depends on the balance of species

505 losses, species gains, and species that persist over time (Dornelas *et al.* 2019), and as we

506 show here, so do changes in ecosystem functioning. Focusing on aggregate measures of

507 biodiversity change alone can lead to underestimation of change and its impacts on the

508 functioning of ecosystems.

509   Rates of change in the metrics investigated here were uncorrelated, supporting the

510 idea that drivers of change can act relatively independently on diversity, composition, and

511 function (Helsen *et al.* 2014). This indicates that increasing biomass associated with

512 fertilization may contribute to diversity loss, and changes in composition can in turn have

513 varying effects associated with biomass (Harpole *et al.* 2016; Leibold *et al.* 2017). Our

514 results support the idea that diversity and functioning changes need to be considered

515 independently, but concomitantly (Ladouceur *et al.* 2020) to better understand how these

516 relationships shift under global change processes and pressures. We've found that the effect

517 of compositional change on ecosystem functioning is dependent on the magnitude and

518 functional contribution of species entering, persisting, and exiting communities. Which

519 species thrive under nutrient addition and which are excluded from fertilized communities, is

520 in part determined by species identities, their traits, and the matching of traits to the

521 environment (Lind *et al.* 2013; Seabloom *et al.* 2015; Morgan *et al.* 2016). Because species

522 contribute to ecosystem function to different extents (Isbell *et al.* 2013; Hautier *et al.* 2018),

523 considering various compositional changes simultaneously and in relation to their individual

524 contributions to function provides a more comprehensive understanding of the effects of

525 global change pressures on ecological communities and ecosystems.

526   Grassland productivity is often limited by multiple nutrients (Fay *et al.* 2015; Harpole *et

527 al.* 2016), and species richness and productivity are controlled by a complex network of

528 processes (Grace *et al.* 2016). Changes in components of compositional change contributes

529 to variation in site-level responses to fertilization in terms of both richness and biomass (Fig.

530 S9, S10). This work presented here points to many interesting avenues surrounding species

531 compositional change and ecosystem functioning for further development and investigation.

532 For example, because the plots used in this analyses were unfenced, we expect that

533 herbivory reduced biomass (Borer *et al.* 2014b, 2020; Hodapp *et al.* 2018; Ebeling *et al.*

534 2021), possibly explaining some variation in the effect of NPK on aboveground biomass in

535 many sites. Further work could investigate composition and biomass relationships under

536 fertilization and with herbivory exclosures. Additionally, some variation in site-level

537 responses of biomass to NPK may be due to water limitation, and may account for some

538 cases where nutrient induced species-loss does not affect biomass (Fig. S11). Opportunities

539 also exist for future work to explore additional mechanisms driving patterns within and

540 across sites (Fig. S11) (Avolio *et al.* 2021), spatial scales (Chase *et al.* 2019; Barry *et al.*

541 2021; Seabloom *et al.* 2021), and according to species' identities and characteristics

542 (Crawford *et al.* 2021). We now know that the risk of a species being lost from a plot

543 decreases with its abundance in both space and time, and varies across lifespans and

544 functional forms (Wilfahrt *et al.* 2021). The degree to which these species' characteristics

545 (e.g., traits, dominance) influence the magnitude of community level species loss and gains

546 and change associated with functioning are beyond the scope of this investigation, but

547 present opportunities for adaptations to the approach taken here to ask these questions

548 explicitly. However, because our temporal approach provides estimates of rates of functional

549 change over time, a similar approach could possibly be adapted to functions that are not

550 additive, such as stability (e.g., estimates of temporal variability within an assemblage), with

551 some substantial adaptations.

552   In sum, we partition measures of species richness and a measure of ecosystem

553 functioning (aboveground live plant biomass) to better understand the underlying

554 mechanisms of community change under pressure from a key driver of global environmental

555 change, nutrient enrichment. Our results demonstrate that the components of compositional

556 change are key to understanding the relationship between diversity and ecosystem

557 functioning, particularly in ecological systems that are experiencing ongoing anthropogenic

558   change. By partitioning the roles of individual species, this work provides a more detailed

559   understanding of the relationships between biodiversity change and ecosystem function in

560   natural systems and how global change drivers can affect them.

561

578

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

583

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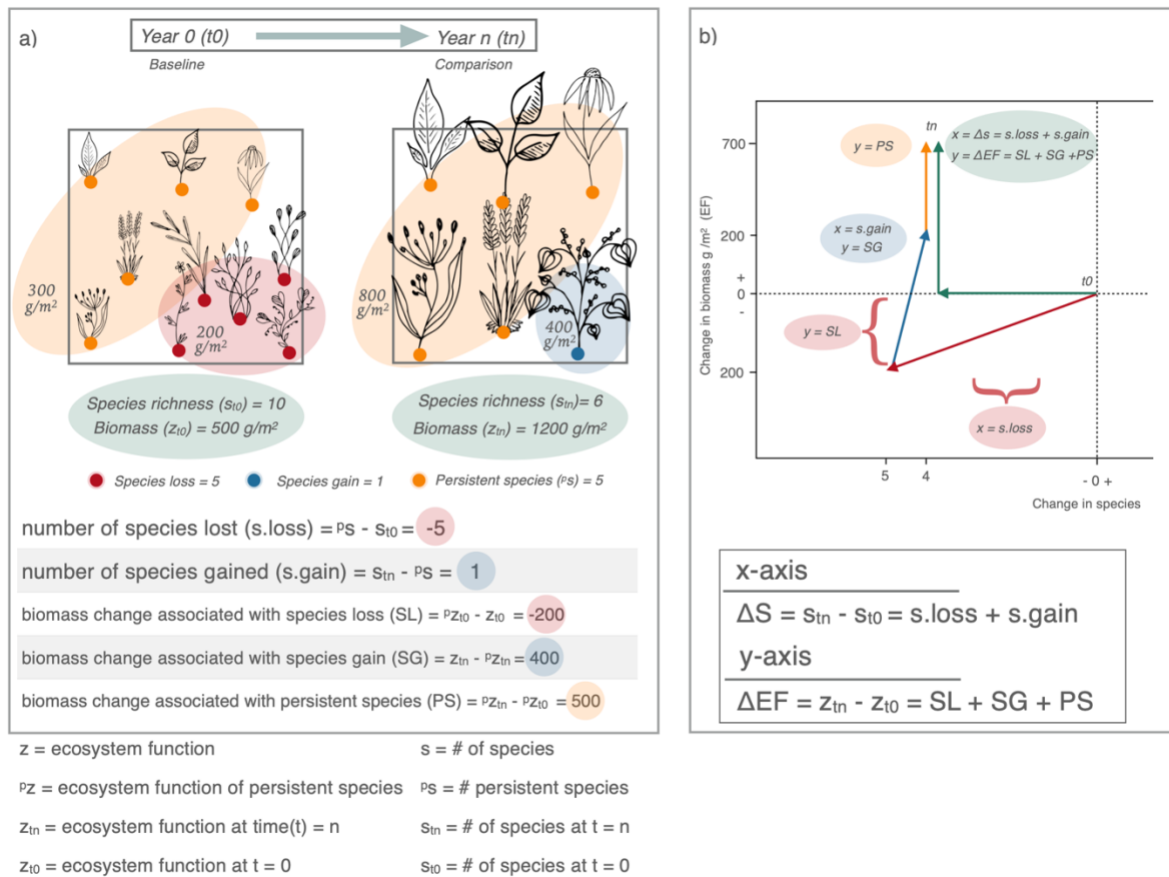735   non-substitutable stabilising effects on biomass production. *Ecology Letters*, 24,
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741 **Figure 1: Schematic illustration of compositional change and the contribution to altered**

742 **functioning based on the 'Community Assembly' 3-part Price equation partition suggested by**

743 **Bannar-Martin et al. (2018)** A) Represents a Nutrient Network plot at year 0 (t=0, t0) on the left

744 before nutrient addition, and on the right represents the same plot at a point in time after NPK addition

745 (Year tn). Species losses (red), species gains (blue), and change in persistent species (orange) are

746 additive components of this composition-functioning relationship and each component affects

747 measures of species richness and community biomass change. B) Observed changes in species and

748 changes in biomass within a community can be together to understand the joint response. This

749 represents our expectations for the overall effect of NPK addition on change in species and biomass

750 as a rate over time, and our expectations for partitioning this effect into biomass lost associated with

751 species loss, biomass gained associated with species gain and the biomass change associated with

752 persistent species. Plant images by Alex Muravev, The Noun Project.

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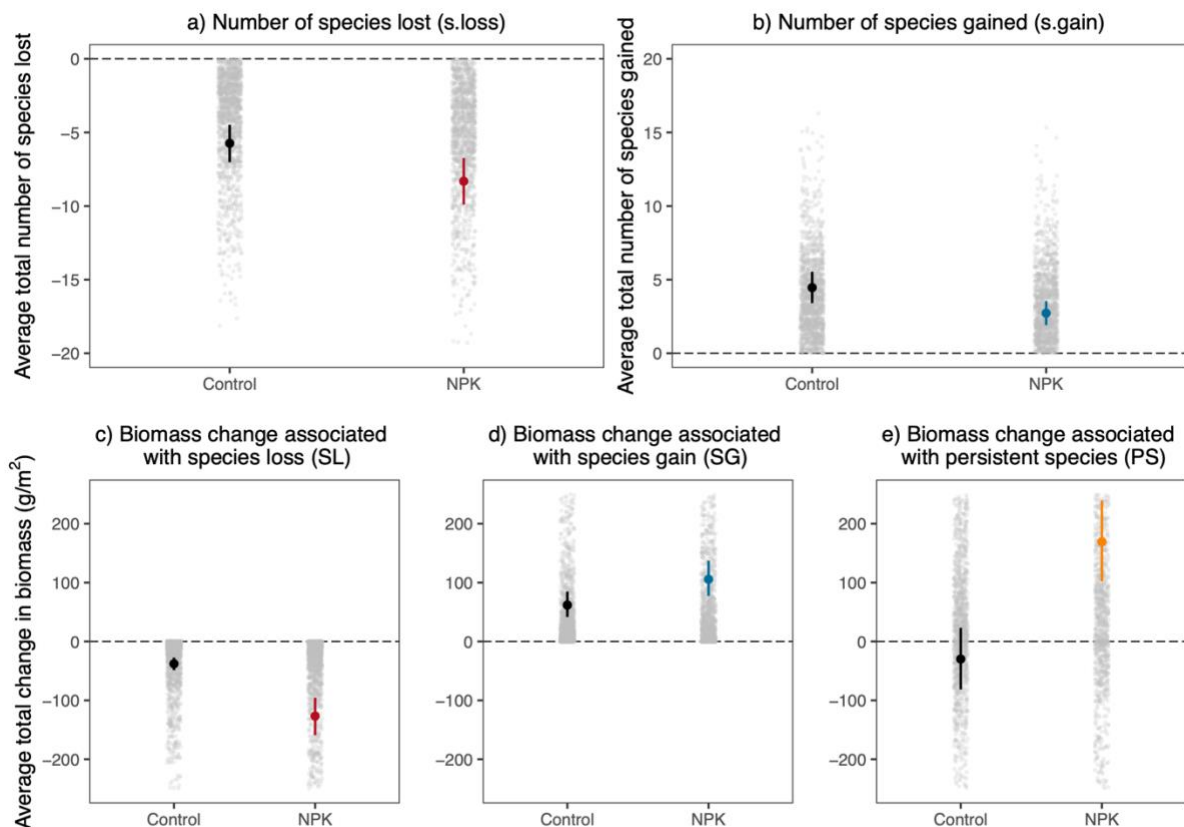754

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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 (average total) of treatment at 13 years (maximum year of experimental measurements across all sites) and colored lines show the 95% credible intervals.
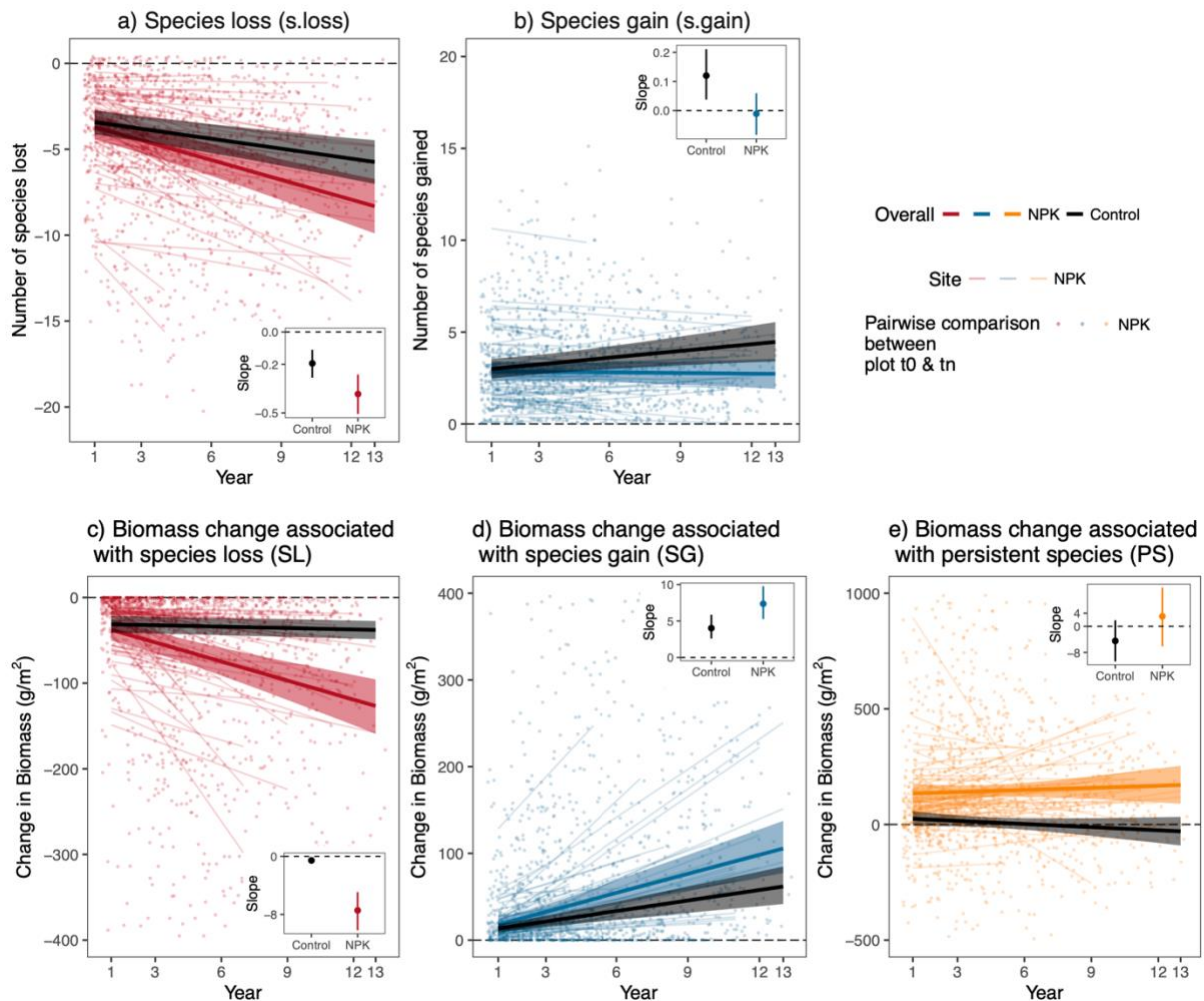

a) Species loss (s.loss)
b) Species gain (s.gain)
c) Biomass change associated with species loss (SL)
d) Biomass change associated with species gain (SG)
e) Biomass change associated with persistent species (PS)

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 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

776 a slope of 0 for each metric.

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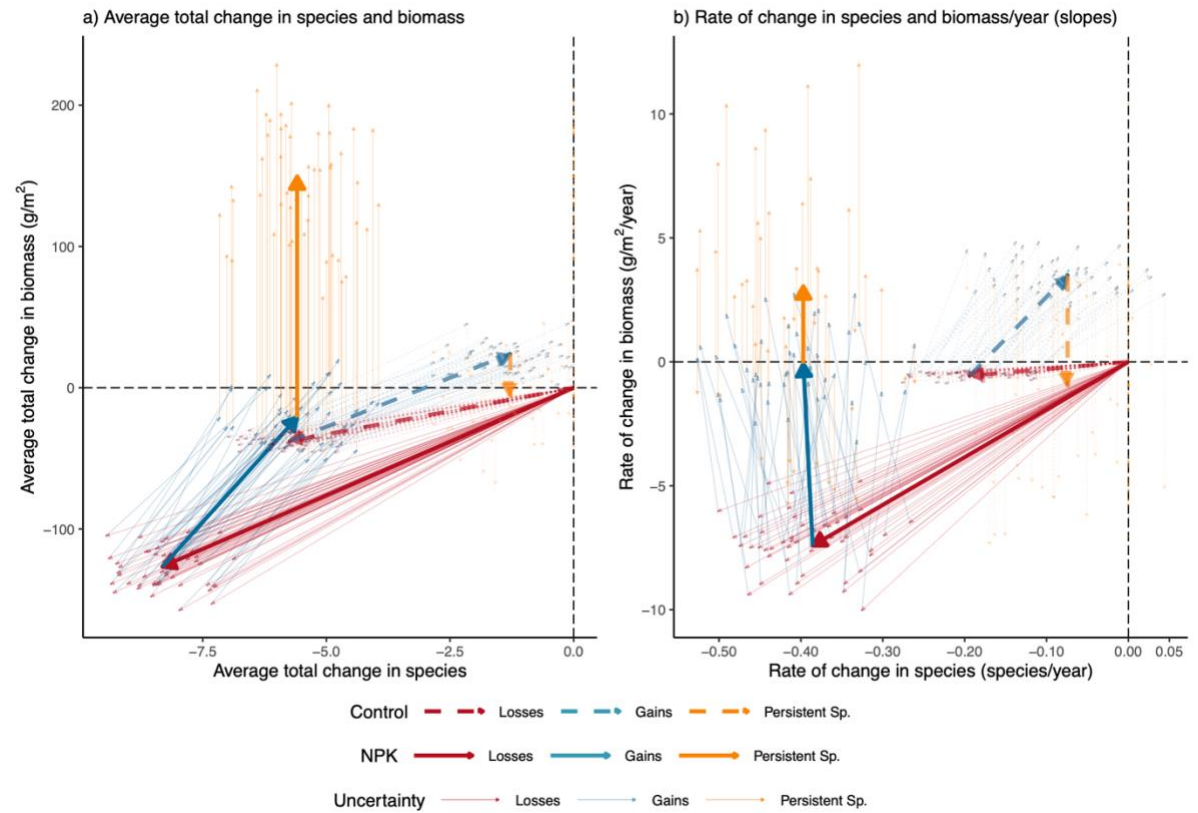778
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Figure 4: Change in species and biomass. Change in control (dashed lines) and fertilized plots (solid lines) on species (x-axis) and biomass change (y-axis) as a) an average overall change after 13 years and b) a rate of change across time (slope). 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.

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Box 1

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796   Thanks to a great deal of previous work on the effect of nutrient deposition addition
797   on ecological communities (REF), and after over a decade of the Nutrient Network (Borer *et*
798   *al.* 2014a) we know that the more resources (Nitrogen, Phosphorus, Potassium) that are
799   added to grasslands, the more species richness declines, and the more aboveground
800   biomass and productivity increases (Fay *et al.* 2015; Harpole *et al.* 2016). We also know that
801   there is an increasing effect of chronic nutrient enrichment on plant diversity loss and
802   ecosystem productivity over time (Seabloom *et al.* 2020) and that species loss due to
803   nutrient addition increases with spatial scale (Seabloom *et al.* 2021). Here, we use an
804   updated dataset that includes more sites and longer time series than in this previous work,
805   so we analyse the relationship between the addition of multiple limiting nutrients (a
806   combination of Nitrogen, Phosphorus, Potassium - NPK hereafter) on species richness over
807   time and biomass over time simply as a reference point with this updated dataset (Fig S5,
808   Table S2, S3, S4, S5)
809   The ecological adaptation of the Price equation enables the partitioning of community
810   change into 5 components, named the '5-part Price partition' or alternatively into 3
811   components (Fox & Kerr 2012; Bannar-Martin *et al.* 2017). Here, we use the 3-part
812   'Community assembly' partition proposed by (Bannar-Martin *et al.* 2017) to understand the
813   effects on biomass change of all lost species unique in the baseline sample (SL), all gained
814   species in the comparison sample (SG), and changes in the function of shared species
815   called the 'Context Dependent Effect' or CDE, but here called persistent species (PS)
816   (Figure 1, Table below). This partition requires two comparable units to quantify additive
817   pairwise differences between the two. Here, we compare every Nutrient Network plot
818   included in this analysis at the year before experimental treatments began as a baseline
819   (year 0 = t0) to itself at every point in time as a comparison (year n = tn) measured since
820   experimental treatments began to quantify cumulative temporal changes in each and every
821   plot.
822   The ecological Price equation used here (Figure 1) uses the number of species in
823   each community (s_{t0} and s_{tn}), the number of species shared ($_ps$), the species-level function in
824   each community (z_{t0}, z_{tn}) and the function of species shared by the baseline ($^pz_{t0}$) and
825   comparison communities ($^pz_{tn}$) (Bannar-Martin *et al.* 2017). Here, we uniquely use the
826   number of species shared between two samples in time (^ps), those unique in the baseline
827   community (s_{t0}) to quantify the number of species lost (s.loss), and those unique in the
828   comparison community (s_{tn}) to quantify the number of species gained (s.gain) (Figure 1).
829   These are the same number of species used to quantify the impacts of these gains and
830   losses on additive measures of ecosystem function in the 3-part Price equation partition.
831   Next, we use this 3-part ecological version of the Price partition to quantify ecosystem
832   function change associated with species loss (SL) ($^pz_{t0} - z_{t0}$), gains (SG) ($z_{tn} - {^pz_{tn}}$) and
833   persistent species (PS) ($^pz_{tn} - {^pz_{t0}}$) (See methods and Figure 1). Slightly different language
834   has been used to describe the components of the mostly commonly used 5-part Price
835   equation partition for different applications and contexts in previous work. Below we describe
836   these differences in relation to what is presented here.
837   Descriptions of Price equation components, the different short names each
838   component has been given in previous literature to address various contexts, and their
839   acronyms compared against the components used in this work. Acronyms for each
840   component are in bold italic. Initials used as a short reference for each paper that uses each
841   acronym for each component (Fox & Kerr 2012) = FK, (Winfree *et al.* 2015) = W, (Bannar-

842   Martin *et al.* 2017) = BM, cited in the order they were published.
843

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

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