- 1 Multiple facets of biodiversity drive the diversity-stability relationship
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122 Abstract

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

156 Introduction

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158 The relationship between the biodiversity and the stability of ecosystems has long been a fundamental subject of ecological research^{1,2,3,4}. More recently, this research topic has gained 159 160 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 ecosystem services they underpin^{5,6,7,8}. Much of this work has examined the relationship 162 between plant species diversity and biomass production, and both theoretical and empirical 163 164 has consistently demonstrated that the productivity of species-rich communities shows lower variation over time than that of less diverse communities^{9,10,11,12,13,14,15,16}. 165 166 167 Temporal stability (or invariability) of ecosystem functioning is an integrative measure of the responses of populations and communities to each other and to environmental variation¹⁷. In 168 169 the case of biomass production, temporal stability is typically defined as mean biomass divided by its temporal standard deviation $(\mu/\sigma)^{18}$. Thus, the higher stability of species-rich 170 171 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) and/or resilience (i.e., biomass returns to average levels rapidly after perturbations)^{3,19,20}. 173 174 Furthermore, numerous statistical mechanisms have been proposed as drivers of stability and tested empirically^{10,11,12}. Of these, perhaps the primary mechanism through which diversity 175 stabilizes biomass production is species asynchrony^{10,12,21,22}, which describes the extent to 176 which species-level productivity is correlated within a community over time. Asynchrony, 177 178 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 interspecific interactions^{12,23}, negative frequency dependence, e.g. due to pathogen 180

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

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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 the production, persistence, and stability of plant biomass³⁵. While plants differ greatly in 192 193 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 (hereafter 'slow' species)^{36,37}. The former typically possess high specific leaf area (SLA), low 197 198 leaf dry matter content (LDMC), and high leaf nitrogen concentrations (N), the latter the opposite^{37,38,39}. There is growing evidence that variation in functional composition along this 199 200 'fast-slow' leaf economics spectrum influences ecosystem stability. For example, 201 communities dominated by species with high LDMC values have been found to increase ecosystem stability in experimental and semi-natural grassland communities⁴⁰. If functional 202 203 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 more stable than those dominated by species with fast leaf economics ('fast communities') 41 . 205

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

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

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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 diversity measures. Traits that reflect a shared co-evolutionary history of biotic interactions 222 often show a high degree of phylogenetic conservatism⁴², such as symbiotic N₂ fixation and 223 mycorrhizal tendency^{32,43}. Closely related species are also known to share pathogens or 224 immune responses via their shared co-evolutionary history^{44,45}. Importantly, phylogenetic 225 226 diversity has been shown to have a positive effect on ecosystem stability in grasslands in most analyses 31,32,34 , but not all²⁸. We therefore hypothesize that greater phylogenetic 227 228 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 attacks, which are strong regulators of biomass production in grasslands⁴⁵. 230

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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 class of mechanism may include the effects of persistent seedbanks⁴⁶, regrowth from 234 belowground storage organs⁴⁷, carbohydrate reserves⁴⁸, variation in rooting depth⁴⁹, and 235 phenology⁵⁰. Plant species richness can also affect ecosystem stability by modifying 236 237 environmental conditions. For example, the higher productivity of species-rich communities is associated with more rapid rates of soil organic matter accumulation^{51,52,53} and soil 238 aggregate formation⁵⁴, which result in a more aerobic, mesic soil environment in which plant 239 240 growth is more constant. We expect that these effects will indirectly enhance ecosystem stability via increased asynchrony¹⁰ and directly via greater mean biomass production over 241 time^{28,55}. 242

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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 general assessment of the contribution of different facets of biodiversity in driving 247 248 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), and which controls for covariation among the different facets of biodiversity^{28,34}. We 252 253 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 by increasing asynchrony and *ii*) species-rich communities with high functional and 255

phylogenetic diversity, and those dominated by species with slow leaf economics, will
increase ecosystem stability directly as they increase the temporal mean of biomass
production, a component of stability, via classical diversity-function mechanisms, e.g.
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 of variation in ecosystem stability (Table S1, marginal R^2), with a larger proportion being 267 explained by the random effects (Tables S1 and S2, conditional R²). In contrast, although 268 269 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).

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These relationships were investigated in more depth with our structural equation model,which provides evidence that asynchrony is a key mechanism mediating the biodiversity-

stability relationship and that asynchrony is driven by multiple facets of biodiversity (Fig. 3).

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 R²), which

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

285

286 The strongest pathway of influence on ecosystem stability was from plant species richness via species asynchrony (standardized indirect effect = 0.21). This effect was larger and more 287 288 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).

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

important effects of climate and found that neither the mean nor inter-annual variation inprecipitation significantly affected asynchrony or ecosystem stability.

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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 above ground 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 above ground 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

In an analysis that only included longer studies (six studies >4 years, n = 454 plots) certain paths became stronger, with notable increases in the effects of fast-slow functional diversity (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 four individual traits making up the fast-slow leaf economics spectrum, we saw positive 335 336 direct effects of leaf P on ecosystem stability and negative effects of leaf N on ecosystem stability, while the effect of LDMC and SLA on ecosystem stability were not statistically 337 338 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.

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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 temporally variable environment^{21,57,58,59}. However, these niche differences were not captured 349 350 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. Such traits may include different rooting strategies, photosynthetic pathways, non-structural 352 carbohydrate concentrations, and traits related to phenology, demographic storage and 353 regeneration^{47,48,50,60,61,62}. Data for some of these traits is relatively sparse⁶³ and the collection 354

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

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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 than effects operating via the standard deviation, which is in line with previous studies^{12,28}. 360 One possible explanation for this direct effect of species richness is the greater accumulation 361 362 of soil organic matter and nutrient stocks and heightened mineralization in diverse communities over time^{51,52,53,55,65}. These effects may be further enhanced by positive effects 363 364 of plant species diversity on the abundance and diversity of soil biota that improve the physical structure of soils^{54,66,67,68}. Further, root biomass – which also increases with species 365 richness 51,69,70 – has been found to stabilize ecosystem productivity⁹ by enhancing water 366 367 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 grasses^{71,72}. Furthermore, our analysis illustrates that the effects of phylogenetic diversity on 379

ecosystem stability are sensitive to the phylogenetic diversity metric used³⁴. Consistent with 380 Venail, Gross²⁸, but in contrast with those presented in Figs. 3 and 4, SEMs using mean 381 pairwise distance (MPD) showed weak direct and indirect effects of phylogenetic diversity on 382 383 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 fact that it better represents recently evolved differences among species⁷³ and, more 385 specifically, recently evolved differentiation in the traits that confer tolerance to specialized 386 pathogens or herbivores, which play a major role in driving grassland productivity^{24,74}. 387

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, such as low nutrient availability or aridity, e.g. the dry grasslands of the experimental sites in 402 Texas included in our study^{75,76}. Site-level information detailing disturbance regimes and the 403 404 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. drought, are more likely to occur in long-term studies²⁰. However, such patterns may also be 413 414 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 more complete understanding of the drivers of ecosystem stability⁴. Furthermore, initial 425 426 investigations indicate a powerful interactive role between environmental conditions and biotic community properties^{79,80}, as abiotic and management factors not only control diversity 427 428 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

complementarity^{22,81}. This means that under natural conditions changes in diversity are not 430 431 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 need to be considered⁶. Threshold-based measures of stability¹⁷ may also be more relevant to 440 441 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, through which plant community properties affect the stability of grassland biomass 448 productivity. In an era of increased climatic variability^{83,84} and biodiversity change, it is 449 450 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. 452

453

455 Methods

456 **Data preparation**

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

463

For each plot within the experiments, we quantified ecosystem stability as the inverse of the coefficient of variation of aboveground plant biomass $(\mu/\sigma)^{18}$, which is the ratio of the mean 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
$$\eta = (1/n) \Sigma_i \operatorname{corr} (Y_i, \Sigma_j \neq i Y_j),$$
 (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 (- η) ranges 472 from -1, where species' aboveground plant biomass is maximally synchronous, to 1, where 473 species' aboveground plant biomass is maximally asynchronous. Further, - η 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

We selected four leaf traits associated with the fast-slow leaf economics spectrum³⁶, specific
leaf area (SLA; mm² mg⁻¹), leaf dry matter content (LDMC; g g⁻¹), foliar N (%), and foliar P
(%). These data were obtained from the TRY database⁸⁷ (Appendix 2) and additional studies

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

We calculated functional diversity in traits associated with the fast-slow leaf economics 497 498 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**

We used the molecular phylogeny from Zanne, Tank⁹⁴ as a backbone to build a phylogeny of 506 all species within the experiments, conservatively binding species into the backbone using 507 dating information from congeners in the tree (using *congeneric.merge*)⁹⁵. We then calculated 508 abundance-weighted phylogenetic diversity as mean nearest taxon distance (MNTD)⁹⁶ and 509 510 mean pairwise distance (MPD) annually for each plot and then calculated the average across years. MNTD has captured competitive differences among species in previous studies⁹⁷ and 511 the sharing of specialized pathogens tends to be confined to closely related species^{44,45}. 512 513 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 Materials. 517

518

519 Climate

As empirical and theoretical studies have shown strong impacts of mean and inter-annual variation in precipitation on ecosystem stability and species asynchrony in grasslands^{10,77}, we included site-level climate data to explain across-site variation in ecosystem stability. To describe environmental conditions during each study in a consistent manner across sites, we calculated mean annual precipitation (MAP) and inter-annual variation in precipitation (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 sizes⁹⁹. Models were fit using the 'nlme' package and model assumptions were checked by 538 539 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 models (SEM)¹⁰⁰ using 'piecewiseSEM'. Testing for relationships with resistance and 546 resilience (as in Isbell, Craven²⁰) was not possible because of the unequal distribution of 547 548 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 represent biological drivers that influence ecosystem stability, e.g. via complementarity 552 effects on the temporal mean of biomass production^{23,56}. Finally, we included direct paths 553 554 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

because variation in these variables can be directly attributed to the experimental

557 manipulation of species richness in all studies³².

558

All initial models contained partial bivariate correlations between fast-slow functional 559 diversity and phylogenetic diversity³⁴. Additional partial bivariate correlations were added to 560 the initial model if they significantly improved model fit using modification indices (P < 561 562 (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 log₂ transformed to meet normality assumptions. Model assumptions of normality were inspected visually. As many of the variables included in our 576 577 SEM were correlated (see Appendix 1), we estimated variance inflation. This demonstrated that multi-collinearity did not affect parameter estimates (VIF < 3). All analyses were 578 performed using R 3.3.1¹⁰¹. 579

580 581	Refere	ences
582	1	May RM Stability and complexity in model ecosystems Princeton University Press
583	1.	(1973).
584		
585	2.	McNaughton SJ. Stability and diversity of ecological communities. <i>Nature</i> 274, 251-
586		253 (1978).
587		
588	3.	Tilman D, Downing JA. Biodiversity and stability in grasslands. <i>Nature</i> 367 , 363-365
589		(1994).
590		
591	4.	Ives AR, Carpenter SR. Stability and diversity of ecosystems. Science 317, 58-62
592		(2007).
593		
594	5.	Balvanera P, et al. Quantifying the evidence for biodiversity effects on ecosystem
595		functioning and services. Ecology Letters 9, 1146 - 1156 (2006).
596		
597	6.	Donohue I, et al. Navigating the complexity of ecological stability. Ecology Letters,
598		(2016).
599	-	
600	7.	Hautier Y, Tilman D, Isbell F, Seabloom EW, Borer ET, Reich PB. Anthropogenic
601		environmental changes affect ecosystem stability via biodiversity. Science 348, 336-
602		340 (2015).
603	0	Libell E Tilmen D Deleter C Lemen M The big dimension dent as services
604 605	8.	Isbell F, Tilman D, Polasky S, Loreau M. The biodiversity-dependent ecosystem
605 606		service debt. <i>Ecology Letters</i> 18, 119-134 (2013).
607	0	Tilman D. Raich DR. Knong IMH. Biodiversity and ecosystem stability in a decade
608	9.	long grassland experiment Nature 441, 629 - 632 (2006)
609		101g grassiand experiment. <i>Wature</i> 441 , 027 - 032 (2000).
610	10	de Mazancourt C. et al. Predicting ecosystem stability from community composition
611	10.	and biodiversity <i>Ecology Letters</i> 16 , 617 - 625 (2013).
612		
613	11.	Hector A, et al. General stabilizing effects of plant diversity on grassland productivity
614		through population asychrony and overyielding. <i>Ecology</i> 91 , 2213 - 2220 (2010).
615		
616	12.	Gross K, et al. Species richness and the temporal stability of biomass production: a
617		new analysis of recent biodiversity experiments. The American Naturalist 183, 1 - 12
618		(2014).
619		
620	13.	Jiang L, Pu Z. Different effects of species diversity on temporal stability in single-
621		trophic and multitrophic communities. The American Naturalist 174, 651-659 (2009).
622		
623	14.	Campbell V, Murphy G, Romanuk TN. Experimental design and the outcome and
624		interpretation of diversity-stability relations. Oikos 120, 399-408 (2011).
625		
626	15.	del Río M, et al. Species interactions increase the temporal stability of community
627		productivity in Pinus sylvestris–Fagus sylvatica mixtures across Europe. <i>Journal of</i>
628		Ecology 105, 1032-1043 (2017).
629		

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

679 680 681 682	30.	Lepš J, Májeková M, Vítová A, Doležal J, de Bello F. Stabilizing effects in temporal fluctuations: management, traits, and species richness in high-diversity communities. <i>Ecology</i> 99 , 360-371 (2018).
683 684 685	31.	Cadotte MW, Dinnage R, Tilman D. Phylogenetic diversity promotes ecosystem stability. <i>Ecology</i> 93 , S223-S233 (2012).
686 687 688 689	32.	Flynn DFB, Mirotchnick N, Jain M, Palmer MI, Naeem S. Fuctional and phylogenetic diversity as predictors of biodiversity - ecosystem - function relationships. <i>Ecology</i> 92 , 1573-1581 (2011).
690 691 692 693	33.	Spasojevic MJ, Suding KN. Inferring community assembly mechanisms from functional diversity patterns: the importance of multiple assembly processes. <i>Journal of Ecology</i> 100 , 652-661 (2012).
694 695 696 697	34.	Cadotte MW. Phylogenetic diversity and productivity: gauging interpretations from experiments that do not manipulate phylogenetic diversity. <i>Functional Ecology</i> 29 , 1603-1606 (2015).
698 699 700	35.	Díaz S, Cabido M. Vive la différence: plant functional diversity matters to ecosystem processes. <i>Trend in Ecology & Evolution</i> 16 , 646 - 655 (2001).
701 702 703	36.	Wright IJ, et al. The worldwide leaf economics spectrum. Nature 428 , 821-827 (2004).
704 705 706	37.	Reich PB. The world-wide 'fast–slow' plant economics spectrum: a traits manifesto. <i>Journal of Ecology</i> 102 , 275-301 (2014).
707 708 709 710	38.	Grime JP. Evidence for the existence of three primary strategies in plants and its relevance to ecological and evolutionary theory. <i>The American Naturalist</i> 111 , 1169-1194 (1977).
711 712 713	39.	Díaz S, <i>et al</i> . The global spectrum of plant form and function. <i>Nature</i> 529 , 167-171 (2016).
714 715 716 717	40.	Polley HW, Isbell FI, Wilsey BJ. Plant functional traits improve diversity-based predictions of temporal stability of grassland productivity. <i>Oikos</i> 122 , 1275-1282 (2013).
718 719 720	41.	Májeková M, de Bello F, Doležal J, Lepš J. Plant functional traits as determinants of population stability. <i>Ecology</i> 95 , 2369-2374 (2014).
721 722 723	42.	Gomez JM, Verdu M, Perfectti F. Ecological interactions are evolutionarily conserved across the entire tree of life. <i>Nature</i> 465 , 918-921 (2010).
724 725 726	43.	Reinhart KO, Wilson GWT, Rinella MJ. Predicting plant responses to mycorrhizae: integrating evolutionary history and plant traits. <i>Ecology Letters</i> 15 , 689-695 (2012).
727 728	44.	Parker IM, <i>et al.</i> Phylogenetic structure and host abundance drive disease pressure in communities. <i>Nature</i> 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-Harquindequy N et al New handbook for standardised measurement of plant
735	10.	functional traits worldwide Australian Journal of Botany 61, 167 - 234 (2013)
735		Tunctional traits worldwide. Australian Journal of Dolany 61 , 107 - 254 (2015).
730	17	Hoover DL Knapp AK Smith MD Resistance and resiliance of a grassland
729	47.	account on a provide the sector of the secto
730		ecosystem to chinate extremes. Ecology 95, 2040-2050 (2014).
739	40	
/40	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. <i>Nature Clim Change</i> 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? <i>Ecology Letters</i> 11 , 338-347 (2008).
746		
747	50.	Fargione J, Tilman D. Niche differences in phenology and rooting depth promote
748		coexistence with a dominant C ₄ bunchgrass. <i>Oecologia</i> 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 Devn 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		10guillos vou nur of 2001089 202, 1100 - 1170 (2017).
757	53	I ange M <i>et al.</i> Plant diversity increases soil microbial activity and soil carbon
758	55.	storage Nature Communications 6 6707 (2015)
750		storage. Watare Commanications 0 , 0707 (2015).
760	54	Gould II Quinton IN Weigelt A De Devn GB Bardgett RD Plant diversity and root
761	54.	traits benefit physical properties key to soil function in grasslands. Ecology Letters 10
762		1140 1140 (2016)
762		1140-1149 (2010).
705	55	Deich DD at al Import of highly ansity loss appolate through time as redundancy
/04 765	55.	fadag. Szimus 226 , 590, 502 (2012)
705		Tades. Science 330 , 589 - 592 (2012).
/00	F (
/6/	56.	Loreau M, Hector A. Partitioning selection and complementarity in biodiversity
768		experiments. <i>Nature</i> 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		

777 778 779	59.	Turnbull LA, Isbell F, Purves DW, Loreau M, Hector A. Undertanding the value of plant diversity for ecosystem functioning through niche theory. <i>Proc R Soc B</i> 283 , 20160536 (2016).
780		
781 782	60.	Edwards EJ, Osborne CP, Strömberg CAE, Smith SA. The Origins of C4 Grasslands: Integrating Evolutionary and Ecosystem Science. <i>Science</i> 328 , 587-591 (2010).
783 784 785 786	61.	Bartlett MK, Scoffoni C, Sack L. The determinants of leaf turgor loss point and prediction of drought tolerance of species and biomes: a global meta-analysis. <i>Ecology Letters</i> 15 , 393-405 (2012).
787		
788 789 790 791	62.	Schroeder-Georgi T, Wirth C, Nadrowski K, Meyer ST, Mommer L, Weigelt A. From pots to plots: hierarchical trait-based prediction of plant performance in a mesic grassland. <i>Journal of Ecology</i> 104 , 206-218 (2016).
792 793 794	63.	Iversen CM, <i>et al.</i> A global Fine-Root Ecology Database to address below-ground challenges in plant ecology. <i>New Phytologist</i> 215 , 15-26 (2017).
795 796 797	64.	Aubin I, <i>et al.</i> Traits to stay, traits to move: a review of functional traits to assess sensitivity and adaptive capacity of temperate and boreal trees to climate change. <i>Environ Rev</i> 24 , 164-186 (2016).
/98		
799 800 801 802	65.	Oelmann Y, <i>et al.</i> Plant diversity effects on aboveground and belowground N pools in temperate grassland ecosystems: Development in the first 5 years after establishment. <i>Global Biogeochemical Cycles</i> 25 , 1 - 11 (2011).
802 803 804 805	66.	van der Heijden MGA, <i>et al.</i> The mycorrhizal contribution to plant productivity, plant nutrition and soil structure in experimental grassland. <i>New Phytologist</i> 172 , 739 - 752 (2006).
806		
807 808 809	67.	Eisenhauer N, <i>et al.</i> Plant diversity effects on soil microorganisms support the singular hypothesis. <i>Ecology</i> 91 , 485 - 496 (2010).
810 811 812	68.	Eisenhauer N, Reich PB, Isbell F. Decomposer diversity and identity influence plant diversity effects on ecosystem functioning. <i>Ecology</i> 93 , 2227 - 2240 (2012).
812 813 814 815	69.	Mueller KE, Tilman D, Fornara DA, Hobbie SE. Root depth distribution and the diversity-productivity relationship in a long-term grassland experiment. <i>Ecology</i> 94 , 787 - 793 (2013).
816 817 818 810	70.	Ravenek JM, <i>et al.</i> Long-term study of root biomass in a biodiversity experiment reveals shifts in diversity effects over time. <i>Oikos</i> 123 , 1528-1536 (2014).
820 821 822	71.	Hoover DL, Duniway MC, Belnap J. Pulse-drought atop press-drought: unexpected plant responses and implications for dryland ecosystems. <i>Oecologia</i> 179 , 1211-1221 (2015).
823824825826	72.	Shi Z, <i>et al.</i> Dual mechanisms regulate ecosystem stability under decade-long warming and hay harvest. <i>Nature Communications</i> 7 , 11973 (2016).

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

877 878 879	88.	Grime JP, Hodgson JG, Hunt R. <i>Comparative plant ecology: a functional approach to common British species</i> . Springer (2007).
875 880 881 882 883	89.	Wacker L, Baudois O, Eichenberger-Glinz S, Schmid B. Diversity effects in early- and mid-successional species pools along a nitrogen gradient. <i>Ecology</i> 90 , 637-648 (2009).
884 885 886	90.	Roscher C, <i>et al.</i> Using plant functional traits to explain diversity–productivity relationships. <i>PLoS ONE</i> 7 , e36760 (2012).
887 888 889 890	91.	Daneshgar PP, Polley HW, Wilsey BJ. Simple plant traits explain functional group diversity decline in novel grassland communities of Texas. <i>Plant Ecology</i> 214 , 231-241 (2013).
891 892 803	92.	Lê S, Josse J, Husson F, others. FactoMineR: an R package for multivariate analysis. <i>Journal of statistical software</i> 25 , 1-18 (2008).
895 894 895 896	93.	Laliberté E, Legendre P. A distance-based framework for measuring functional diversity from multiple traits. <i>Ecology</i> 91 , 299-305 (2010).
897 898 898	94.	Zanne AE, <i>et al.</i> Three keys to the radiation of angiosperms into freezing environments. <i>Nature</i> 506 , 89 (2014).
900 901 902	95.	Pearse WD, <i>et al.</i> pez: phylogenetics for the environmental sciences. <i>Bioinformatics</i> 31 , 2888-2890 (2015).
903 904 905	96.	Webb CO, Ackerly DD, McPeek MA, Donoghue MJ. Phylogenies and Community Ecology. <i>Annual Review of Ecology and Systematics</i> 33 , 475-505 (2002).
905 906 907	97.	Godoy O, Kraft NJB, Levine JM. Phylogenetic relatedness and the determinants of competitive outcomes. <i>Ecology Letters</i> 17 , 836-844 (2014).
909 910 911 912	98.	Harris I, Jones PD, Osborn TJ, Lister DH. Updated high-resolution grids of monthly climatic observations – the CRU TS3.10 Dataset. <i>International Journal of Climatology</i> 34 , 623-642 (2014).
913 914 915	99.	Burnham KP, Anderson DR. <i>Model Selection and Multimodel Inference: a practical information-theoretic approach</i> , 2nd edn. Springer Science & Business Media (2003).
916 917 918 919	100.	Lefcheck JS. piecewiseSEM: Piecewise structural equation modelling in r for ecology, evolution, and systematics. <i>Methods in Ecology and Evolution</i> 7 , 573-579 (2016).
920 921 922 923 924 925 926	101.	R Development Core Team: A Language and Environment for Statistical Computing (R Foundation for Statistical Computing, Vienna, 2016).

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947 Authorship contributions

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.

Competing interests

958 The authors have no competing interests.



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

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1015 Figure 2. Phylogenetic (a; PD) and fast-slow functional diversity (b; Fast-Slow FD) and 1016 community-weighted mean of fast-slow traits (c; CWM Fast-Slow) effects on ecosystem 1017 stability of aboveground biomass production across 39 experimental grassland studies. Phylogenetic diversity is abundance-weighted mean nearest taxon distance (MNTD) and 1018 1019 Fast-Slow FD is abundance-weighted functional dispersion of fast-slow traits. CWM Fast-1020 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 1021 1022 (SLA), leaf matter dry content (LMDC), and leaf N and P concentrations. Low values of the 1023 fast-slow spectrum correspond to communities dominated by 'slow' species, i.e. low SLA 1024 and leaf N and P and high LDMC and high values to communities dominated 'fast species, 1025 i.e. high SLA and leaf N and P and low LDMC. Lines are mixed-effects model fits for each 1026 study (light gray lines) or across all studies (black lines; $P \le 0.05$). 1027



$\begin{array}{c} 1029 \\ 1030 \end{array}$

1031 Figure 3. Structural equation model (SEM) exploring the effects of plant species richness, 1032 fast-slow functional diversity (Fast-Slow FD; abundance-weighted functional dispersion), 1033 phylogenetic diversity (abundance-weighted mean nearest taxon distance, functional 1034 composition (CWM Fast-Slow), mean annual precipitation (\bar{x}_{Precip}), and interannual variation 1035 in precipitation (CV_{Precip}) on asynchrony and ecosystem stability of aboveground biomass 1036 production across 39 experimental grassland studies. The model fit the data well (Fisher's C 1037 = 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 1038 1039 significant ($P \le 0.05$), positive and negative standardized path coefficients, respectively, and 1040 gray arrows represent non-significant standardized path coefficients. Standardized path coefficients are given next to each (significant) path. Conditional R² (based on both fixed and 1041 random effects) for asynchrony and ecosystem stability is reported in the corresponding box. 1042 1043 The SEM was fitted using 'piecewise SEM' where 'study' was treated as a random group 1044 factor term and plant species richness as a random slope term, allowing regression slopes and 1045 intercepts to vary between studies. 1046





Figure 4. 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 (\overline{x}_{Precip}), and interannual variation in precipitation (CV_{Precip}) on asynchrony, mean ($\overline{x}_{\text{biomass}}$) and variation in (SD _{biomass}) aboveground biomass production and ecosystem stability of aboveground biomass production across 39 experimental grassland studies. The model fit the data well (Fisher's C = 24.52, df = 22, P =0.32; K = 49, n = 1,699). Boxes represent measured variables and arrows represent relationships among variables. Solid green and dashed red arrows represent significant ($P \le P$ 0.05), positive and negative standardized path coefficients, respectively, and gray arrows represent non-significant standardized path coefficients. Standardized path coefficient are given next to each (significant) path. Conditional R^2 (based on both fixed and random effects) for asynchrony, $\overline{x}_{\text{biomass}}$, SD _{biomass}, 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.