

1 **Multiple facets of biodiversity drive the diversity-stability relationship**

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122 **Abstract**

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124 A significant body of evidence has demonstrated that biodiversity stabilizes ecosystem
125 functioning over time in grassland ecosystems. However, the relative importance of different
126 facets of biodiversity underlying the diversity-stability relationship remains unclear. Here we
127 used data from 39 biodiversity experiments and structural equation modeling to investigate
128 the roles of species richness, phylogenetic diversity, and both the diversity and community-
129 weighted mean of functional traits representing the ‘fast-slow’ leaf economics spectrum in
130 driving the diversity-stability relationship. We found that high species richness and
131 phylogenetic diversity stabilize biomass production via enhanced asynchrony. Contrary to
132 our hypothesis, low phylogenetic diversity also enhances ecosystem stability directly, albeit
133 weakly. While the diversity of fast-slow functional traits has a weak effect on ecosystem
134 stability, communities dominated by slow species enhance ecosystem stability by increasing
135 mean biomass production relative to the standard deviation of biomass over time. Our results
136 demonstrate that biodiversity influences ecosystem stability via a variety of facets, thus
137 highlighting a more multicausal relationship than has been previously acknowledged.

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156 **Introduction**

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158 The relationship between the biodiversity and the stability of ecosystems has long been a
159 fundamental subject of ecological research^{1,2,3,4}. More recently, this research topic has gained
160 new impetus due to concerns about the consequences of global environmental change and
161 biodiversity loss, both of which threaten the stability of ecosystem functions and the
162 ecosystem services they underpin^{5,6,7,8}. Much of this work has examined the relationship
163 between plant species diversity and biomass production, and both theoretical and empirical
164 has consistently demonstrated that the productivity of species-rich communities shows lower
165 variation over time than that of less diverse communities^{9,10,11,12,13,14,15,16}.

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167 Temporal stability (or invariability) of ecosystem functioning is an integrative measure of the
168 responses of populations and communities to each other and to environmental variation¹⁷. In
169 the case of biomass production, temporal stability is typically defined as mean biomass
170 divided by its temporal standard deviation (μ/σ)¹⁸. Thus, the higher stability of species-rich
171 ecosystems can be attributed to several properties including their greater biomass, higher
172 resistance (i.e., biomass shows little deviation from average levels during perturbations)
173 and/or resilience (i.e., biomass returns to average levels rapidly after perturbations)^{3,19,20}.

174 Furthermore, numerous statistical mechanisms have been proposed as drivers of stability and
175 tested empirically^{10,11,12}. Of these, perhaps the primary mechanism through which diversity
176 stabilizes biomass production is species asynchrony^{10,12,21,22}, which describes the extent to
177 which species-level productivity is correlated within a community over time. Asynchrony,
178 where decreases in the productivity of some species are compensated by increases in the
179 productivity of other species, can promote ecosystem stability to increase as a consequence of
180 interspecific interactions^{12,23}, negative frequency dependence, e.g. due to pathogen

181 outbreaks^{24,25}, and/or the greater likelihood that diverse communities contain a wider range of
182 species' responses to environmental conditions^{10,26}. Accordingly, it is likely that multiple and
183 correlated facets of biodiversity²⁷ underpin species asynchrony, including taxonomic
184 diversity²⁸, functional diversity^{29,30} and phylogenetic diversity³¹, which collectively may
185 influence ecosystem stability^{32,33,34}. We hypothesize that the relationship between
186 biodiversity and ecosystem stability is mediated by four classes of biological drivers and that
187 these operate both directly, e.g. by affecting biomass production, and indirectly, via species
188 asynchrony.

189

190 The first class of biological drivers is functional composition, which may play a key role in
191 stabilizing biomass production in grasslands because growth-related traits strongly influence
192 the production, persistence, and stability of plant biomass³⁵. While plants differ greatly in
193 their trait values and strategies, a large proportion of global plant trait variation is correlated
194 along a single leaf economics axis that distinguishes between exploitative species that are
195 capable of rapid resource uptake, growth, and tissue turnover (hereafter 'fast' species) and
196 conservative species with slower rates of growth, resource uptake, and tissue turnover
197 (hereafter 'slow' species)^{36,37}. The former typically possess high specific leaf area (SLA), low
198 leaf dry matter content (LDMC), and high leaf nitrogen concentrations (N), the latter the
199 opposite^{37,38,39}. There is growing evidence that variation in functional composition along this
200 'fast-slow' leaf economics spectrum influences ecosystem stability. For example,
201 communities dominated by species with high LDMC values have been found to increase
202 ecosystem stability in experimental and semi-natural grassland communities⁴⁰. If functional
203 composition were a key driver of ecosystem stability, we may therefore expect that
204 communities dominated by species with slow leaf economics ('slow communities') will be
205 more stable than those dominated by species with fast leaf economics ('fast communities')⁴¹.

206 However, the net effect of functional composition on ecosystem stability across multiple
207 communities may be low because the opposing effects of fast communities, which should be
208 more resilient, and slow communities, which should be more resistant, may cancel each other
209 out.

210

211 Variation in fast-slow plant ecological strategies within a community, which can be
212 quantified using functional diversity metrics, is the second class of biological drivers that
213 may explain ecosystem stability. As fast species are likely to recover rapidly following
214 disturbance (resilience), and slow species will be better able to tolerate environmental
215 stresses and perturbations (resistance)^{37,38}, we hypothesize that functionally diverse
216 communities will exhibit both resistance and resilience, thus increasing ecosystem stability.

217

218 The third class of biological drivers that we propose as underlying the diversity-stability
219 relationship are those associated with phylogenetic diversity. Generally, phylogenetic
220 diversity can be seen as representing the diversity of phylogenetically conserved functional
221 traits, but may represent a broader set of traits than is typically included in functional
222 diversity measures. Traits that reflect a shared co-evolutionary history of biotic interactions
223 often show a high degree of phylogenetic conservatism⁴², such as symbiotic N₂ fixation and
224 mycorrhizal tendency^{32,43}. Closely related species are also known to share pathogens or
225 immune responses via their shared co-evolutionary history^{44,45}. Importantly, phylogenetic
226 diversity has been shown to have a positive effect on ecosystem stability in grasslands in
227 most analyses^{31,32,34}, but not all²⁸. We therefore hypothesize that greater phylogenetic
228 diversity will stabilize biomass production over time by increasing (measured and
229 unmeasured) trait diversity and by diluting the effects of pathogen outbreaks and herbivore
230 attacks, which are strong regulators of biomass production in grasslands⁴⁵.

231

232 Finally, plant species richness may affect ecosystem stability via pathways that are trait-based
233 but not associated with the leaf economics spectrum and not phylogenetically conserved. This
234 class of mechanism may include the effects of persistent seedbanks⁴⁶, regrowth from
235 belowground storage organs⁴⁷, carbohydrate reserves⁴⁸, variation in rooting depth⁴⁹, and
236 phenology⁵⁰. Plant species richness can also affect ecosystem stability by modifying
237 environmental conditions. For example, the higher productivity of species-rich communities
238 is associated with more rapid rates of soil organic matter accumulation^{51,52,53} and soil
239 aggregate formation⁵⁴, which result in a more aerobic, mesic soil environment in which plant
240 growth is more constant. We expect that these effects will indirectly enhance ecosystem
241 stability via increased asynchrony¹⁰ and directly via greater mean biomass production over
242 time^{28,55}.

243

244 While there is empirical evidence that each of the aforementioned biological drivers
245 contributes to the overall relationship between diversity and stability, they likely operate
246 concurrently and their relative importance has not been investigated. Here, we made the first
247 general assessment of the contribution of different facets of biodiversity in driving
248 biodiversity-stability relationships by performing a meta-level analysis using data from 39
249 grassland biodiversity-ecosystem function experiments distributed across North America and
250 Europe. Direct and indirect effects of the biological drivers were assessed using structural
251 equation models (SEM), which represented the relationships described above (Fig. S1 & S2),
252 and which controls for covariation among the different facets of biodiversity^{28,34}. We
253 hypothesized that: *i*) greater plant species richness, diversity in leaf traits that capture the fast-
254 slow leaf economics spectrum, and phylogenetic diversity will increase ecosystem stability
255 by increasing asynchrony and *ii*) species-rich communities with high functional and

256 phylogenetic diversity, and those dominated by species with slow leaf economics, will
257 increase ecosystem stability directly as they increase the temporal mean of biomass
258 production, a component of stability, via classical diversity-function mechanisms, e.g.
259 complementarity and selection effects^{23,56}.

260

261 **Results**

262 Our analysis shows that the bivariate relationships between stability, asynchrony and several
263 biodiversity facets: species richness, phylogenetic diversity (calculated as mean nearest taxon
264 distance, MNTD, see Methods), fast-slow functional diversity (calculated using traits
265 associated with the fast-slow leaf economics spectrum) are positive and significant and
266 generally consistent across experiments (Figs. 1 and 2). These drivers explained low amounts
267 of variation in ecosystem stability (Table S1, marginal R^2), with a larger proportion being
268 explained by the random effects (Tables S1 and S2, conditional R^2). In contrast, although
269 fast-slow functional diversity enhanced ecosystem stability, there was no consistent effect of
270 the community-weighted mean of fast-slow traits on ecosystem stability ($P > 0.10$; Fig. 2c).
271 However, there was evidence that communities dominated by slow species stabilized
272 productivity at certain experimental sites (Fig. 2c), while fast species stabilized production at
273 other sites, as the effect of the community-weighted mean of fast-slow traits was highly
274 variable across all experimental sites (Table S2).

275

276 These relationships were investigated in more depth with our structural equation model,
277 which provides evidence that asynchrony is a key mechanism mediating the biodiversity-
278 stability relationship and that asynchrony is driven by multiple facets of biodiversity (Fig. 3).
279 Overall, the data fit our model well (Fisher's $C = 9.25$, $df = 12$, $P = 0.68$; $K = 34$, $n = 1,699$).
280 Fixed effects explained 19% of variation in ecosystem stability (marginal R^2), which

281 increased to 58% (conditional R^2) when accounting for fixed and random effects. In total,
282 species richness, phylogenetic diversity, and fast-slow functional diversity explained 52% of
283 variation in species asynchrony (marginal R^2), which increased to 79% when random effects
284 were accounted for (conditional R^2).

285

286 The strongest pathway of influence on ecosystem stability was from plant species richness
287 via species asynchrony (standardized indirect effect = 0.21). This effect was larger and more
288 consistent across experimental sites than the direct effect of species richness (standardized
289 path coefficient of direct effect = 0.03, $P = 0.61$), thus suggesting that much of the effect of
290 plant species richness on ecosystem stability is explained by species asynchrony.

291 Phylogenetic diversity also had strong yet opposing effects on ecosystem stability in that it
292 indirectly increased ecosystem stability via asynchrony (standardized path coefficient of
293 indirect effect = 0.12). Conversely, the direct pathway between phylogenetic diversity and
294 ecosystem stability was negative (standardized path coefficient of direct effect = - 0.10; $P <$
295 0.001). This negative effect was weaker than the positive indirect effect via species
296 asynchrony, thus explaining the overall positive relationship between phylogenetic diversity
297 and ecosystem stability, along with covariance with species richness (Fig. 2a).

298

299 The community-weighted mean of fast-slow traits had a direct negative effect on ecosystem
300 stability, meaning that communities dominated by slow species were more stable than those
301 dominated by fast species (Fig. 3). Contrary to our expectations, the SEM revealed that fast-
302 slow functional diversity did not directly or indirectly (via asynchrony) stabilize ecosystem
303 productivity ($P > 0.05$). These weak effects of fast-slow functional diversity on ecosystem
304 stability were also generally robust to the use of an alternative measure of fast-slow
305 functional diversity, functional richness (Fig. S3). Finally, we also looked at potentially

306 important effects of climate and found that neither the mean nor inter-annual variation in
307 precipitation significantly affected asynchrony or ecosystem stability.
308
309 Further analyses provided added insight into mechanisms underlying the biodiversity-
310 stability relationship. By including the two components of stability in a separate SEM, i.e.,
311 mean and standard deviation of biomass production, we found that species richness,
312 phylogenetic diversity, and the community-weighted mean of fast-slow traits stabilized mean
313 aboveground biomass production while also affecting asynchrony (Fig. 4; Fisher's $C = 24.52$,
314 $df = 22$, $P = 0.32$; $K = 49$, $n = 1,699$). Species richness promoted ecosystem stability by
315 increasing mean aboveground biomass production, while the direct effect of phylogenetic
316 diversity on ecosystem stability operated via effects on the standard deviation of biomass.
317 Furthermore, these analyses revealed that the weak negative effect of the community-
318 weighted mean of fast-slow traits on ecosystem stability masked contrasting effects on the
319 components of ecosystem stability; communities dominated by species with fast trait values
320 decreased mean biomass (standardized path coefficient of direct effect = -0.12) to a greater
321 extent than they decreased standard deviation of biomass (standardized path coefficient of
322 direct effect = -0.07). Asynchrony increased ecosystem stability via effects on the standard
323 deviation of biomass. Finally, inter-annual variation in precipitation destabilized biomass
324 production by increasing the standard deviation of biomass. These relationships were
325 generally robust to the use of different combinations of phylogenetic and functional diversity
326 indices (Fig. S4).
327
328 In an analysis that only included longer studies (six studies >4 years, $n = 454$ plots) certain
329 paths became stronger, with notable increases in the effects of fast-slow functional diversity
330 (Fig. S5). In long-term studies, fast-slow functional diversity had both a direct positive effect

331 on ecosystem stability and a negative effect operating on asynchrony (Fig. S5a). The strength
332 of the effects of the community-weighted mean of fast-slow traits on ecosystem stability also
333 increased, with fast communities having a direct negative effect on ecosystem stability (Fig
334 S5a). Furthermore, trait identity affected path strength and direction (Figs. S6 - 9). Of the
335 four individual traits making up the fast-slow leaf economics spectrum, we saw positive
336 direct effects of leaf P on ecosystem stability and negative effects of leaf N on ecosystem
337 stability, while the effect of LDMC and SLA on ecosystem stability were not statistically
338 significant.

339

340 **Discussion**

341 The results support our overall hypothesis that multiple facets of biodiversity mediate the
342 diversity-stability relationship, principally via their effects on species asynchrony. However,
343 the relative importance of certain biological drivers, e.g. community-weighted mean of fast-
344 slow leaf traits, varied substantially across studies.

345

346 The strongest and most consistent driver of stability across the 39 experiments examined in
347 our study was that of species richness, operating via species asynchrony. This likely reflects
348 niche differences among species that affect their relative performance over time in a
349 temporally variable environment^{21,57,58,59}. However, these niche differences were not captured
350 by the functional diversity of fast-slow leaf traits or phylogenetic diversity. Instead, the
351 species richness-asynchrony-stability relationship points to traits that stabilize productivity.
352 Such traits may include different rooting strategies, photosynthetic pathways, non-structural
353 carbohydrate concentrations, and traits related to phenology, demographic storage and
354 regeneration^{47,48,50,60,61,62}. Data for some of these traits is relatively sparse⁶³ and the collection

355 of such information should be a priority in addressing the current question and those related
356 to the components of ecosystem stability, i.e. resistance and resilience⁶⁴.

357

358 Species richness also affected ecosystem stability directly. We found that species richness
359 stabilizes biomass production via its stronger effects on mean biomass production over time
360 than effects operating via the standard deviation, which is in line with previous studies^{12,28}.

361 One possible explanation for this direct effect of species richness is the greater accumulation
362 of soil organic matter and nutrient stocks and heightened mineralization in diverse
363 communities over time^{51,52,53,55,65}. These effects may be further enhanced by positive effects
364 of plant species diversity on the abundance and diversity of soil biota that improve the
365 physical structure of soils^{54,66,67,68}. Further, root biomass – which also increases with species
366 richness^{51,69,70} – has been found to stabilize ecosystem productivity⁹ by enhancing water
367 uptake, nutrient foraging and storage, and carbohydrate reserves.

368

369 The next most important driver of diversity-stability relationships was phylogenetic diversity.
370 Interestingly, phylogenetic diversity influences ecosystem stability via two different
371 pathways, one positive and operating indirectly via species asynchrony, and one negative and
372 operating directly. The indirect asynchrony pathway was the stronger of the two, resulting in
373 a positive overall effect and is likely due to a range of phylogenetically conserved traits.

374 These conserved traits may limit susceptibility to pathogen and herbivore outbreaks to just a
375 few species in more phylogenetically diverse communities such that only a small proportion
376 of community biomass is affected. The weaker direct negative effect operated via standard
377 deviation in biomass. This path may reflect experimental communities that are dominated by
378 more inherently stable and phylogenetically clustered plant functional groups, such as
379 grasses^{71,72}. Furthermore, our analysis illustrates that the effects of phylogenetic diversity on

380 ecosystem stability are sensitive to the phylogenetic diversity metric used³⁴. Consistent with
381 Venail, Gross²⁸, but in contrast with those presented in Figs. 3 and 4, SEMs using mean
382 pairwise distance (MPD) showed weak direct and indirect effects of phylogenetic diversity on
383 ecosystem stability, probably due to its strong, positive correlation with plant species richness
384 (Figs. S3 & S4, Appendix 1). We also suggest that the stronger effects of MNTD reflect the
385 fact that it better represents recently evolved differences among species⁷³ and, more
386 specifically, recently evolved differentiation in the traits that confer tolerance to specialized
387 pathogens or herbivores, which play a major role in driving grassland productivity^{24,74}.
388
389 Evidence for the fast-slow leaf economics spectrum affecting ecosystem stability as an
390 overall strategy (community-weighted mean) was weak across the full dataset. However, this
391 relationship masked effects of fast traits that reduced both mean aboveground biomass
392 production and its standard deviation, resulting in communities dominated by species with
393 fast trait values that were marginally less stable than those dominated by species with slow
394 trait values. Furthermore, individual site-level relationships between the community-weighted
395 mean of fast-slow traits and ecosystem stability were often very strong, but extremely
396 variable across sites. These findings suggest that the relationship between the fast-slow leaf
397 economics spectrum and ecosystem stability is heavily dependent upon site specific factors,
398 which could include the study duration, environmental conditions, and the ‘matching’ of
399 appropriate functional strategies to a site. For example, fast traits may confer ecosystem
400 stability at sites subject to repeated disturbances due to their ability to allow fast recovery,
401 while slow traits may confer ecosystem stability in the face of chronic environmental stresses,
402 such as low nutrient availability or aridity, e.g. the dry grasslands of the experimental sites in
403 Texas included in our study^{75,76}. Site-level information detailing disturbance regimes and the
404 constancy of soil water availability and nutrient supply at a finer temporal resolution may

405 clarify in which environmental conditions particular plant strategies stabilize (or destabilize)
406 biomass production⁷⁷.

407

408 The effect of fast-slow functional diversity and the community-weighted mean of fast-slow
409 traits became markedly stronger when only long-term studies were considered. We
410 hypothesize that this is due to the strengthening of biodiversity effects on mean community
411 biomass production over time⁷⁸. Furthermore, the hypothesized effects of fast and slow traits
412 on resilience and resistance have a greater chance of detection because extreme events, e.g.
413 drought, are more likely to occur in long-term studies²⁰. However, such patterns may also be
414 driven by ecological differences in the sites where long and short-term studies were
415 conducted, as long-term sites tended to include more communities dominated by slow species
416 (Fig. S10).

417

418 The final driver of ecosystem stability in our models was climate. Inter-annual variation in
419 precipitation – but not mean annual precipitation – destabilized biomass production by
420 increasing the standard deviation of biomass production. This is likely to represent the strong
421 annual variation in the timing and intensity of aboveground biomass production in such
422 environments, e.g. inter-annual variation in the timing and intensity of seasonal rains, and
423 provides evidence that inter-annual variation in climate may be a key driver of ecosystem
424 stability⁷⁷. As mentioned above, a better characterization of site conditions may provide a
425 more complete understanding of the drivers of ecosystem stability⁴. Furthermore, initial
426 investigations indicate a powerful interactive role between environmental conditions and
427 biotic community properties^{79,80}, as abiotic and management factors not only control diversity
428 and productivity but also influence the capacity for diversity to stabilize ecosystem function
429 by altering diversity-enhancing mechanisms such as asynchrony and resource-use

430 complementarity^{22,81}. This means that under natural conditions changes in diversity are not
431 the ultimate cause of ecosystem stability, but are an intermediate property of ecosystem
432 response to global change drivers that might also influence ecosystem stability via other
433 pathways. A greater understanding of these interactions and how they operate in natural
434 ecosystems is required to improve both our fundamental understanding of ecosystem stability
435 and to integrate knowledge of diversity-stability relationship into agroecosystem
436 management⁸². With respect to this, our results indicate that certain facets of diversity (e.g.
437 phylogenetic diversity) would play a greater role than others (e.g. fast-slow functional
438 diversity) in promoting the stability of fodder production. However, the effect of such
439 management on the delivery and stability of other services (e.g. carbon storage) would also
440 need to be considered⁶. Threshold-based measures of stability¹⁷ may also be more relevant to
441 such applications than the variability measures employed here, as a threshold-based view of
442 ecosystem stability allows under- and overproduction to be considered differently.

443

444 In conclusion, our study is the first to make a general multi-site assessment of how multiple
445 facets of biodiversity, e.g. taxonomic, functional, and phylogenetic diversity, drive diversity-
446 stability relationships. Doing this identified that there are several important pathways,
447 including those related to phylogenetic diversity and the fast-slow leaf economics spectrum,
448 through which plant community properties affect the stability of grassland biomass
449 productivity. In an era of increased climatic variability^{83,84} and biodiversity change, it is
450 important to gain a deeper understanding of each of these component processes so that the
451 functional benefits of biodiversity may be effectively conserved and promoted.

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453

454

455 **Methods**

456 **Data preparation**

457 We assembled a database by combining data from biodiversity experiments that manipulated
458 plant species richness in grasslands and measured community- and species-level aboveground
459 plant biomass for at least three years. In total, we used data from 39 studies across North
460 America and Europe (Table S3) from Isbell, Craven²⁰ and Craven, Isbell⁸¹. Our dataset
461 comprises observations from 1,699 plots and 165 plant species, which were standardized
462 using the Taxonomic Name Resolution Service (<http://trns.iplantcollaborative.org>)⁸⁵.

463

464 For each plot within the experiments, we quantified ecosystem stability as the inverse of the
465 coefficient of variation of aboveground plant biomass (μ/σ)¹⁸, which is the ratio of the mean
466 to the standard deviation of aboveground plant biomass over time. Following Gross,
467 Cardinale¹², species synchrony (η) was quantified as the average correlation across species
468 between the biomass of each species and the total biomass of all other species in a plot:

469
$$\eta = (1/n) \sum_i \text{corr} (Y_i, \sum_{j \neq i} Y_j) , \quad (\text{Eq.1})$$

470 where Y_i is the biomass of species i in a plot containing n species. Because asynchrony
471 implies negative synchrony, we multiplied η by -1. Thus, species asynchrony ($-\eta$) ranges
472 from -1, where species' aboveground plant biomass is maximally synchronous, to 1, where
473 species' aboveground plant biomass is maximally asynchronous. Further, $-\eta$ is independent of
474 the number of species and their individual variances¹², which contrasts with species
475 asynchrony as calculated by Loreau and de Mazancourt⁸⁶.

476

477 We selected four leaf traits associated with the fast-slow leaf economics spectrum³⁶, specific
478 leaf area (SLA; $\text{mm}^2 \text{mg}^{-1}$), leaf dry matter content (LDMC; g g^{-1}), foliar N (%), and foliar P
479 (%). These data were obtained from the TRY database⁸⁷ (Appendix 2) and additional studies

480 in our database that measured traits^{88,89,90,91}. Trait values were converted to consistent units
481 and outliers were excluded (z -score > 4). Values were then averaged by trait data contributor
482 and then by species. Genus-level means were used when species-level data were not
483 available; species-level data for SLA, LDMC, leaf N, and leaf P were available for 98%, 83
484 %, 92 %, and 62 % of species, respectively. Combining species- and genus-level values, our
485 final trait data set included SLA, LDMC, and foliar N values for more than 96% of the
486 species and leaf P values for 93% of the species.

487

488 **Fast-slow functional composition and diversity**

489 We used the first axis of a principal component analysis (PCA) of community-weighted
490 means of SLA, LDMC, leaf N, and leaf P to represent the fast-slow leaf economics spectrum
491 (hereafter ‘community-weighted mean (CWM) of fast-slow traits’)³⁷. PCA was performed
492 using the *PCA* function in ‘FactoMineR’⁹². The first PCA captured 60.4% of variation among
493 the four traits (Fig. S11) and represents the fast-slow leaf economics spectrum of
494 communities, from those dominated by slow species with low SLA and leaf N and P and high
495 LDMC to those dominated by fast species with high SLA and leaf N and P and low LDMC.

496

497 We calculated functional diversity in traits associated with the fast-slow leaf economics
498 spectrum (hereafter ‘fast-slow functional diversity’) as either abundance-weighted functional
499 dispersion or functional richness to represent complementarity among co-occurring species
500 and volume of trait space, respectively, using the ‘FD’ package⁹³. Results for both measures
501 of fast-slow functional diversity were qualitatively similar. Therefore, we present results for
502 functional dispersion in the main text and for functional richness in Supplementary Materials.
503 Functional composition and functional diversity were calculated annually for each plot and
504 then averaged across years.

505 **Phylogenetic diversity**

506 We used the molecular phylogeny from Zanne, Tank⁹⁴ as a backbone to build a phylogeny of
507 all species within the experiments, conservatively binding species into the backbone using
508 dating information from congeners in the tree (using *congeneric.merge*)⁹⁵. We then calculated
509 abundance-weighted phylogenetic diversity as mean nearest taxon distance (MNTD)⁹⁶ and
510 mean pairwise distance (MPD) annually for each plot and then calculated the average across
511 years. MNTD has captured competitive differences among species in previous studies⁹⁷ and
512 the sharing of specialized pathogens tends to be confined to closely related species^{44,45}.
513 MNTD, therefore, is a good metric to test our hypotheses about the mechanisms that explain
514 variation in species asynchrony and ecosystem stability. Furthermore, there was a strong,
515 positive correlation between MPD and plant species richness ($r = 0.86$; Appendix 1). We
516 therefore present results for MNTD in the main text and for MPD in Supplementary
517 Materials.

518

519 **Climate**

520 As empirical and theoretical studies have shown strong impacts of mean and inter-annual
521 variation in precipitation on ecosystem stability and species asynchrony in grasslands^{10,77}, we
522 included site-level climate data to explain across-site variation in ecosystem stability. To
523 describe environmental conditions during each study in a consistent manner across sites, we
524 calculated mean annual precipitation (MAP) and inter-annual variation in precipitation
525 (coefficient of variation of MAP) using data from CRU TS 3.2.3 (Table S3)⁹⁸.

526

527 **Data analysis**

528 To explore bivariate relationships between each of our hypothesized drivers and ecosystem
529 stability, we fit separate linear mixed-effects models (independently of SEMs) that tested for

530 the effects of plant species richness, phylogenetic diversity, fast-slow functional diversity,
531 community-weighted mean of fast-slow traits, and species asynchrony on ecosystem stability.
532 Multiple random effect structures were tested for each model, first using a basic structure
533 defined by the experimental design of all studies where study was treated as a random
534 intercept and species richness as a random slope. We also tested for interactions of predictor
535 variables with plant species richness and included them as random slopes when supported by
536 model selection. We used AICc to select the most parsimonious random effects structure.
537 AICc is a second-order bias correction to Akaike's information criterion for small sample
538 sizes⁹⁹. Models were fit using the 'nlme' package and model assumptions were checked by
539 visually inspecting residual plots for homogeneity and quantile-quantile plots for normality.
540 Intra-class correlation (ICC) was calculated to compare variability within a study to
541 variability across studies.

542

543 To test the relative importance of the different mechanisms represented by the community-
544 weighted mean of fast-slow traits, fast-slow functional diversity, phylogenetic diversity,
545 climate, and asynchrony in driving temporal stability, we fit piecewise structural equation
546 models (SEM)¹⁰⁰ using 'piecewiseSEM'. Testing for relationships with resistance and
547 resilience (as in Isbell, Craven²⁰) was not possible because of the unequal distribution of
548 extreme climate events across sites, which prevented fitting a general SEM. We formulated a
549 hypothetical causal model (Fig. S1) based on *a priori* knowledge of grassland ecosystems and
550 used this to test the fit of the model to the data. We also included direct paths from species
551 richness, fast-slow functional diversity, and phylogenetic diversity to ecosystem stability to
552 represent biological drivers that influence ecosystem stability, e.g. via complementarity
553 effects on the temporal mean of biomass production^{23,56}. Finally, we included direct paths
554 from mean and inter-annual variation in precipitation to ecosystem stability. We included

555 direct paths from species richness to fast-slow functional diversity and phylogenetic diversity
556 because variation in these variables can be directly attributed to the experimental
557 manipulation of species richness in all studies³².

558

559 All initial models contained partial bivariate correlations between fast-slow functional
560 diversity and phylogenetic diversity³⁴. Additional partial bivariate correlations were added to
561 the initial model if they significantly improved model fit using modification indices ($P <$
562 0.05). To test the sensitivity of our model to functional and phylogenetic indices, the duration
563 of the time series, and the choice of traits, we fit additional models for each combination of
564 functional and phylogenetic diversity indices, using only data from long-term experiments
565 (>4 years), and for each functional trait separately. Finally, we fit another SEM to see if
566 stabilizing effects on biomass production operated via the two components of ecosystem
567 stability, mean and standard deviation of biomass production (Fig. S2). In this model, we
568 added direct paths from species richness, phylogenetic diversity, fast-slow functional
569 diversity, and species asynchrony to the mean and standard deviation of biomass and from
570 mean precipitation to mean biomass and from inter-annual variation in precipitation to
571 standard deviation of biomass production. Model fit was assessed using Fisher's C statistic (P
572 > 0.10). SEMs were fit using linear mixed-effects models where study was treated as a
573 random factor and species richness as a random slope. Random effect structures allowed the
574 intercepts and slopes to vary among studies. In all analyses, plant species richness and
575 ecosystem stability were \log_2 transformed to meet normality assumptions. Model
576 assumptions of normality were inspected visually. As many of the variables included in our
577 SEM were correlated (see Appendix 1), we estimated variance inflation. This demonstrated
578 that multi-collinearity did not affect parameter estimates ($VIF < 3$). All analyses were
579 performed using R 3.3.1¹⁰¹.

580 **References**

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629

1. May RM. *Stability and complexity in model ecosystems*. Princeton University Press (1973).
2. McNaughton SJ. Stability and diversity of ecological communities. *Nature* **274**, 251-253 (1978).
3. Tilman D, Downing JA. Biodiversity and stability in grasslands. *Nature* **367**, 363-365 (1994).
4. Ives AR, Carpenter SR. Stability and diversity of ecosystems. *Science* **317**, 58-62 (2007).
5. Balvanera P, *et al.* Quantifying the evidence for biodiversity effects on ecosystem functioning and services. *Ecology Letters* **9**, 1146 - 1156 (2006).
6. Donohue I, *et al.* Navigating the complexity of ecological stability. *Ecology Letters*, (2016).
7. Hautier Y, Tilman D, Isbell F, Seabloom EW, Borer ET, Reich PB. Anthropogenic environmental changes affect ecosystem stability via biodiversity. *Science* **348**, 336-340 (2015).
8. Isbell F, Tilman D, Polasky S, Loreau M. The biodiversity-dependent ecosystem service debt. *Ecology Letters* **18**, 119-134 (2015).
9. Tilman D, Reich PB, Knops JMH. Biodiversity and ecosystem stability in a decade-long grassland experiment. *Nature* **441**, 629 - 632 (2006).
10. de Mazancourt C, *et al.* Predicting ecosystem stability from community composition and biodiversity *Ecology Letters* **16**, 617 - 625 (2013).
11. Hector A, *et al.* General stabilizing effects of plant diversity on grassland productivity through population asynchrony andoveryielding. *Ecology* **91**, 2213 - 2220 (2010).
12. Gross K, *et al.* Species richness and the temporal stability of biomass production: a new analysis of recent biodiversity experiments. *The American Naturalist* **183**, 1 - 12 (2014).
13. Jiang L, Pu Z. Different effects of species diversity on temporal stability in single-trophic and multitrophic communities. *The American Naturalist* **174**, 651-659 (2009).
14. Campbell V, Murphy G, Romanuk TN. Experimental design and the outcome and interpretation of diversity–stability relations. *Oikos* **120**, 399-408 (2011).
15. del Río M, *et al.* Species interactions increase the temporal stability of community productivity in *Pinus sylvestris*–*Fagus sylvatica* mixtures across Europe. *Journal of Ecology* **105**, 1032-1043 (2017).

- 630 16. Aussenac R, Bergeron Y, Ghotsa Mekontchou C, Gravel D, Pilch K, Drobyshev I.
631 Intraspecific variability in growth response to environmental fluctuations modulates
632 the stabilizing effect of species diversity on forest growth. *Journal of Ecology* **105**,
633 1010-1020 (2017).
634
- 635 17. Oliver TH, *et al.* Biodiversity and resilience of ecosystem functions. *Trends in*
636 *Ecology & Evolution* **30**, 673-684 (2015).
637
- 638 18. Tilman D. The ecological consequences of changes in biodiversity: a search for
639 general principles. *Ecology* **80**, 1455 - 1474 (1999).
640
- 641 19. van Ruijven J, Berendse F. Diversity enhances community recovery, but not
642 resistance, after drought. *Journal of Ecology* **98**, 81 - 86 (2010).
643
- 644 20. Isbell F, *et al.* Biodiversity increases the resistance of ecosystem productivity to
645 climate extremes. *Nature* **526**, 574 - 577 (2015).
646
- 647 21. Yachi S, Loreau M. Biodiversity and ecosystem productivity in a fluctuating
648 environment: The insurance hypothesis. *PNAS* **96**, 1463 - 1468 (1999).
649
- 650 22. Hautier Y, *et al.* Eutrophication weakens stabilizing effects of diversity in natural
651 grasslands. *Nature* **508**, 521 - 525 (2014).
652
- 653 23. Lehman Clarence L, Tilman D. Biodiversity, stability, and productivity in competitive
654 communities. *The American Naturalist* **156**, 534-552 (2000).
655
- 656 24. Maron JL, Marler M, Klironomos JN, Cleveland CC. Soil fungal pathogens and the
657 relationship between plant diversity and productivity. *Ecology Letters* **14**, 36 - 41
658 (2011).
659
- 660 25. Schnitzer SA, *et al.* Soil microbes drive the classic plant diversity-productivity
661 pattern. *Ecology* **92**, 296 - 303 (2011).
662
- 663 26. Tredennick AT, de Mazancourt C, Loreau M, Adler PB. Environmental responses, not
664 species interactions, determine synchrony of dominant species in semiarid grasslands.
665 *Ecology* **98**, 971-981 (2017).
666
- 667 27. Naeem S, *et al.* Biodiversity as a multidimensional construct: a review, framework
668 and case study of herbivory's impact on plant biodiversity. *Proc R Soc B* **283**,
669 20153005 (2016).
670
- 671 28. Venail P, *et al.* Species richness, but not phylogenetic diversity, influences
672 community biomass production and temporal stability in a re-examination of 16
673 grassland biodiversity studies. *Functional Ecology* **29**, 615-626 (2015).
674
- 675 29. Roscher C, *et al.* Identifying population- and community-level mechanisms of
676 diversity-stability relationships in experimental grasslands. *Journal of Ecology* **99**,
677 1460 - 1469 (2011).
678

- 679 30. Lepš J, Májektivá M, Vítová A, Doležal J, de Bello F. Stabilizing effects in temporal
680 fluctuations: management, traits, and species richness in high-diversity communities.
681 *Ecology* **99**, 360-371 (2018).
682
- 683 31. Cadotte MW, Dinnage R, Tilman D. Phylogenetic diversity promotes ecosystem
684 stability. *Ecology* **93**, S223-S233 (2012).
685
- 686 32. Flynn DFB, Mirotchnick N, Jain M, Palmer MI, Naeem S. Functional and phylogenetic
687 diversity as predictors of biodiversity - ecosystem - function relationships. *Ecology*
688 **92**, 1573-1581 (2011).
689
- 690 33. Spasojevic MJ, Suding KN. Inferring community assembly mechanisms from
691 functional diversity patterns: the importance of multiple assembly processes. *Journal*
692 *of Ecology* **100**, 652-661 (2012).
693
- 694 34. Cadotte MW. Phylogenetic diversity and productivity: gauging interpretations from
695 experiments that do not manipulate phylogenetic diversity. *Functional Ecology* **29**,
696 1603-1606 (2015).
697
- 698 35. Díaz S, Cabido M. Vive la différence: plant functional diversity matters to ecosystem
699 processes. *Trend in Ecology & Evolution* **16**, 646 - 655 (2001).
700
- 701 36. Wright IJ, *et al.* The worldwide leaf economics spectrum. *Nature* **428**, 821-827
702 (2004).
703
- 704 37. Reich PB. The world-wide 'fast-slow' plant economics spectrum: a traits manifesto.
705 *Journal of Ecology* **102**, 275-301 (2014).
706
- 707 38. Grime JP. Evidence for the existence of three primary strategies in plants and its
708 relevance to ecological and evolutionary theory. *The American Naturalist* **111**, 1169-
709 1194 (1977).
710
- 711 39. Díaz S, *et al.* The global spectrum of plant form and function. *Nature* **529**, 167-171
712 (2016).
713
- 714 40. Polley HW, Isbell FI, Wilsey BJ. Plant functional traits improve diversity-based
715 predictions of temporal stability of grassland productivity. *Oikos* **122**, 1275-1282
716 (2013).
717
- 718 41. Májektivá M, de Bello F, Doležal J, Lepš J. Plant functional traits as determinants of
719 population stability. *Ecology* **95**, 2369-2374 (2014).
720
- 721 42. Gomez JM, Verdu M, Perfectti F. Ecological interactions are evolutionarily conserved
722 across the entire tree of life. *Nature* **465**, 918-921 (2010).
723
- 724 43. Reinhart KO, Wilson GWT, Rinella MJ. Predicting plant responses to mycorrhizae:
725 integrating evolutionary history and plant traits. *Ecology Letters* **15**, 689-695 (2012).
726
- 727 44. Parker IM, *et al.* Phylogenetic structure and host abundance drive disease pressure in
728 communities. *Nature* **520**, 542 - 544 (2015).

- 729
730 45. Gilbert GS, Magarey R, Suiter K, Webb CO. Evolutionary tools for phytosanitary risk
731 analysis: phylogenetic signal as a predictor of host range of plant pests and pathogens.
732 *Evolutionary applications* **5**, 869-878 (2012).
733
- 734 46. Pérez-Harguindeguy N, *et al.* New handbook for standardised measurement of plant
735 functional traits worldwide. *Australian Journal of Botany* **61**, 167 - 234 (2013).
736
- 737 47. Hoover DL, Knapp AK, Smith MD. Resistance and resilience of a grassland
738 ecosystem to climate extremes. *Ecology* **95**, 2646-2656 (2014).
739
- 740 48. O'Brien MJ, Leuzinger S, Philipson CD, Tay J, Hector A. Drought survival of tropical
741 tree seedlings enhanced by non-structural carbohydrate levels. *Nature Clim Change* **4**,
742 710-714 (2014).
743
- 744 49. Weigelt A, Schumacher J, Roscher C, Schmid B. Does biodiversity increase spatial
745 stability in plant community biomass? *Ecology Letters* **11**, 338-347 (2008).
746
- 747 50. Fargione J, Tilman D. Niche differences in phenology and rooting depth promote
748 coexistence with a dominant C₄ bunchgrass. *Oecologia* **143**, 598 - 606 (2005).
749
- 750 51. Fornara DA, Tilman D. Plant functional composition influences rates of soil carbon
751 and nitrogen accumulation. *Journal of Ecology* **96**, 314 - 322 (2008).
752
- 753 52. Cong W-F, van Ruijven J, Mommer L, De Deyn GB, Berendse F, Hoffland E. Plant
754 species richness promotes soil carbon and nitrogen stocks in grasslands without
755 legumes. *Journal of Ecology* **102**, 1163 - 1170 (2014).
756
- 757 53. Lange M, *et al.* Plant diversity increases soil microbial activity and soil carbon
758 storage. *Nature Communications* **6**, 6707 (2015).
759
- 760 54. Gould IJ, Quinton JN, Weigelt A, De Deyn GB, Bardgett RD. Plant diversity and root
761 traits benefit physical properties key to soil function in grasslands. *Ecology Letters* **19**,
762 1140-1149 (2016).
763
- 764 55. Reich PB, *et al.* Impact of biodiversity loss escalate through time as redundancy
765 fades. *Science* **336**, 589 - 592 (2012).
766
- 767 56. Loreau M, Hector A. Partitioning selection and complementarity in biodiversity
768 experiments. *Nature* **412**, 72 - 76 (2001).
769
- 770 57. Allan E, Weisser W, Weigelt A, Roscher C, Fischer M, Hillebrand H. More diverse
771 plant communities have higher functioning over time due to turnover in
772 complementary dominant species. *PNAS* **108**, 17034 - 17039 (2011).
773
- 774 58. Isbell F, *et al.* High plant diversity is needed to maintain ecosystem services. *Nature*
775 (2011).
776

- 777 59. Turnbull LA, Isbell F, Purves DW, Loreau M, Hector A. Understanding the value of
778 plant diversity for ecosystem functioning through niche theory. *Proc R Soc B* **283**,
779 20160536 (2016).
780
- 781 60. Edwards EJ, Osborne CP, Strömberg CAE, Smith SA. The Origins of C4 Grasslands:
782 Integrating Evolutionary and Ecosystem Science. *Science* **328**, 587-591 (2010).
783
- 784 61. Bartlett MK, Scoffoni C, Sack L. The determinants of leaf turgor loss point and
785 prediction of drought tolerance of species and biomes: a global meta-analysis.
786 *Ecology Letters* **15**, 393-405 (2012).
787
- 788 62. Schroeder-Georgi T, Wirth C, Nadrowski K, Meyer ST, Mommer L, Weigelt A. From
789 pots to plots: hierarchical trait-based prediction of plant performance in a mesic
790 grassland. *Journal of Ecology* **104**, 206-218 (2016).
791
- 792 63. Iversen CM, *et al.* A global Fine-Root Ecology Database to address below-ground
793 challenges in plant ecology. *New Phytologist* **215**, 15-26 (2017).
794
- 795 64. Aubin I, *et al.* Traits to stay, traits to move: a review of functional traits to assess
796 sensitivity and adaptive capacity of temperate and boreal trees to climate change.
797 *Environ Rev* **24**, 164-186 (2016).
798
- 799 65. Oelmann Y, *et al.* Plant diversity effects on aboveground and belowground N pools in
800 temperate grassland ecosystems: Development in the first 5 years after establishment.
801 *Global Biogeochemical Cycles* **25**, 1 - 11 (2011).
802
- 803 66. van der Heijden MGA, *et al.* The mycorrhizal contribution to plant productivity, plant
804 nutrition and soil structure in experimental grassland. *New Phytologist* **172**, 739 - 752
805 (2006).
806
- 807 67. Eisenhauer N, *et al.* Plant diversity effects on soil microorganisms support the
808 singular hypothesis. *Ecology* **91**, 485 - 496 (2010).
809
- 810 68. Eisenhauer N, Reich PB, Isbell F. Decomposer diversity and identity influence plant
811 diversity effects on ecosystem functioning. *Ecology* **93**, 2227 - 2240 (2012).
812
- 813 69. Mueller KE, Tilman D, Fornara DA, Hobbie SE. Root depth distribution and the
814 diversity-productivity relationship in a long-term grassland experiment. *Ecology* **94**,
815 787 - 793 (2013).
816
- 817 70. Ravenek JM, *et al.* Long-term study of root biomass in a biodiversity experiment
818 reveals shifts in diversity effects over time. *Oikos* **123**, 1528-1536 (2014).
819
- 820 71. Hoover DL, Duniway MC, Belnap J. Pulse-drought atop press-drought: unexpected
821 plant responses and implications for dryland ecosystems. *Oecologia* **179**, 1211-1221
822 (2015).
823
- 824 72. Shi Z, *et al.* Dual mechanisms regulate ecosystem stability under decade-long
825 warming and hay harvest. *Nature Communications* **7**, 11973 (2016).
826

- 827 73. Mazel F, *et al.* Influence of tree shape and evolutionary time-scale on phylogenetic
828 diversity metrics. *Ecography* **39**, 913-920 (2016).
829
- 830 74. Mitchell CE, Tilman D, Groth JV. Effects of grassland plant species diversity,
831 abundance, and composition on foliar fungal disease. *Ecology* **83**, 1713-1726 (2002).
832
- 833 75. Wilsey BJ, Polley W. Realistically low species evenness does not alter grassland
834 species-richness-productivity relationships. *Ecology* **85**, 2693 - 2700 (2004).
835
- 836 76. Wilsey BJ, Teaschner TB, Daneshgar PP, Isbell FI, Polley HW. Biodiversity
837 maintenance mechanisms differ between native and novel exotic-dominated
838 communities. *Ecology Letters* **12**, 432-442 (2009).
839
- 840 77. Hallett LM, *et al.* Biotic mechanisms of community stability shift along a
841 precipitation gradient. *Ecology* **95**, 1693-1700 (2014).
842
- 843 78. Guerrero-Ramirez NR, *et al.* Diversity-dependent temporal divergence of ecosystem
844 functioning in experimental ecosystems. *Nature Ecology and Evolution* **1**, 1639 -
845 1642 (2017).
846
- 847 79. Xu Z, *et al.* Environmental changes drive the temporal stability of semi-arid natural
848 grasslands through altering species asynchrony. *Journal of Ecology* **103**, 1308-1316
849 (2015).
850
- 851 80. Yang Z, *et al.* Daytime warming lowers community temporal stability by reducing the
852 abundance of dominant, stable species. *Global change biology* **23**, 154-163 (2017).
853
- 854 81. Craven D, *et al.* Plant diversity effects on grassland productivity are robust to both
855 nutrient enrichment and drought. *Philosophical Transactions B* **371**, 1 - 8 (2016).
856
- 857 82. Isbell F, *et al.* Benefits of increasing plant diversity in sustainable agroecosystems.
858 *Journal of Ecology* **105**, 871-879 (2017).
859
- 860 83. Goodess CM. How is the frequency, location and severity of extreme events likely to
861 change up to 2060? *Environmental Science & Policy* **27**, Supplement 1, S4-S14
862 (2013).
863
- 864 84. Stott P. How climate change affects extreme weather events. *Science* **352**, 1517 -
865 1518 (2016).
866
- 867 85. Boyle B, *et al.* The taxonomic name resolution service: an online tool for automated
868 standardization of plant names. *BMC Bioinformatics* **14**, 16 (2013).
869
- 870 86. Loreau M, de Mazancourt C. Species synchrony and its drivers: Neutral and
871 nonneutral community dynamics in fluctuating environments. *The American*
872 *Naturalist* **172**, E48-E66 (2008).
873
- 874 87. Kattge J, *et al.* TRY - a global database of plant traits. *Global Change Biology* **17**,
875 2905-2935 (2011).
876

- 877 88. Grime JP, Hodgson JG, Hunt R. *Comparative plant ecology: a functional approach to*
878 *common British species*. Springer (2007).
879
- 880 89. Wacker L, Baudois O, Eichenberger-Glinz S, Schmid B. Diversity effects in early-
881 and mid-successional species pools along a nitrogen gradient. *Ecology* **90**, 637-648
882 (2009).
883
- 884 90. Roscher C, *et al.* Using plant functional traits to explain diversity–productivity
885 relationships. *PLoS ONE* **7**, e36760 (2012).
886
- 887 91. Daneshgar PP, Polley HW, Wilsey BJ. Simple plant traits explain functional group
888 diversity decline in novel grassland communities of Texas. *Plant Ecology* **214**, 231-
889 241 (2013).
890
- 891 92. Lê S, Josse J, Husson F, others. FactoMineR: an R package for multivariate analysis.
892 *Journal of statistical software* **25**, 1-18 (2008).
893
- 894 93. Laliberté E, Legendre P. A distance-based framework for measuring functional
895 diversity from multiple traits. *Ecology* **91**, 299-305 (2010).
896
- 897 94. Zanne AE, *et al.* Three keys to the radiation of angiosperms into freezing
898 environments. *Nature* **506**, 89 (2014).
899
- 900 95. Pearse WD, *et al.* pez: phylogenetics for the environmental sciences. *Bioinformatics*
901 **31**, 2888-2890 (2015).
902
- 903 96. Webb CO, Ackerly DD, McPeck MA, Donoghue MJ. Phylogenies and Community
904 Ecology. *Annual Review of Ecology and Systematics* **33**, 475-505 (2002).
905
- 906 97. Godoy O, Kraft NJB, Levine JM. Phylogenetic relatedness and the determinants of
907 competitive outcomes. *Ecology Letters* **17**, 836-844 (2014).
908
- 909 98. Harris I, Jones PD, Osborn TJ, Lister DH. Updated high-resolution grids of monthly
910 climatic observations – the CRU TS3.10 Dataset. *International Journal of*
911 *Climatology* **34**, 623-642 (2014).
912
- 913 99. Burnham KP, Anderson DR. *Model Selection and Multimodel Inference: a practical*
914 *information-theoretic approach*, 2nd edn. Springer Science & Business Media (2003).
915
- 916 100. Lefcheck JS. piecewiseSEM: Piecewise structural equation modelling in r for
917 ecology, evolution, and systematics. *Methods in Ecology and Evolution* **7**, 573-579
918 (2016).
919
- 920 101. R Development Core Team: *A Language and Environment for Statistical Computing*
921 (R Foundation for Statistical Computing, Vienna, 2016).
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927 **Acknowledgements**

928 This paper is a joint effort of the sTABILITY group funded by sDiv (www.idiv.de/stability),
929 the Synthesis Centre of the German Centre for Integrative Biodiversity Research (iDiv)
930 Halle-Jena-Leipzig (DFG FZT 118). The Jena Experiment is funded by the Deutsche
931 Forschungsgemeinschaft (DFG, German Research Foundation; FOR 1451) and the Swiss
932 National Science Foundation. The Cedar Creek biodiversity experiments were supported by
933 awards from the Andrew Mellon Foundation, the U.S. National Science Foundation (NSF)
934 Long-Term Ecological Research (DEB-9411972, DEB-0080382, DEB-0620652, and DEB-
935 1234162), Biocomplexity Coupled Biogeochemical Cycles (DEB-0322057), Long-Term
936 Research in Environmental Biology (DEB-0716587, DEB-1242531), and Ecosystem
937 Sciences (NSF DEB- 1120064) Programs; as well as the U.S. Department of Energy
938 Programs for Ecosystem Research (DE-FG02-96ER62291), and National Institute for
939 Climatic Change Research (DE-FC02-06ER64158). The Texas MEND study was funded by
940 US-NSF DEB-0639417 and USDA-NIFA-2014-67003-22067. The study has been supported
941 by the TRY initiative on plant traits (<http://www.try-db.org>). TRY is currently supported by
942 DIVERSITAS/Future Earth and the German Centre for Integrative Biodiversity Research
943 (iDiv) Halle-Jena-Leipzig. V.O. received financial support from the Russian Science
944 Foundation (#14-50-00029). The authors would also like to thank Jon Lefcheck for his help
945 in revising the structural equation model.

946
947 **Authorship contributions**

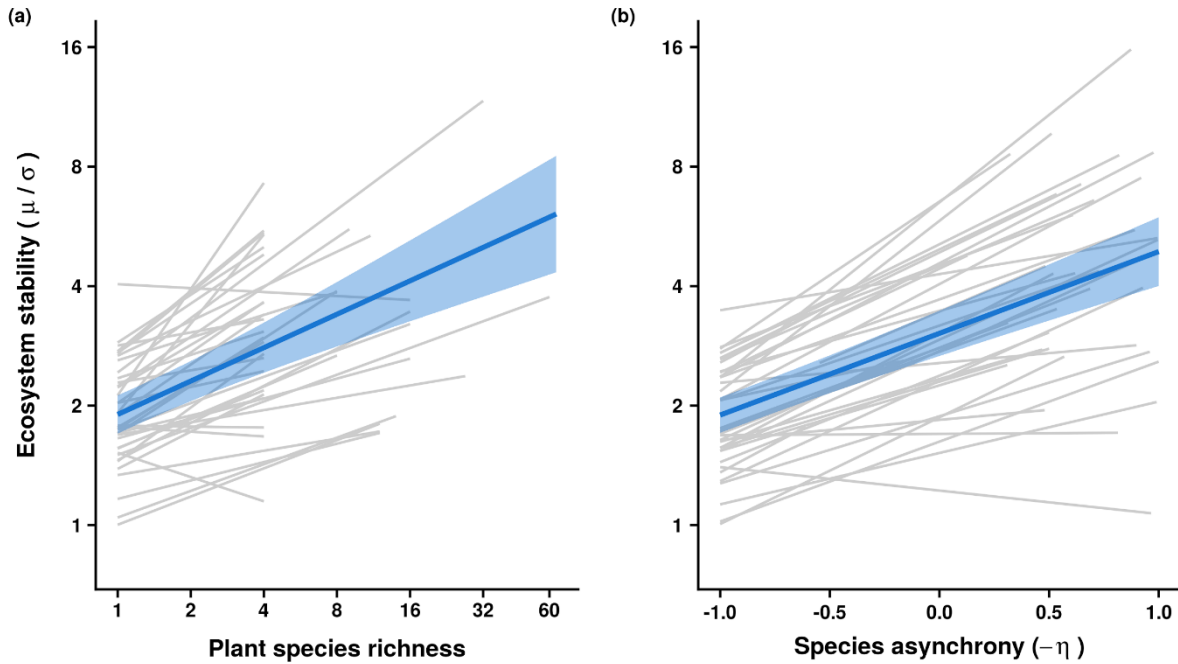
948
949 DC, NE, and FI conceived the project, DC, PM, NE, WDP, YH, CR, FI, AE, JNG, JH, AJ,
950 NL, STM, JvR, AW, and MDS further developed the project in a workshop; NE, CR, FI, MB,
951 CB, GB, NB, CB, BELC, JAC, JHCC, JMC, EDL, AH, AJ, JK, JK, VL, VM, VO, HWP,
952 PBR, JvR, BS, NAS, DT, AW, and BW contributed experimental and functional trait data;
953 DC compiled data; DC analyzed data with significant input from PM, NE, WDP, and YH.

954 DC and PM wrote the first draft of the manuscript and all co-authors contributed substantially
955 to revisions.

956
957 **Competing interests**

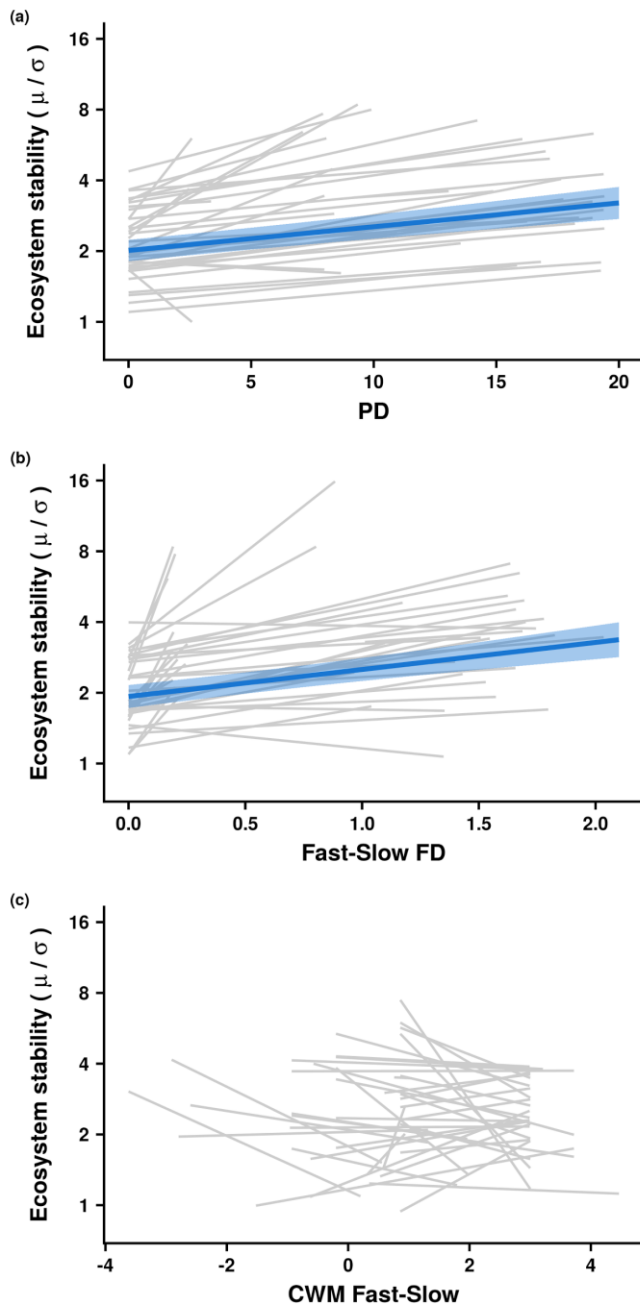
958 The authors have no competing interests.

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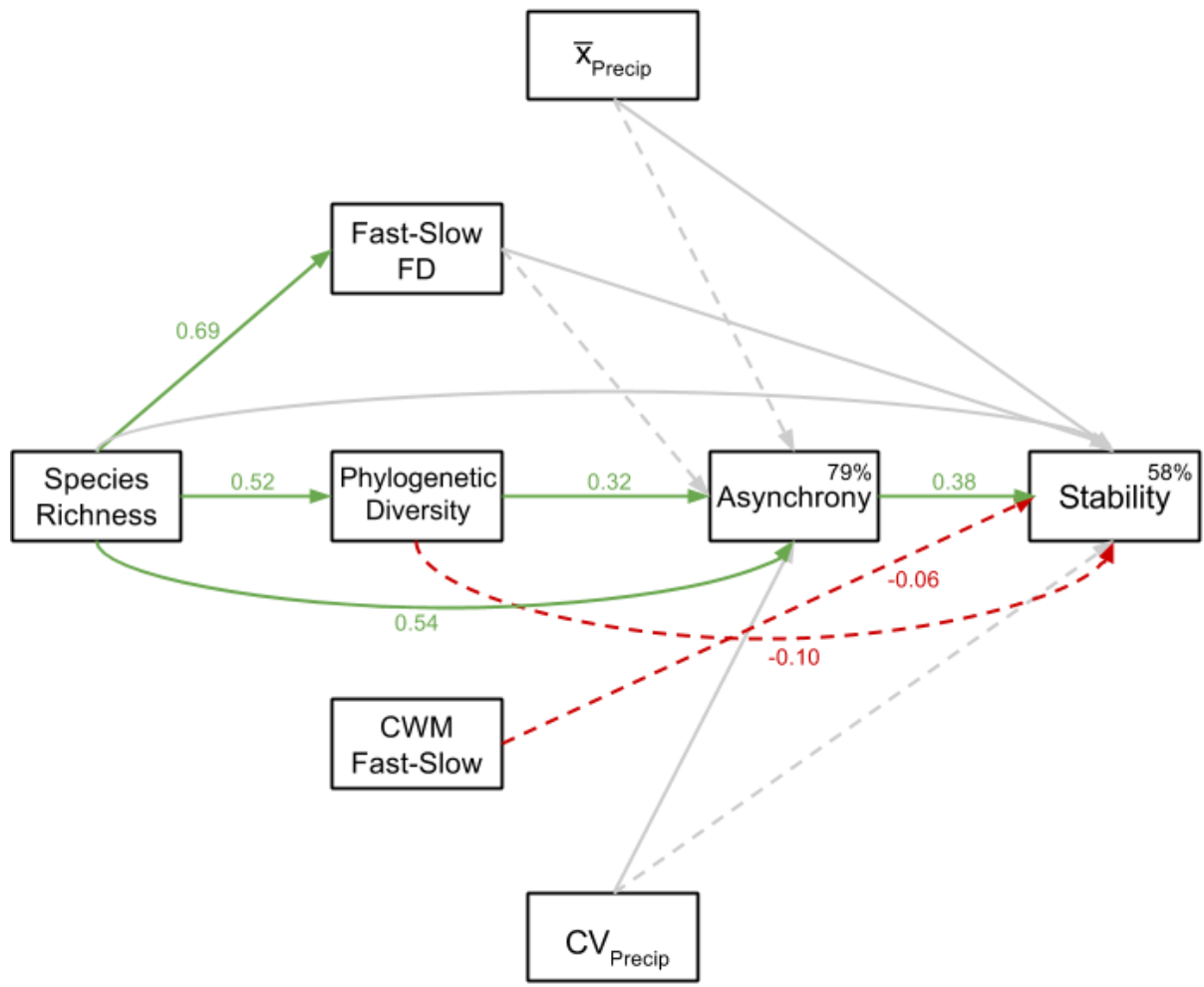
988 **Figure 1.** Plant species richness (a) and species asynchrony (b) effects on ecosystem stability
 989 of aboveground biomass production across 39 experimental grassland studies. Lines are
 990 mixed-effects model fits for each study (light gray lines) or across all studies (black lines).
 991 Synchrony ranges from -1 to 1, where -1 represents maximum synchrony and +1 maximum
 992 asynchrony.

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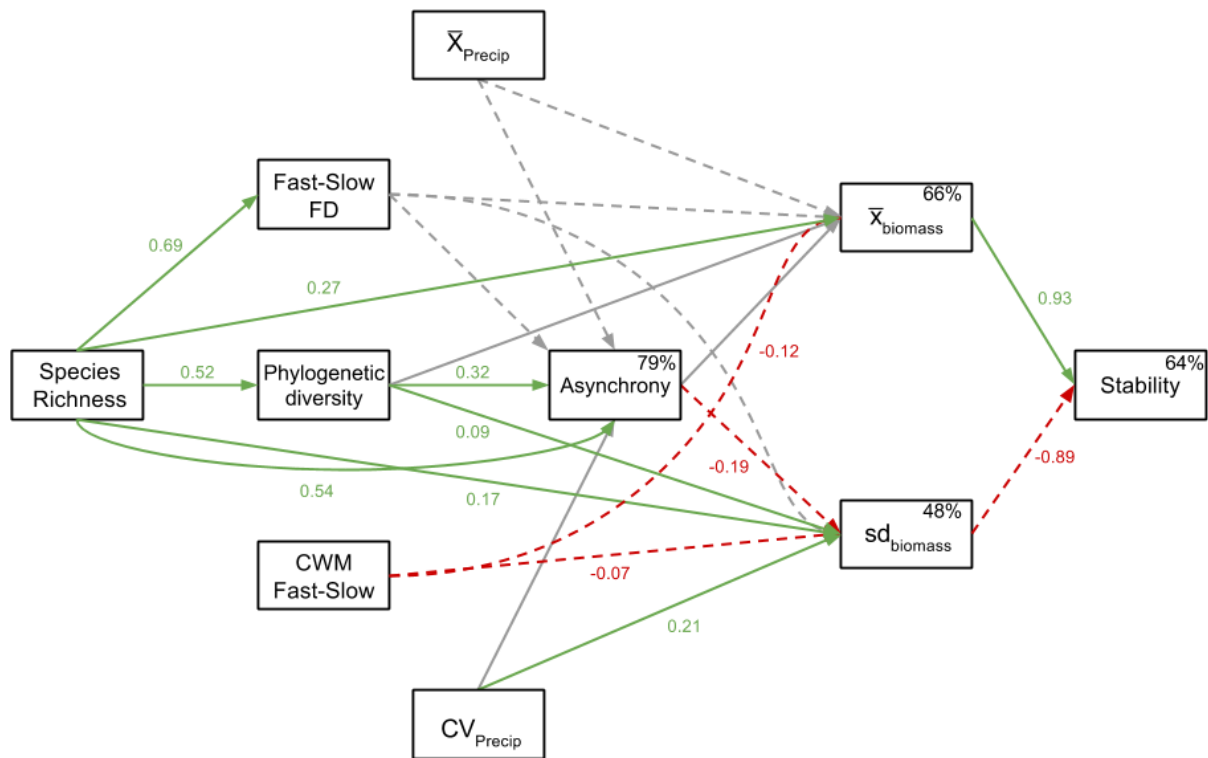
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Figure 2. Phylogenetic (**a**; PD) and fast-slow functional diversity (**b**; Fast-Slow FD) and community-weighted mean of fast-slow traits (**c**; CWM Fast-Slow) effects on ecosystem stability of aboveground biomass production across 39 experimental grassland studies. Phylogenetic diversity is abundance-weighted mean nearest taxon distance (MNTD) and Fast-Slow FD is abundance-weighted functional dispersion of fast-slow traits. CWM Fast-Slow is the first axis of a principal component analysis of community-weighted means of key leaf functional traits associated with ‘fast’ and ‘slow’ ecological strategies: specific leaf area (SLA), leaf matter dry content (LMDC), and leaf N and P concentrations. Low values of the fast-slow spectrum correspond to communities dominated by ‘slow’ species, i.e. low SLA and leaf N and P and high LDMC and high values to communities dominated ‘fast species, i.e. high SLA and leaf N and P and low LDMC. Lines are mixed-effects model fits for each study (light gray lines) or across all studies (black lines; $P \leq 0.05$).



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Figure 3. Structural equation model (SEM) exploring the effects of plant species richness, fast-slow functional diversity (Fast-Slow FD; abundance-weighted functional dispersion), phylogenetic diversity (abundance-weighted mean nearest taxon distance, functional composition (CWM Fast-Slow), mean annual precipitation (\bar{x}_{Precip}), and interannual variation in precipitation (CV_{Precip}) on asynchrony and ecosystem stability of aboveground biomass production across 39 experimental grassland studies. The model fit the data well (Fisher’s $C = 9.25$, $df = 12$, $P = 0.68$; $K = 34$, $n = 1,699$). Boxes represent measured variables and arrows represent relationships among variables. Solid green and dashed red arrows represent significant ($P \leq 0.05$), positive and negative standardized path coefficients, respectively, and gray arrows represent non-significant standardized path coefficients. Standardized path coefficients are given next to each (significant) path. Conditional R^2 (based on both fixed and random effects) for asynchrony and ecosystem stability is reported in the corresponding box. The SEM was fitted using ‘piecewise SEM’ where ‘study’ was treated as a random group factor term and plant species richness as a random slope term, allowing regression slopes and intercepts to vary between studies.



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1050 **Figure 4.** Structural equation model (SEM) exploring the effects of plant species richness,
 1051 fast-slow functional diversity (Fast-Slow FD; abundance-weighted functional dispersion),
 1052 phylogenetic diversity (abundance-weighted mean nearest taxon distance, functional
 1053 composition (CWM Fast-Slow), mean annual precipitation (\bar{x}_{Precip}), and interannual variation
 1054 in precipitation ($\text{CV}_{\text{Precip}}$) on asynchrony, mean (\bar{x}_{biomass}) and variation in ($\text{SD}_{\text{biomass}}$)
 1055 aboveground biomass production and ecosystem stability of aboveground biomass production
 1056 across 39 experimental grassland studies. The model fit the data well (Fisher's $C = 24.52$, $\text{df} = 22$, $P = 0.32$; $K = 49$, $n = 1,699$). Boxes represent measured variables and arrows represent
 1058 relationships among variables. Solid green and dashed red arrows represent significant ($P \leq$
 1059 0.05), positive and negative standardized path coefficients, respectively, and gray arrows
 1060 represent non-significant standardized path coefficients. Standardized path coefficient are
 1061 given next to each (significant) path. Conditional R^2 (based on both fixed and random effects)
 1062 for asynchrony, \bar{x}_{biomass} , $\text{SD}_{\text{biomass}}$, and ecosystem stability is reported in the corresponding
 1063 box. The SEM was fitted using 'piecewise SEM' where 'study' was treated as a random
 1064 group factor term and plant species richness as a random slope term, allowing regression
 1065 slopes and intercepts to vary between studies.

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