

1 **Title:** Change in functional trait diversity mediates the effects of nutrient addition on grassland
2 stability

3

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41

42 **Abstract**

43 1. Nutrient enrichment impacts grassland plant diversity such as species richness, functional trait
44 composition and diversity, but whether and how these changes affect ecosystem stability in the face
45 of increasing climate extremes remains largely unknown.

46 2. We quantify the direct and diversity-mediated effects of nutrient addition (by nitrogen,
47 phosphorus, and potassium) on the stability of aboveground biomass production in 10 long-term
48 grassland experimental sites. We measure stability as the temporal invariability, resistance during
49 and recovery after extreme dry and wet growing seasons.

50 3. Leaf traits (leaf carbon, nitrogen, phosphorus, potassium, and specific leaf area) were
51 measured under ambient and nutrient addition conditions in the field and used to construct the leaf
52 economic spectrum (LES). We calculated functional trait composition and diversity of LES and of
53 single leaf traits. We quantified the contribution of intraspecific trait shifts and species replacement
54 to change in functional trait composition as responses to nutrient addition and its implications for
55 ecosystem stability.

56 4. Nutrient addition decreased functional trait diversity and drove grassland communities to the
57 faster end of the LES primarily through intraspecific trait shifts. Moreover, the change in functional
58 trait diversity of the LES in turn influenced different facets of stability. That said, these diversity-
59 mediated effects were overall weak and/or overwhelmed by the direct effects of nutrient addition on
60 stability. As a result, nutrient addition did not strongly impact any of the stability facets. These
61 results were generally consistent using individual leaf traits but the dominant pathways differed.
62 **Importantly**, major influencing pathways differed using **average** traits extracted from global **trait**
63 databases (e.g. TRY), suggesting that intraspecific trait shifts should be included for accurately
64 predicting ecosystem stability.

65 5. Synthesis. Investigating changes in multiple facets of plant diversity and their impacts on
66 multidimensional stability under global changes such as nutrient enrichment can improve our
67 understanding of the processes and mechanisms maintaining ecosystem stability.

68

69 **Keywords**

70 Nutrient deposition; drought; heavy rainfall; biodiversity; functional traits; ecosystem service,
71 Nutrient Network (NutNet)

72

73

74 **Introduction**

75
76 Earth is undergoing multiple global changes such as nutrient enrichment and climate extremes,
77 which threaten both the diversity and stability of ecosystems (IPCC, 2023). For instance,
78 agricultural fertilization and atmospheric nutrient deposition have led to increased availability and
79 redistribution of soil nutrients such as **nitrogen (N)**, **phosphorous (P)**, and **potassium (K)** globally
80 (Galloway et al., 2021; Sardans & Peñuelas, 2015; Yuan et al., 2018). Meanwhile, climate extremes
81 are increasing in both intensity and frequency (IPCC, 2023). Mounting evidence shows that these
82 global changes can reduce ecosystem stability via increasing community fluctuations or indirectly
83 via decreasing diversity (Chen et al., 2022; Hautier et al., 2015; **Xu et al., 2022**). However, our
84 understanding of ecosystem stability is limited because diversity and stability are both multifaceted
85 concepts, yet most studies only analyzed one or a few facets in isolation (Chase et al., 2018;
86 Donohue et al., 2013; Kéfi et al., 2019). Stability characterizes ecosystem responses to different
87 types of perturbations (Pimm, 1984). In the context of climate extremes, stability of an ecosystem
88 function (e.g., aboveground biomass production) can be defined as temporal invariability, resistance
89 during and recovery after climate extremes (Isbell et al., 2015; Pimm, 1984). Temporal invariability
90 indicates the degree of fluctuation and is often quantified as the ratio of the temporal mean of
91 aboveground biomass to its standard deviation (Pimm, 1984; Tilman, 1996). While this measure is
92 commonly termed as temporal stability in the literature, here we use temporal invariability to avoid
93 confusion because all stability facets we investigate involve temporal dynamics. To enable
94 comparison among sites with varying biotic and abiotic factors, resistance can be quantified as the
95 inverse of the proportional deviation of aboveground biomass during a climate extreme from the
96 normal level (Isbell et al., 2015). Recovery can be quantified as the proportional deviation from a
97 normal level during a climate extreme to that after the climate extreme. Here, a normal level refers
98 to the mean value of aboveground biomass during non-climate extremes (Isbell et al., 2015). As
99 both resistance and recovery maintain a function around its normal level, increased resistance
100 and/or recovery may increase temporal invariability (Isbell et al., 2015; Ives & Carpenter, 2007).
101 Similarly, plant diversity can be quantified in multiple dimensions, for instance, species richness,
102 functional trait diversity, and functional trait composition (Bazzichetto et al., 2024; Craven et al.,
103 2018). Different facets of diversity have been shown to respond differently to global changes and
104 have different effects on ecosystem stability (Bazzichetto et al., 2024; Chen et al., 2022; Pichon et
105 al., 2022; Suonan et al., 2023). Disentangling the direct and diversity-mediated indirect effects of
106 global changes on multiple facets of stability is essential to understand processes and mechanisms
107 maintaining ecosystem stability.

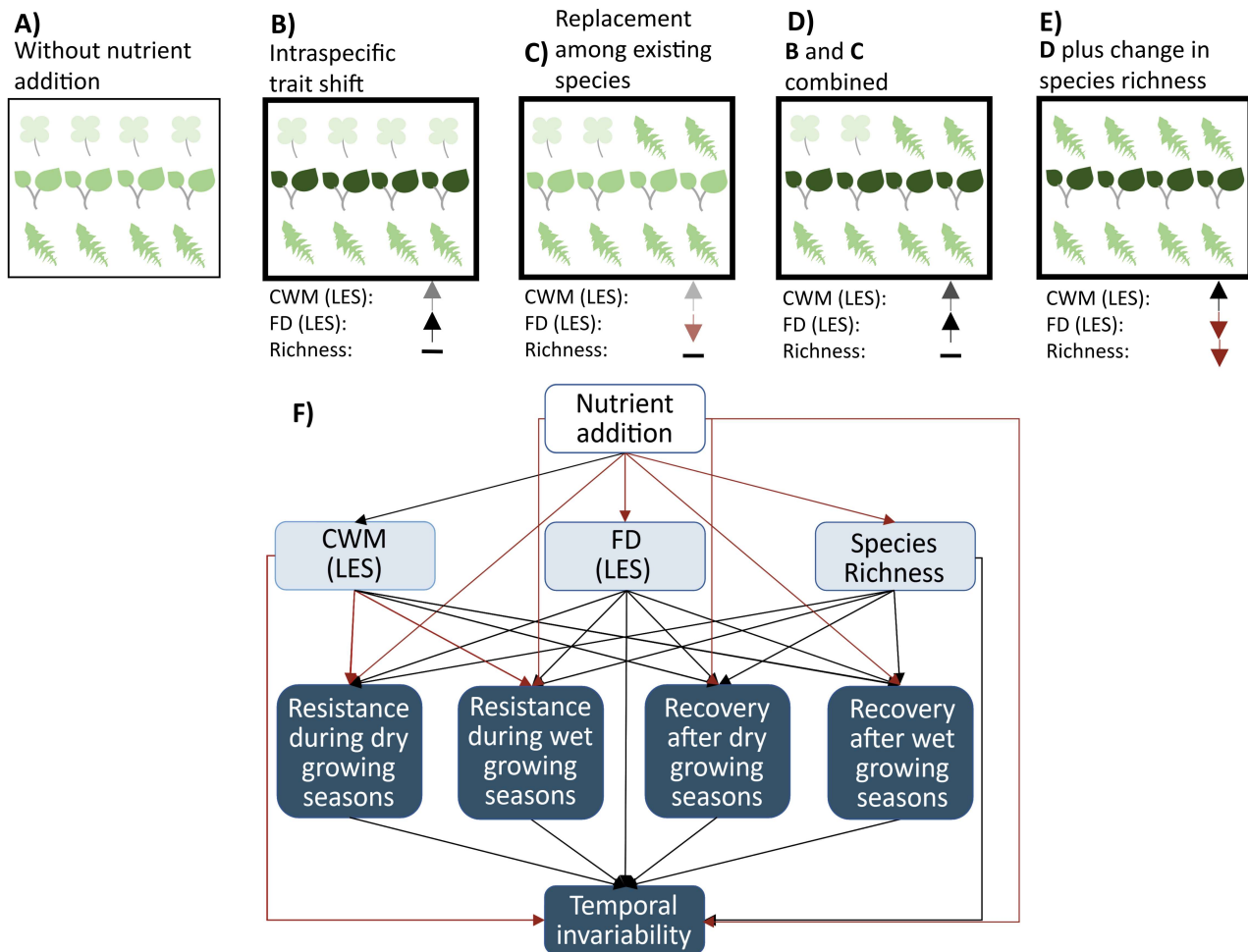
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109 Past studies have highlighted the role of functional trait composition and diversity of the leaf
110 economic spectrum (hereafter LES) in ecosystem stability (Craven et al., 2018; de Bello et al.,
111 2021; Reich, 2014). The LES framework integrates leaf morphological, physiological, and chemical
112 traits related to carbon acquisition and use to locate plant species along a spectrum that ranges from
113 slow (conservative) to fast (acquisitive) strategies. Fast species can take up resources more rapidly
114 and are typically associated with high leaf nutrients (e.g. N, P, K) and specific leaf area (Reich,
115 2014; Wright et al., 2004). These fast species may take advantage of increased pulses of resources
116 and therefore recover faster after climate extremes (Bazzichetto et al., 2024; Craven et al., 2018). In
117 contrast, slow species invest more in cell walls and secondary metabolites, having lower rates of
118 photosynthesis and respiration (Reich, 2014; Wright et al., 2004). These features may help them
119 endure unfavorable environments such that they may have higher resistance during climate
120 extremes (Oram et al., 2020; Reich, 2014; Wright et al., 2004). While the
121 ecological significance of leaf N and P has been well documented, other key elements remain less
122 investigated (Kaspari, 2021). In particular, K is essential for regulating stomata that control gas
123 exchange and water vapor release as well as activating enzymes for photosynthesis and protein
124 synthesis (Kaspari, 2021). Previous single-site experiments show that nutrient addition may
125 promote fast communities through either increasing dominance of fast species and/or shifting
126 intraspecific traits towards fast strategies (Lepš et al., 2011; Pichon et al., 2022; Siefert & Ritchie,
127 2016; Tatarko & Knops, 2018; Zhou et al., 2018). However, few ecological studies on stability have
128 as yet accounted for intraspecific trait variation, likely because of the extreme effort required to
129 measure plant traits repeatedly. Some previous studies found that plant traits have limited
130 explanatory power for ecosystem functioning, processes, and stability (Craven et al., 2018; van der
131 Plas et al., 2020). These studies used species trait values from global databases (e.g. TRY) or
132 measured in other growing environments assuming one species has a fixed trait value. Accounting
133 for intraspecific trait shifts is important to disentangle the processes driving changes in functional
134 trait composition and may improve prediction for ecosystem functions and stability.

135
136 Here, we use ten long-term (ranging from 10 to 15 years) standardized nutrient addition
137 experiments to investigate the direct and diversity-mediated effects of nutrient enrichment on
138 multidimensional ecosystem stability. We focus on five stability facets including temporal
139 invariability of aboveground plant biomass, its resistance during and recovery after dry and wet
140 climate extremes aggregated across a growing season (hereafter dry and wet growing seasons). We
141 define an extreme growing season as the event occurs once per decade. We use three diversity
142 measures including functional trait composition and diversity and species richness. We use five
143 morphological and chemical leaf traits measured in the field accounting for intraspecific trait shifts
144 to construct LES and calculate functional trait composition and diversity of LES and single leaf

145 traits. To facilitate comparison with previous studies, we also use traits extracted from global trait
146 databases.

147
148 We hypothesize that nutrient addition decreases resistance during dry and wet growing seasons.
149 This is because nutrient addition often increases aboveground biomass, resulting in a higher normal
150 level (Chen et al., 2023). Higher normal levels of biomass can lead to larger deviations during
151 extreme growing seasons (e.g., decrease under dry and increase under wet growing seasons) that
152 may exceed the nutrient-induced biomass increase in normal levels (Chen et al., 2023). During dry
153 growing seasons, reduced water availability may reduce uptake of soluble nutrients by plants.
154 Meanwhile, nutrient addition often increases leaf N that promotes photosynthesis and growth,
155 which in turn increases water demands (Harpole et al., 2007). This reduced supply and increased
156 demand of water may lead to a larger decrease in biomass (relative to the normal level) under
157 nutrient addition than the control treatment. During wet growing seasons, increased nutrients and
158 water availability may lead to a larger increase in biomass (relative to the normal level) under
159 nutrient addition than the control treatment (Chen et al., 2023). Nutrient addition may also decrease
160 recovery after dry growing seasons because increased plant mortality (due to increased normal
161 level) can increase litter accumulation and thereby limit species colonization (Meng et al., 2021;
162 Southon et al., 2012). Nutrient addition may decrease recovery after wet growing seasons because
163 increased aboveground biomass due to increased nutrients and water availability may persist or
164 even amplify in later years (Sala et al., 2012; Wheeler et al., 2021). Moreover, nutrient addition may
165 indirectly decrease resistance during, but increase recovery after, dry and wet growing seasons by
166 promoting fast communities (Bazzichetto et al., 2024; Craven et al., 2018). The impact of nutrient
167 addition on temporal invariability can, however, be weak because nutrient-induced fast
168 communities have opposing effects on resistance and recovery (Craven et al., 2018). Furthermore,
169 nutrient addition may indirectly decrease temporal invariability, resistance during and recovery
170 from dry and wet growing seasons by decreasing the diversity of LES and species richness (Fig.1F).
171 Species richness may capture diversity in **phylogenetically conserved traits (e.g. plants associated**
172 **with nitrogen fixation bacteria) and not conserved traits** (e.g. root and size-related traits) that cannot
173 be captured by LES. Communities with higher diversity in LES or species richness are more likely
174 to include species that are better adapted to climate extremes. Thus, population decreases in some
175 species may be compensated by increases in others during and after extreme growing seasons
176 (Loreau & de Mazancourt, 2013). This leads to less aboveground biomass deviation from normal
177 levels, which increases resistance and recovery (Bazzichetto et al., 2024) as well as temporal
178 invariability (Craven et al., 2018). Overall, we hypothesize that nutrient addition decreases all these
179 stability facets and that such effects are primarily mediated by changes in functional trait
180 composition and diversity of the LES.



182

183 **Fig. 1. Conceptual framework illustrating how nutrient addition may impact different facets**
 184 **of plant diversity (A-E) and stability through its direct and diversity-mediated indirect effects**
 185 **(F). Darker color in A-E represents faster species. Thick boxes represent nutrient addition**
 186 **conditions. Black and red arrows represent increase and decrease (darker color represents a larger**
 187 **change). CWM (LES): functional trait composition as measured by community-weighted mean of**
 188 **leaf economics spectrum (LES); FD (LES): functional diversity of LES. Line color in F represents**
 189 **positive (black) and negative (red) effects. See Table 1 for the calculation and interpretation of each**
 190 **variable.**

191

192 **Materials and Methods**

193 *Experimental Design*

194 We used a **coordinated, multisite, and multiyear nutrient addition** and herbivore manipulation
 195 experiment (NutNet; www.nutnet.org) initiated in 2007 (Borer et al., 2014, 2017). The original
 196 design includes a factorial manipulation of nutrients (N, P & K) plus two fences to exclude
 197 herbivores (one without nutrients addition and the other with NPK). Each treatment was imposed to
 198 a 25 m² plot and replicated in at least three blocks. N was supplied as slow-release urea ((NH₂)₂CO),
 199 P was supplied as triple superphosphate (Ca(H₂PO₄)₂), and K as potassium sulfate (K₂SO₄). N, P,

200 and K were added annually at a rate of $10 \text{ g m}^{-2} \text{ y}^{-1}$ (i.e. 100 kg/ha/year). A micronutrient and
201 macronutrient mix (Fe, S, Mg, Mn, Cu, Zn, B, and Mo in combination) was applied at a rate of 100
202 g m^{-2} once at the start of the experiment, as part of the K addition. Further details on the design are
203 available in (Borer et al., 2014). We use traits measured in all treatments (see section ‘Leaf trait
204 measurements’ for details), we focus on exploring stability in the control and nutrient addition
205 (NPK) treatments.

206

207 *Site selection*

208 We selected ten long-term (ranging from 10 to 15 years) sites because they have: 1) both control
209 and nutrient addition (NPK) treatments and the occurrence of at least one extreme dry and one
210 extreme wet growing season during the experiment. See section ‘Defining climate extremes and
211 stability facets’ for detail in classifying dry and wet growing seasons; 2) three blocks. For sites with
212 more than three blocks, we used the first three blocks according to the block number recorded by
213 site PIs; 3) more than three plant species measured for leaf traits in both control and nutrient
214 addition conditions; 4) >50% proportional cover of species with trait **values** in a plant community
215 averaged across blocks and experimental years. So, the community-weighted mean (CWM) and
216 functional diversity (FD) of traits can reasonably represent the whole plant community. See section
217 ‘Leaf trait measurements’ for details. These sites are distributed in North America (8 sites) and
218 Australia (2 sites) (Fig. S1; Table S1). These sites are dominated by herbaceous plant species,
219 covering montane, alpine, and semiarid grasslands as well as prairies and old fields, which we refer
220 to as grasslands for simplicity (see Table S1 for geolocation, climate, and experimental duration for
221 these sites).

222

223 *Sampling protocol*

224 All sites followed standard NutNet sampling protocols. A $1 \times 1 \text{ m}$ subplot was permanently marked
225 within a 25 m^2 plot. Number of species, species identity, and their covers were recorded once per
226 year in these $1 \times 1 \text{ m}$ subplots at most sites. At a few sites with strong seasonality, cover and biomass
227 were recorded twice per year to include a full list of species and follow typical management
228 procedures. For those sites, the maximum cover for each species and total biomass for a community
229 were used in the analysis. The taxonomy was checked and adjusted within sites to ensure consistent
230 naming over time. For instance, when individuals could not be identified as species in all years,
231 they were aggregated at the genus level but referred to as taxa for simplicity. Meanwhile,
232 aboveground biomass was measured adjacent to these permanent subplots within two $1 \times 0.1 \text{ m}$
233 strips (in total 0.2 m^2), which were moved from year to year to avoid resampling. All aboveground
234 biomass was clipped, sorted into dead and live, and dried at $60 \text{ }^\circ\text{C}$ to constant mass before weighing
235 to the nearest 0.01 g.

236

237 *Leaf trait measurements*

238 Leaf morphological and chemical traits including leaf carbon, leaf nitrogen, leaf phosphorus, leaf
239 potassium, specific leaf area (hereafter leaf C, N, P, K, SLA) were measured after 2, 3, or 4 years of
240 nutrient addition at most sites (Table S2). Traits were measured for 3 to 5 of the most abundant
241 species (ranked by cover) in each subplot according to standard protocols (Pérez-Harguindeguy et
242 al., 2016). A detailed description of these trait measurements can be found in (Firn et al., 2019).
243 Briefly, for each species measured for leaf traits, five fully grown leaves without clear grazing
244 marks were randomly selected. Leaf area (mm^2) was measured using a leaf area meter or a scanner.
245 After that, dry weight (g) of leaves was measured after oven-drying at 60 °C for 48 h. Specific leaf
246 area (SLA; mm^2g^{-1}) was calculated as leaf area divided by dry weight. Then, leaf nutrient
247 concentrations (%) including C, N, P, and K were determined. Leaf P, K, and C were determined
248 using laser ablation inductively coupled plasma mass spectrometry following (Duodu et al., 2015).
249 Leaf N was determined using a LECO TruMac, based on a combustion technique using thermal
250 conductivity relative to pure gas with an error < 1%.

251

252 We separated leaf traits measured in ambient (control, Fence) and nutrient-enriched conditions (N,
253 P, K, NP, NK, PK, NPK, NPK+Fence). Additionally, multiple trait measurements for the same
254 species at one site (e.g., from different blocks or nutrient treatments) were averaged. We did this to
255 maximize the number of species with available trait data and because previous results found little
256 variation in leaf traits among blocks within the ambient and nutrient-enriched conditions at 27
257 NutNet sites (Firn et al., 2019). Due to this aggregation, a larger number of species measured for
258 traits and proportional cover of species with traits in plant communities were found under nutrient
259 addition than ambient conditions at nearly all 10 sites (Table S2). Across all sites, plant species with
260 trait values account for >52% of the cover; at 6 of 10 sites this proportion was similar under control
261 and nutrient addition treatments (Table S2). Overall, 102 plant species were measured for the five
262 leaf traits and 92 species have data for all these traits.

263

264 *The leaf economic spectrum, community-weighted mean traits, and functional trait diversity*

265 We used the five leaf traits from the 92 species to construct leaf economic spectrum (LES) using
266 principal component analysis (PCA) as coded in the “PCA” function from the R package
267 “FactoMineR” (Lê et al., 2008). We extracted the first axis of the PCA, which explained 34.7% of
268 the variance, to represent the LES. Higher values (i.e. lower leaf C, higher N, P, K, and SLA)
269 indicate faster species (Fig. S2a). Due to relatively low variance explained in the first axis of the
270 PCA, we calculated CWM and FD of LES as well as of individual leaf traits. CWM is the average
271 of each trait weighted by the relative cover of that species in a community (Garnier, et al., 2004).

272 FD is cover-weighted dispersion of each trait relative to CWM (Laliberte & Legendre, 2010). We
273 calculated CWM and FD using the function “dbFD” from the R package “FD” (Laliberté et al.,
274 2014). See Table 1 for mathematical formulas for CWM and FD and their interpretations. These
275 variables were calculated annually for each subplot and then averaged across years.

276
277 *Partitioning community-weighted mean traits into intraspecific trait shift and species replacement*
278 In addition to calculating CWM and FD based on all species with trait data, we recalculated them
279 for shared species (species that were present in both the control and nutrient addition subplots). This
280 allowed us to partition CWM based on shared species into intraspecific trait shift and replacement
281 of existing species following (Jung et al., 2014). See Table 1 for mathematical formulas for
282 calculating and interpreting these variables.

283 **Table 1. Variables used in this study with their mathematical definitions and interpretations.**

284 We used leaf economic spectrum (LES) as an example, we also quantified community-weighted
 285 mean (CWM) and functional diversity (FD) of single leaf traits.

Variables	Methods	Parameters explained	Interpretations	References
CWM (LES)	$\sum_{i=1}^s a_i \cdot x_i$	a_i is the relative cover of species i , x_i is the LES for species i . S is the number of species.	A higher value indicates that a plant community is dominated By fast-growing species.	Garnier <i>et al.</i> 2004)
CWM induced by intraspecific trait shift	$CWM_{Nut} - CWM_{Nut*}$	CWM_{Nut} and $CWM_{control}$ are CWM in the nutrient addition and control treatment. CWM_{Nut*} is the CWM in the nutrient addition treatment recalculated using LES in the control treatment.	A higher value of replacement indicates that a change in CWM is more induced by a change in relative cover among existing species while less induced by intraspecific trait shift.	(Jung <i>et al.</i> 2014)
CWM induced by replacement among existing species	$CWM_{Nut*} - CWM_{control}$			
FD (LES)	$\sum_{i=1}^s a_i \cdot z_i$	a_i is cover of species i , z_i is the distance of LES of species i to community-weighted mean trait (CWM). S is the number of species.	A higher value indicates that a plant community has higher diversity in LES.	(Laliberte & Legendre 2010)
Temporal invariability	u/σ	μ is the mean of aboveground biomass, σ is the standard deviation of it over time.	A higher value indicates that a plant community fluctuates less in aboveground biomass over time.	(Pimm 1984)
Resistance during dry/wet growing seasons	$\frac{\bar{Y}_n}{ Y_e - \bar{Y}_n }$	\bar{Y}_n , Y_e , and Y_{e+1} are aboveground biomass during normal growing seasons, during a dry or wet growing season, and one year after a dry or wet growing season, respectively.	A higher value indicates that aboveground biomass deviates less under a dry or wet growing season from that of the average of normal growing seasons.	(Isbell <i>et al.</i> 2015)
Recovery After dry/wet growing seasons	$\frac{ Y_e - \bar{Y}_n }{ Y_{e+1} - \bar{Y}_n }$		A higher value indicates that aboveground biomass deviates less one year after a dry or wet growing season relative to that during a dry or wet growing season.	(Isbell <i>et al.</i> 2015)

286

287

288 *Compare results using trait values extracted from global trait databases*

289 To compare with previous studies that quantify LES based on global trait databases and also include
 290 leaf dry matter content (LDMC), we compiled species-level trait data (leaf C, N, P, K, SLA,
 291 LDMC) from TRY (Version 6), BIEN (Version 1.2.6), AusTraits (Version 5.0.0) for NutNet
 292 species. Following (Craven *et al.*, 2018), all traits were first averaged within databases and then

293 across them for each species regardless of their geolocation. Overall, species-level traits covered
294 less than 50% of the species occurring at these 10 sites. But species with extracted leaf N and SLA
295 data accounted for > 50% of community cover at most NutNet sites (Table S3), thus we use these
296 two species-level traits to calculate CWM and FD. We compared these results to those based on
297 traits directly measured in the field. Moreover, only 31 species have data for all these six leaf traits.
298 To increase trait coverage, following (Craven et al., 2018), missing species-level traits were filled
299 using the average trait value from other species in the same genus for which trait values were
300 available. To ensure that filled trait values *were* not biased towards species with a higher number of
301 records, trait values were first averaged for each species, then averaged across species within a
302 genus. Because of low coverage of leaf K data for species from these 10 NutNet sites, here we used
303 leaf C, leaf N, leaf P, SLA, and LDMC to construct LES. Similarly, we extracted the first axis of
304 PCA, which explained 40.3% of the variance, to represent the LES (Fig. S2b).

305

306 *Defining climate extremes and stability facets*

307 We used the standardized precipitation–evapotranspiration index (SPEI) to classify climate
308 extremes for each site. SPEI was calculated as the standardized (z-score) water balance
309 (precipitation – evapotranspiration; mm) over the growing season from 1901 to 2022. We used
310 water balance during growing seasons because previous studies show it is better correlated with
311 aboveground biomass than total annual water balance (Robinson et al., 2013). Growing seasons
312 were defined by the site PIs (Table S1). Precipitation and potential evapotranspiration used to
313 calculate SPEI were downloaded from https://crudata.uea.ac.uk/cru/data/hrg/cru_ts_4.07/ (*accessed*
314 *on 14/03/2024*) (Harris et al., 2020). Following (Isbell et al., 2015), we categorized each growing
315 season into normal, dry, and wet using the cutoffs of 1.28 and 0.67 SD (1.28: occurring once per
316 decade; 0.67: once every four years; SD: standard deviation). That is, normal growing season: -0.67
317 $SD < SPEI < 0.67 SD$; dry: $SPEI \leq -1.28 SD$; and wet: $SPEI \geq 1.28 SD$. In total, 64, 19, and 19
318 normal, dry, and wet growing seasons across sites were detected in our data. When two (or more)
319 extreme growing seasons of the same kind happen consecutively (e.g., wet followed by wet),
320 recovery was only calculated for the last growing season, which must be followed by a normal or a
321 less extreme growing season (those between normal and extreme).

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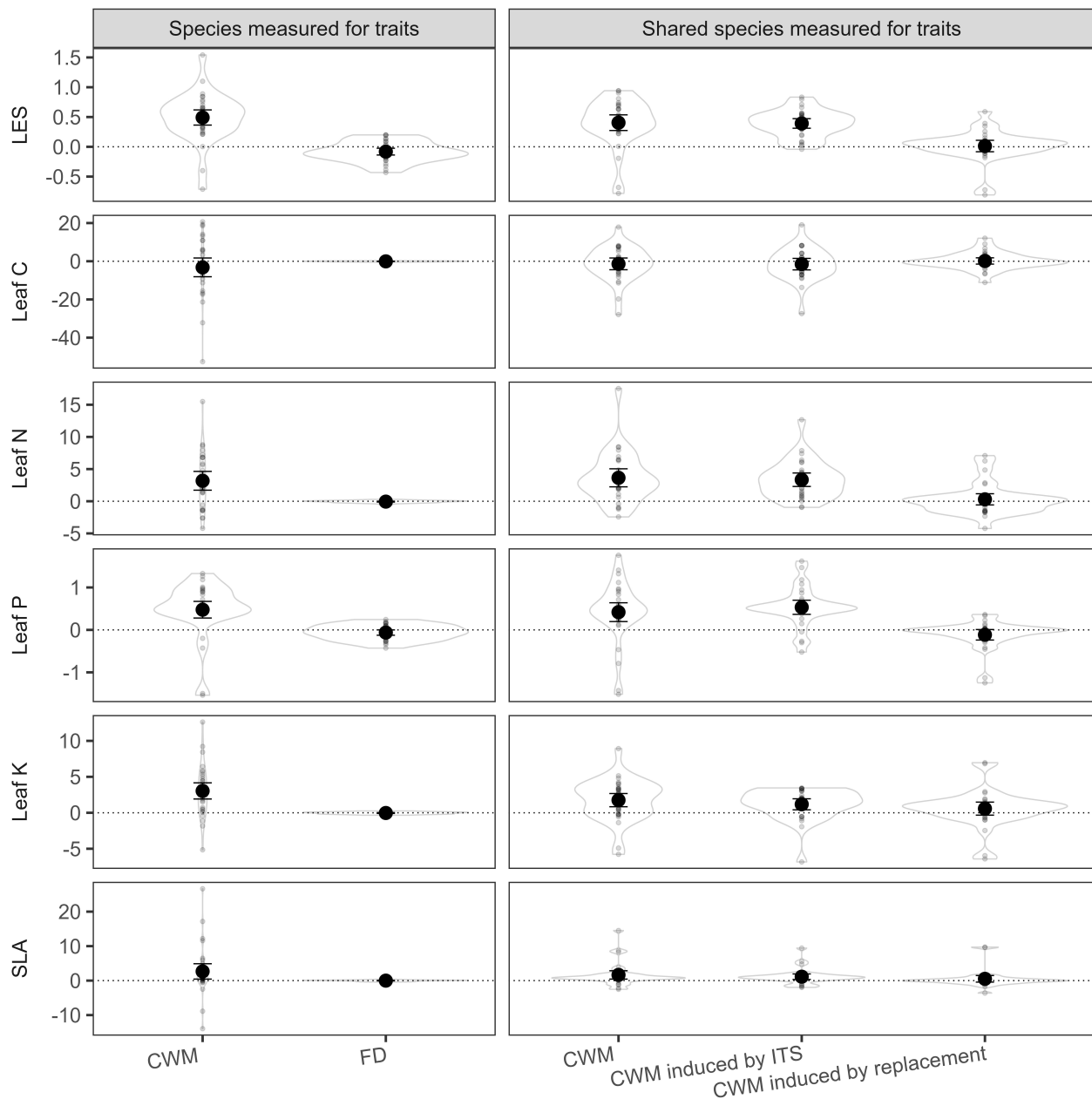
323 We quantified resistance as the inverse of the proportional deviation of aboveground biomass from
324 normal levels during a dry or wet growing season. Also, we quantified recovery as the inverse of
325 the proportional lack of recovery in aboveground biomass during the year after a dry or wet
326 growing season following (Isbell et al., 2015). We treated resistance during and recovery after dry
327 and wet growing seasons individually, and averaged each over experimental years to match the data
328 structure of temporal invariability. We quantified temporal invariability as the ratio of the temporal

329 mean to the standard deviation of aboveground biomass in each plant community (Pimm, 1984). To
330 eliminate potential trends in aboveground biomass over time, we calculated detrended standard
331 deviation from the residuals of a linear model (function “lm”) regressing aboveground biomass
332 against experimental years (Tilman et al., 2006). See Table 1 for mathematical formulas for
333 calculating stability metrics and their interpretations.

334
335 *Statistical analysis*
336 All analyses were performed in R v.4.1.6 (R Core Team., 2022). We used linear mixed-effects
337 models (function “lme”) from the R package “nlme” (Pinheiro et al., 2017) for the following
338 analyses. We built models where site and block nested within the site were the random effects and
339 treatment was the fixed effect. First, we tested whether nutrient addition impacted CWM and FD of
340 various traits using all species with trait data and the shared species. We also tested whether nutrient
341 addition impacted intraspecific trait shifts and species replacement (drivers for CWM) of various
342 traits based on shared species. Second, we examined the effects of nutrient addition on each
343 stability facet. To that end, we first disentangled how nutrient addition impacted resistance and
344 recovery through aboveground biomass deviation under extreme growing seasons from that during
345 normal growing seasons. We aggregated aboveground biomass and the magnitude of aboveground
346 biomass deviation (values are positive only) from normal levels during and one year after dry and
347 wet growing seasons, in control and nutrient addition treatments across sites. We present raw data
348 for aboveground biomass under different growing seasons over the experimental years at each site
349 (Fig. S3). Then, we tested whether nutrient addition impacted stability facets.

350
351 We built structural equation models (SEMs) to evaluate the direct effects of nutrient addition on
352 stability facets as well as its indirect effects through CWM, FD, and species richness. The SEMs
353 were built using the function “psem” from the R package piecewiseSEM (Lefcheck, 2016). An
354 initial model was built based on prior knowledge (Fig. 1F). For each component model in SEM, we
355 used the function “lme” with site and block nested within site as random effects. We estimated
356 variance inflation for each component model to check whether multicollinearity affects parameter
357 estimates, which were smaller than 2 in all component models. The goodness of fit of SEM models
358 were assessed by Fisher’s C statistic, with a higher p value (e.g. ≥ 0.05) indicating a good model fit.
359 We used CWM and FD of LES and each measured leaf trait in the model to link to facets of
360 stability under nutrient addition. We also used species-level leaf N, SLA, and LES based on
361 species- and genus-level filled traits from global trait databases to link them to facets of stability
362 under nutrient addition.

363
364



365

366 **Fig. 2. Effects of nutrient addition on community-weighted mean (CWM) and functional**
 367 **diversity (FD) of the leaf economic spectrum (LES) and single leaf traits used to construct**
 368 **LES.** For shared species (i.e. species present in both control and nutrient addition treatments),
 369 change in CWM was further attributable to intraspecific trait shifts (ITS) and replacement among
 370 existing species. Small points are effects of nutrient addition on each community-level trait from
 371 each block at each site. Large black points are mean values over all 10 sites estimated from linear
 372 mixed effect models, error bars are 95% confidence intervals. Violin shapes show distribution of
 373 values. See Table S4 for test statistics.

374

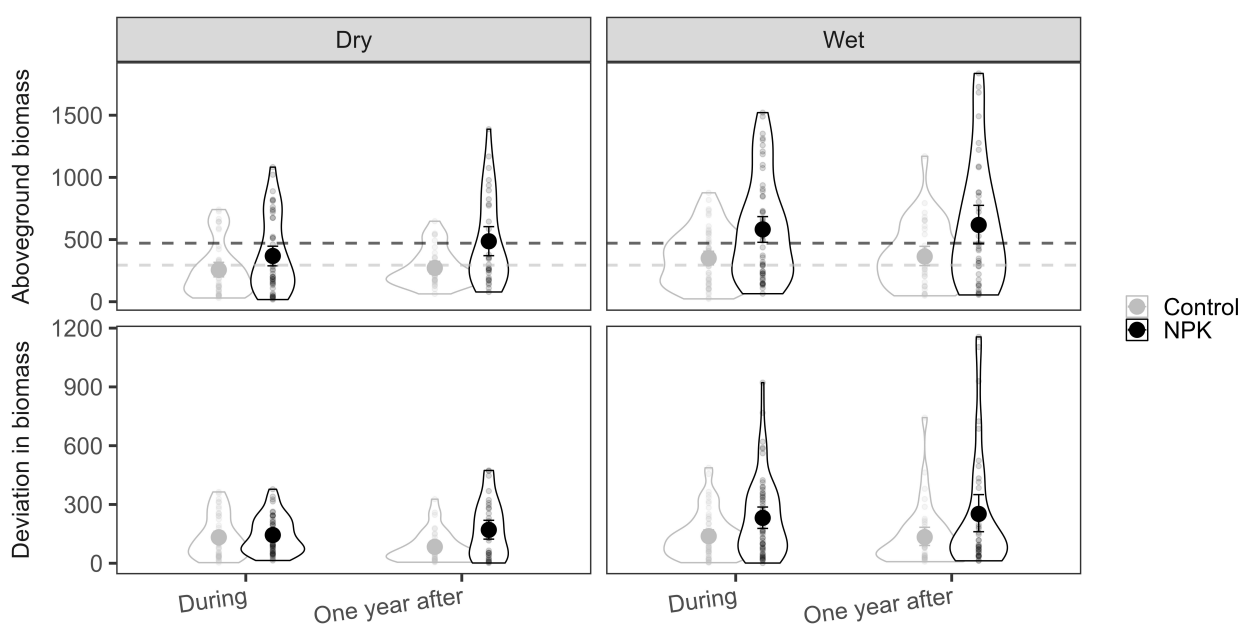
375 Results

376 Using all species having traits, nutrient addition decreased FD of LES while increasing CWM (Fig.
 377 2). That is, nutrient addition led to faster communities. The result for **CWM** was similar using only
 378 shared species (i.e., species occurring in both control and nutrient addition treatments). Using the

379 shared species, we further found that the increased CWM of LES under nutrient addition was driven
 380 mainly by intraspecific trait shifts rather than replacement among existing species (Fig. 2; Table
 381 S4). Nutrient addition also decreased FD of leaf C, N, P, but had no effects on FD of leaf K and
 382 SLA (p values of 0.08 and 0.1 for leaf C and N; Fig. 2; Table S4). Nutrient addition also increased
 383 the CWM of leaf N, P, K, and SLA, but had no effect on the CWM of leaf C. Using the shared
 384 species, we found changes were again mainly driven by intraspecific trait shifts, but the increased
 385 CWM of leaf P was also partly driven by species replacement among existing species (Fig. 2; Table
 386 S4).

387
 388 During normal growing seasons, nutrient addition significantly increased aboveground biomass by
 389 60% (Fig. 3; Table S5). During dry growing seasons, aboveground biomass decreased relative to
 390 their normal levels under both control and nutrient addition treatments, but this decrease was more
 391 pronounced under nutrient addition. Nutrient addition weakly increased aboveground biomass
 392 deviation (i.e., absolute difference between dry and normal seasons) by 9% (Table S5). One year
 393 after dry growing seasons, biomass generally returned to their normal levels. The deviation in
 394 biomass was, however, 104% higher under nutrient addition than the control, suggesting the
 395 biomass recovery was more variable (some sites increased while others decreased) under nutrient
 396 addition. During wet growing seasons, aboveground biomass increased relative to normal levels
 397 under both control and nutrient addition treatments. This increase was more pronounced under
 398 nutrient addition, with biomass deviation 68% higher under nutrient addition than the control. These
 399 deviations persisted to the year following a wet growing season (Fig. 3; Table S5).

400



401
 402 **Fig. 3. Aboveground biomass (gm^{-2}) and the magnitude of its deviation (gm^{-2}) during dry and**
 403 **wet growing seasons from normal levels that were used to quantify resistance and recovery.**

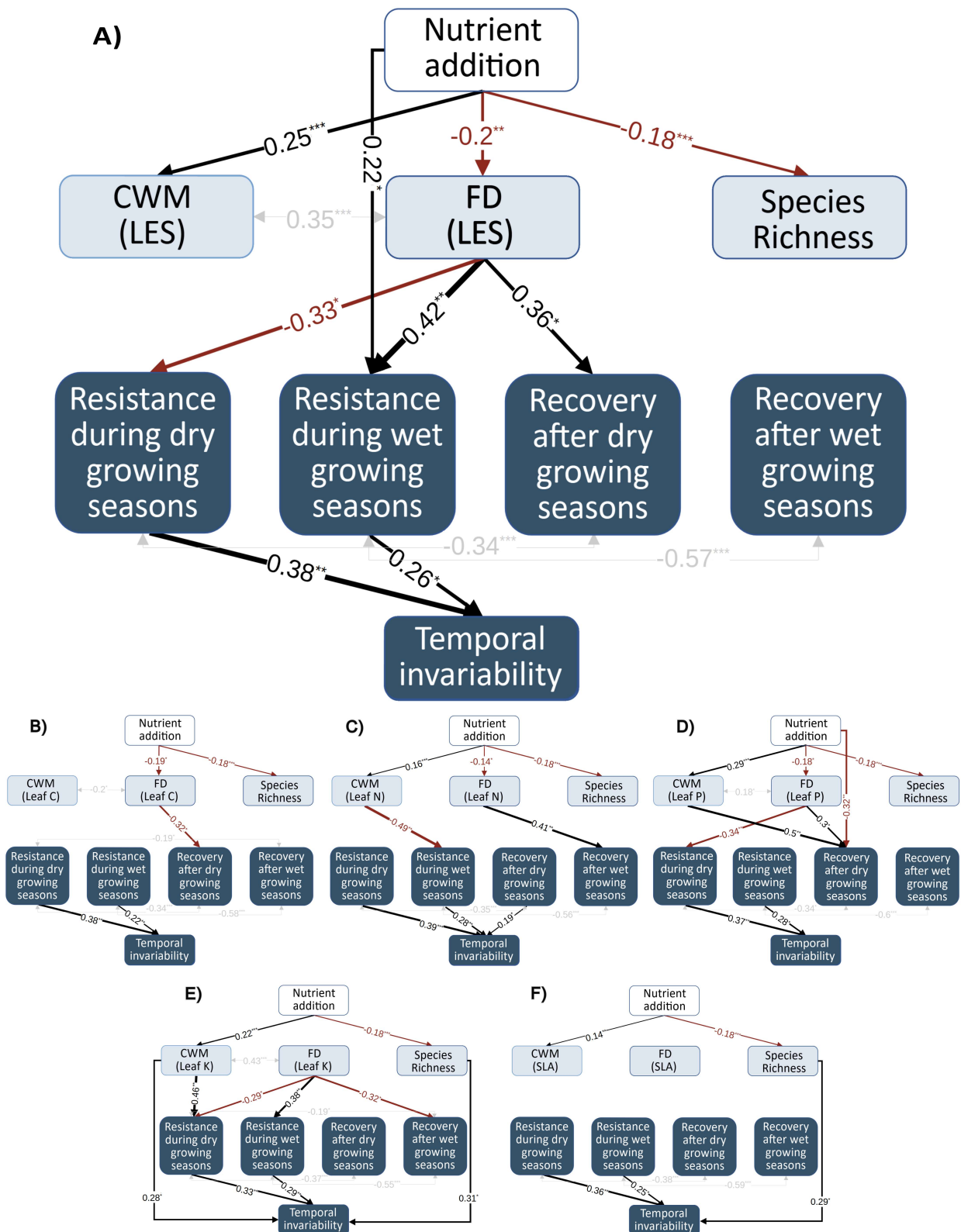
404 Deviation in biomass refers to absolute change in aboveground biomass from normal levels. Dashed
405 lines indicate mean aboveground biomass during normal growing seasons (i.e., normal levels).
406 Note, each treatment in each block at each site had its own normal level. Small points are values
407 from each block at each site. Large points indicate average values across 10 sites. Error bars are
408 95% bootstrapped confidence intervals. Violin shapes show distribution of values. See Table S5 for
409 test statistics.

410
411 The SEM revealed that nutrient addition impacted facets of stability directly and indirectly through
412 different facets of plant diversity (Fig. 4A; Table 2). When using CWM and FD of LES in the SEM,
413 nutrient addition increased resistance during dry growing seasons mainly through decreasing FD of
414 LES. Nutrient addition influenced resistance during wet growing seasons both directly and
415 indirectly, with the positive direct effects partially offset by the negative indirect effects through
416 reducing FD of LES. This resulted in a weak overall increase in resistance during wet growing
417 seasons under nutrient addition. Nutrient addition decreased recovery after dry growing seasons
418 through decreasing FD of LES, but had no effect on the recovery after wet growing seasons.
419 Nutrient addition impacted temporal invariability weakly through the indirect effects mediated by
420 resistance and diversity facets. Overall, these pathways resulted in weak effects of nutrient addition
421 on all facets of stability (Fig. 4A; Table 2; Fig. S4; Table S6).

422
423 Similar results were revealed when using CWM and FD of single leaf traits, although the dominant
424 influencing pathways differed (Fig. 4B-4F; Table 2). Also, the diversity-mediated indirect pathways
425 were stronger using leaf N and leaf P than leaf K, leaf C, and SLA. For instance, nutrient addition
426 did not strongly impact any stability facet through FD of leaf K and SLA. When using CWM and
427 FD of traits extracted from global databases (Fig. S5; Fig. S6; Fig. S7; Table S7; Table S8), nutrient
428 addition did not alter CWM whereas it had a strong negative effect on temporal invariability
429 through decreasing species richness. When including CWM and FD of leaf N and SLA based on
430 species-level traits extracted from global trait databases, nutrient addition had strong effects on
431 some stability facets through FD (Fig. S6; Fig. S7; Table S7; Table S8).

432

433



434
 435 **Fig. 4. Direct and diversity-mediated effects of nutrient addition on facets of stability, where**
 436 **diversity is based on the leaf economics spectrum (LES; A), leaf C (B), leaf K (C), leaf N (D),**
 437 **leaf P (E) specific leaf area (SLA; F).** Arrows represent relationships among variables. The
 438 displayed numbers are standardized path coefficients. The width of arrows indicates the strength of
 439 the pathways. Line color represents positive (black) and negative (red) effects. Non-significant
 440 paths are not shown. Grey lines and text show correlated errors. Asterisks indicate significant paths:
 441 * $p \leq 0.1$; ** $p \leq 0.05$; *** $p \leq 0.001$. All stability facets were on the log scale to improve normality

442 and homogeneity of variance. See Table 2 for the breakdown of direct and diversity-mediated
 443 indirect effects of nutrient addition on facets of stability. All models fit the data well, see Table S7
 444 for variance explained (R^2) for each component model and goodness of model fit.

445

446 **Table 2. Direct and diversity-mediated effects (standardized path coefficients) of nutrient**
 447 **addition on facets of stability.** Results were summarized from both significant and non-significant
 448 paths from structure equation models in Fig. 4.

Trait name	Effects/pathways	Resistance during dry growing seasons	Resistance during wet growing seasons	Recovery after dry growing seasons	Recovery after wet growing seasons	Temporal invariability
LES	Direct effects	0	0.22	-0.17	-0.18	-0.1
	Direct effects through resistance and recovery					0.01
	Indirect effects through diversity facets	0.16	-0.14	-0.01	0.05	-0.02
	Indirect effects through resistance and recovery (and through diversity facets)					0.03
	Total effects	0.16	0.08	-0.18	-0.13	-0.09
Leaf C	Direct effects	0.1	0.13	-0.21	-0.12	-0.05
	Direct effects through resistance and recovery					0.01
	Indirect effects through diversity facets	0.05	-0.05	0.03	-0.01	-0.06
	Indirect effects through resistance and recovery (and through diversity facets)					0.01
	Total effects	0.16	0.08	-0.18	-0.13	-0.09
Leaf N	Direct effects	0.1	0.15	-0.17	-0.13	-0.09
	Direct effects through resistance and recovery					0.03
	Indirect effects through diversity facets	0.05	-0.07	-0.01	0	-0.03
	Indirect effects through resistance and recovery (and through diversity facets)					0
	Total effects	0.16	0.08	-0.18	-0.13	-0.09
Leaf P	Direct effects	0.01	0.15	-0.32	-0.16	-0.11
	Direct effects through resistance and recovery					-0.04
	Indirect effects through diversity facets	0.14	-0.07	0.14	0.03	0
	Indirect effects through resistance and recovery (and through diversity facets)					0.06
	Total effects	0.16	0.08	-0.18	-0.13	-0.09
Leaf K	Direct effects	0.02	0.12	-0.2	-0.14	-0.12
	Direct effects through resistance and recovery					-0.01
	Indirect effects through diversity facets	0.14	-0.04	0.02	0.01	0.01
	Indirect effects through resistance and recovery (and through diversity facets)					0.04
	Total effects	0.16	0.08	-0.18	-0.13	-0.09
SLA	Direct effects	0.1	0.1	-0.21	-0.12	-0.07
	Direct effects through resistance and recovery					0.01
	Indirect effects through diversity facets	0.05	-0.02	0.03	-0.01	-0.04
	Indirect effects through resistance and recovery (and through diversity facets)					0.02
	Total effects	0.16	0.08	-0.18	-0.13	-0.09

450

451 **Discussion**

452 Our study tested the role of the leaf economic spectrum (LES) and single leaf traits **by accounting**
453 **for intraspecific trait variations** in mediating ecosystem stability following nutrient addition. Using
454 leaf traits measured in the field, we quantified the contribution of intraspecific trait shifts and
455 species replacement to change in functional trait composition as responses to nutrient addition and
456 its implications for ecosystem stability. Our study also expanded the scope of stability analyses by
457 including five facets (resistance during and recovery after dry and wet growing seasons, and
458 temporal invariability). Among these, resistance during and recovery after wet growing seasons
459 have been largely overlooked by previous studies. We found that nutrient addition strongly
460 impacted functional trait composition and diversity of LES and single leaf traits, and change in
461 functional trait composition was mainly driven by intraspecific trait shifts. The changes in plant
462 diversity mediated changes in different facets of ecosystem stability under nutrient addition. The
463 major influencing pathways differed using traits measured on-site and that extracted from global
464 databases, suggesting intraspecific trait shifts need to be included for accurately predicting
465 ecosystem stability.

466

467 *The role of intraspecific trait shifts in community trait change*

468 Nutrient addition promoted fast communities while decreasing FD of LES through intraspecific trait
469 shifts and changing species richness (Fig. 1E). The change in CWM of LES was mainly induced by
470 intraspecific trait shifts corroborates results from previous studies under other global change
471 scenarios (Jung et al., 2014; Duodu et al., 2015; Niu et al., 2016; Tatarko & Knops, 2018; Oram et
472 al., 2020). These results indicate that plant species may rapidly adapt/acclimate to global change
473 factors including flooding, drought, and nutrient enrichment. At many NutNet sites, leaf traits were
474 measured after 4 years of nutrient addition, possibly resulting in higher intraspecific trait shifts.
475 Although lacking a test, species replacement that takes longer to manifest may become more
476 important than intraspecific trait shifts in determining community traits in the longer term. A
477 previous NutNet study shows that leaf nutrients, but not SLA, of abundant species are consistent
478 indicators of increased soil nutrients (Firn et al., 2019). Extending that, our results suggest
479 community-level leaf P and leaf N were more responsive than leaf K, leaf C, and SLA to nutrient
480 addition.

481

482 *Diversity-mediated effects on facets of stability*

483 Plant traits have long been viewed as a common currency to link ecosystem processes, functions,
484 and stability (de Bello et al., 2021; Funk et al., 2017). Past studies have shown that FD and CWM
485 of LES and single leaf traits can be tightly linked to temporal invariability (Craven et al., 2018;

486 Schnabel et al., 2021; Suonan et al., 2023), resistance during and recovery after dry and wet climate
487 extremes (Bazzichetto et al., 2024; Oram et al., 2020). **For instance, using bivariate analysis, (Oram**
488 **et al., 2020) found that CWM, but not FD, of LES was strongly related to resistance during and**
489 **recovery from floods. (Mariotte et al., 2013) also found that subordinate plant species enhance**
490 **community resistance during a summer drought in a semi-natural grassland. However, (Bazzichetto**
491 **et al., 2024) found that FD of LES was positively related to drought resistance, but CWM of LES**
492 **was positively related to recovery after short-term droughts (aggregated over 3 months prior to**
493 **biomass harvest). Surprisingly, the commonly-assumed trade-off between CWM of LES (i.e. slow**
494 **and fast communities) on resistance and recovery was not supported in these studies as well as not**
495 **in ours (Bazzichetto et al., 2024; Craven et al., 2018; Oram et al., 2020).** We found that FD of LES
496 was better linked to stability than CWM of LES and species richness under nutrient addition (Fig.
497 4A), suggesting that compensatory dynamics among species may be more important than dominant
498 species in driving community stability at these sites. Interestingly, we found that nutrient addition
499 had opposing effects on resistance during dry and wet growing seasons through decreasing FD of
500 LES (Fig. 4A). That is, plant communities with higher functional diversity of LES exhibited higher
501 resistance (smaller biomass deviation) than those with less diverse LES during wet growing
502 seasons, likely attributed to compensatory dynamics. The opposite effects during dry growing
503 seasons may be because more diverse communities lost more biomass. As different traits respond
504 differently to climate extremes, they could mediate ecosystem functions and stability in different
505 ways (de Bello et al., 2021; Funk et al., 2017). Indeed, we found that results based on LES differed
506 from those based on single leaf traits in dominant pathways. Results also differ among single leaf
507 traits with leaf P and leaf N showing stronger links.

508
509 That said, the effects of nutrient addition on stability mediated by functional trait composition and
510 diversity were relatively weak. This may be due to the following reasons. First, although the LES is
511 a well-established concept and its potential connection to community stability is well described (de
512 Bello et al., 2021), the link between LES and biomass production is only suggestive. Indeed, from a
513 physiological perspective, plants could increase aboveground biomass by structural elements (e.g.
514 increasing the number of leaves, stems) instead of increasing SLA and leaf nutrients (Firn et al.,
515 2019). Second, we may miss some potentially important traits such as root size or metabolic traits
516 (Bazzichetto et al., 2024; Schnabel et al., 2021). Root traits are particularly important for plant
517 species to access soil water and nutrients. However, a greenhouse experiment found that the LES
518 can better predict biomass resistance during and recovery from flooding than the root economic
519 spectrum (Oram et al., 2020). So far, a lack of studies focusing on root and metabolic traits limits
520 our ability to draw any solid conclusions (Oram et al., 2020; Schnabel et al., 2021), and future work
521 resolving the role of such traits could offer new insights into the trait-stability framework. Third, we

522 did not measure traits for all species and those rarer species may strengthen or alter the results
523 found here (Sun et al., 2022) (Table S2). Fourth, we did not consider intraspecific trait shifts over
524 time, which can be a major source of community-level trait shifts (Wheeler et al., 2022), and further
525 impact the prediction of community-level traits on ecosystem stability. This temporal intraspecific
526 trait shift is ignored in many ecological studies using traits to predict ecosystem functions and
527 stability, likely because of the extreme effort required. Last but not least, as our study focused on
528 patterns across sites, we partially accounted for the heterogeneity of climate conditions at each site
529 using site-specific normal levels and extreme growing seasons. Considering environmental
530 dependence together with trait responses, and ecosystem functions, processes, and stability
531 simultaneously would improve our understanding of their links and underlying mechanisms.

532
533 *Comparison between analyses using trait values from different sources*
534 To our knowledge, no studies so far have compared the effects of community-level traits measured
535 in the field accounting for intraspecific trait variation with that extracted from global trait databases
536 often do not account for intraspecific trait variation on ecosystem stability. Increasing accumulation
537 of measured plant traits globally (e.g. TRY database) have greatly advanced the field of trait-based
538 studies (Kattge et al., 2020). Previous studies using trait values extracted from global trait databases
539 to explain ecosystem functions and stability often assume one species has one fixed trait value
540 (Bazzichetto et al., 2024; Craven et al., 2018; van der Plas et al., 2020). It is well acknowledged that
541 intraspecific trait shift is prevalent and play a significant role in shaping plant community response
542 to biotic and abiotic environmental perturbations (Chen et al., 2021; de Bello et al., 2021; Funk et
543 al., 2017; Mitchell & Bakker, 2014; Siefert et al., 2015). Using traits extracted from global
544 databases, we found that species-level leaf N, and to a lesser extent SLA, were more tightly linked
545 to facets of stability than the LES that included LDMC but was based on species- and genus-level
546 trait values. Thus, using species-level traits may be essential to link to ecosystem stability.
547 However, major pathways in which nutrient addition impacted community-level traits and stability
548 differed from those based on traits measured in the field (e.g. leaf N). While traits extracted from
549 global databases allow for broader comparisons and generalizations across different ecosystems and
550 regions, they may not accurately represent plant traits measured on-site. Our results suggest that
551 caution should be taken in interpreting results based on traits extracted from global databases for
552 ecosystem functions and stability because they may fail to capture important ecological processes
553 induced by intraspecific trait shifts.

554
555 *Stability facets and the influencing pathways*
556 Our results showed that nutrient addition could impact different facets of stability through different
557 pathways. This is consistent with a previous study showing that these facets of stability are overall

558 weakly correlated under control and nutrient addition treatments (Chen et al., 2023). Nutrient
559 addition may impact resistance more than recovery and temporal invariability through diversity-
560 mediated indirect effects. Past studies often investigate temporal invariability through mean and
561 standard deviation (Hautier et al., 2015; Suonan et al., 2023). It is also well-established that global
562 changes such as nutrient enrichment can impact community stability through changing species
563 asynchrony (i.e. increase in biomass of some species being compensated by decrease in others)
564 and/or population stability (Loreau & de Mazancourt, 2013). Here we disentangle the drivers
565 underlying long-term temporal stability (i.e. temporal invariability) into two processes, resistance
566 during and recovery after short-term extreme perturbations. In doing so, we linked plant
567 communities' short-term responses to long-term ones, which were often studied separately in
568 previous studies (Donohue et al., 2013; Kéfi et al., 2019). Our results suggest that management
569 strategies aiming at increasing resistance may be more important than those increasing recovery for
570 maintaining temporal invariability of grassland aboveground biomass production.

571

572 **Conclusion**

573 Our study filled an important knowledge gap by exploring the role of multifaceted plant diversity in
574 predicting multidimensional ecosystem stability under nutrient addition. Our results suggested that
575 intraspecific trait shift was a major driver for change in functional trait composition under nutrient
576 addition, which may further impact ecosystem stability. But the diversity of functional traits was
577 more important than functional trait composition in linking to ecosystem functioning and stability.
578 Such diversity-mediated indirect effects, though weak, should be taken into account together with
579 the direct effects of nutrient addition for more accurate predictions for ecosystem stability under
580 global changes.

581

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606 Visualization: QC

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611

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615 **manuscript is accepted.**

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