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

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3

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

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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<sup>1-4</sup>. 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<sup>5-8</sup>. Much of this work has examined the relationship  
163 between plant species diversity and biomass production, often in grasslands. Both theoretical  
164 and empirical research has consistently demonstrated that the primary productivity of  
165 species-rich communities shows lower variation over time than that of less diverse  
166 communities, a finding that has been attributed to a wide range of non-exclusive  
167 mechanisms<sup>9-16</sup>.

168

169 Temporal stability (or invariability) of ecosystem functioning is an integrative measure of the  
170 responses of populations and communities to each other and to environmental variation<sup>17</sup>.  
171 While there are many means of measuring stability<sup>8,18</sup>, temporal stability of primary biomass  
172 production is typically defined as mean biomass divided by its temporal standard deviation  
173 ( $\mu/\sigma$ <sup>19</sup>), and it is this invariability measure that we use throughout this paper. Thus, the higher  
174 stability of species-rich ecosystems is related to several properties including  
175 their greater biomass, higher resistance (i.e., biomass shows little deviation from average  
176 levels during perturbations) and/or resilience (i.e., biomass returns to average levels rapidly  
177 after perturbations)<sup>3,20,21</sup>. Furthermore, numerous statistical mechanisms have been proposed  
178 as drivers of stability and tested empirically<sup>11,13,14</sup>. Of these, perhaps the primary mechanism  
179 through which diversity stabilizes biomass production is species asynchrony<sup>13,14,22,23</sup>, which  
180 describes the extent to which species-level productivity is correlated within a community  
181 over time. Asynchrony, where decreases in the productivity of some species are compensated  
182 by increases in the productivity of other species, can promote ecosystem stability as a

183 consequence of interspecific interactions<sup>14,24</sup>, negative frequency dependence, e.g. due to  
184 pathogen outbreaks<sup>25,26</sup>, and/or the greater likelihood that diverse communities contain a  
185 wider range of species' responses to environmental conditions<sup>13,27</sup>. Accordingly, it is likely  
186 that multiple and correlated facets of biodiversity<sup>28</sup> underpin species asynchrony, including  
187 taxonomic diversity<sup>29</sup>, functional diversity<sup>30,31</sup>, and phylogenetic diversity<sup>32</sup>, which  
188 collectively may influence ecosystem stability<sup>33-35</sup>. We hypothesize that the relationship  
189 between biodiversity and ecosystem stability is mediated by four classes of biological drivers  
190 and that these operate both directly, e.g. by affecting biomass production, and indirectly, via  
191 species asynchrony.

192

193 The first class of biological drivers is functional composition, which may stabilize biomass  
194 production in grasslands because growth-related traits strongly influence the production,  
195 persistence, and stability of plant biomass<sup>36</sup>. While plants differ greatly in their trait values  
196 and strategies, a large proportion of global plant trait variation is correlated along a single leaf  
197 economics axis that distinguishes between exploitative species that are capable of rapid  
198 resource uptake, growth, and tissue turnover (hereafter 'fast' species) and conservative  
199 species with slower rates of growth, resource uptake, and tissue turnover (hereafter 'slow'  
200 species<sup>37,38</sup>). The former typically possess high specific leaf area (SLA), low leaf dry matter  
201 content (LDMC), and high leaf nitrogen concentrations (N), the latter the opposite<sup>38-40</sup>. There  
202 is growing evidence that variation in functional composition along this 'fast-slow' leaf  
203 economics spectrum influences ecosystem stability. For example, communities dominated by  
204 species with high LDMC values have been found to increase ecosystem stability in  
205 experimental and semi-natural grassland communities<sup>41</sup>. As high ecosystem resistance may  
206 limit the capacity for high resilience to be expressed by preventing perturbations from  
207 affecting baseline conditions, we may therefore expect that communities dominated by

208 species with slow leaf economics ('slow communities') will be more stable than those  
209 dominated by species with fast leaf economics ('fast communities')<sup>42</sup>. However, the net effect  
210 of fast-slow functional composition on ecosystem stability across multiple communities may  
211 be low because the opposing effects of fast communities, which should be more resilient, and  
212 slow communities, which should be more resistant, may cancel each other out.

213

214 Variation in fast-slow plant ecological strategies within a community, which can be  
215 quantified using functional diversity metrics, is the second class of biological drivers that  
216 may explain ecosystem stability. As fast species are likely to recover rapidly following  
217 disturbance (resilience), and slow species will be better able to tolerate environmental  
218 stresses and perturbations (resistance<sup>38,39</sup>), we hypothesize that communities with a diversity  
219 of fast-slow traits will exhibit both greater resistance and higher resilience, thus increasing  
220 ecosystem stability.

221

222 The third class of biological drivers that we propose as underlying the diversity-stability  
223 relationship are those associated with phylogenetic diversity. Generally, phylogenetic  
224 diversity can be seen as representing the diversity of phylogenetically conserved functional  
225 traits, which may constitute a broader set of traits than is typically included in functional  
226 diversity measures. Traits that reflect a shared co-evolutionary history of biotic interactions  
227 often show a high degree of phylogenetic conservatism<sup>43</sup>, such as symbiotic N<sub>2</sub> fixation and  
228 mycorrhizal tendency<sup>33,44</sup>. Closely related species are also known to share pathogens or  
229 immune responses via their shared co-evolutionary history<sup>45,46</sup>. Importantly, phylogenetic  
230 diversity has been shown to positively affect ecosystem stability in grasslands in most  
231 analyses<sup>32,33,35</sup>, but not all<sup>29</sup>. We therefore hypothesize that greater phylogenetic diversity will  
232 stabilize biomass production over time by increasing (measured and unmeasured) trait



233 diversity and by diluting the effects of pathogen outbreaks and herbivore attacks, which are  
234 strong regulators of biomass production in grasslands<sup>46</sup>.

235

236 Finally, plant species richness may affect ecosystem stability via pathways that are trait-based  
237 but not associated with the leaf economics spectrum and not phylogenetically conserved. This  
238 class of mechanism may include the effects of persistent seedbanks<sup>47</sup>, regrowth from  
239 belowground storage organs<sup>48</sup>, carbohydrate reserves<sup>49</sup>, variation in rooting depth<sup>50</sup>, and  
240 phenology<sup>51</sup>. We expect that these effects will indirectly enhance ecosystem stability via  
241 increased asynchrony<sup>13</sup> and directly via greater mean biomass production over time<sup>29,52</sup>.

242

243 While there is empirical evidence, typically from single sites, that each of the aforementioned  
244 biological drivers contributes to the overall relationship between diversity and stability, they  
245 likely operate concurrently and their relative importance and interrelationships have not been  
246 investigated. Here, we make a general, integrative assessment of the contribution of different  
247 facets of biodiversity in driving biodiversity-stability relationships. This was achieved by  
248 performing a meta-level analysis using data from 39 grassland biodiversity-ecosystem  
249 function experiments distributed across North America and Europe. Direct and indirect  
250 effects of the biological drivers were assessed using structural equation models (SEM), which  
251 represented the relationships described above (Supplementary Figs. 1 & 2), and which control  
252 for covariation among the different facets of biodiversity<sup>29,35</sup>. We hypothesized that: *i*) greater  
253 plant species richness, diversity in traits that capture the fast-slow leaf economics spectrum,  
254 and phylogenetic diversity will increase ecosystem stability by increasing asynchrony and  
255 that *ii*) species-rich communities with high fast-slow functional diversity and phylogenetic  
256 diversity, and those dominated by species with slow leaf economics, will increase ecosystem  
257 stability directly as they increase the temporal mean of biomass production, a component of

258 stability, via classical diversity-function mechanisms, e.g. complementarity and selection  
259 effects<sup>24,53</sup>.

260

## 261 **Results**

262 Our analysis shows positive 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), and that these are significant and  
266 generally consistent across experiments (Figs. 1 & 2). These drivers explained low amounts  
267 of variation in ecosystem stability (Supplementary Table 1, marginal  $R^2$ ), with a larger  
268 proportion being explained by the random effects (Supplementary Tables 1 and 2, conditional  
269  $R^2$ ). In contrast, although phylogenetic diversity and fast-slow functional diversity were  
270 positively related to ecosystem stability, there was no consistent effect of the community-  
271 weighted mean of fast-slow traits on ecosystem stability ( $P > 0.10$ ; Fig. 2c). However, the  
272 effect of the community-weighted mean of fast-slow traits was highly variable across all  
273 experimental sites; at certain experimental sites dominance by species with slow traits  
274 stabilized productivity (Fig. 2c), while fast species stabilized production at others.

275

276 These relationships were investigated in more depth with our structural equation model,  
277 which provides strong evidence that asynchrony is a key mechanism mediating the  
278 biodiversity-stability relationship and that asynchrony is driven by multiple facets of  
279 biodiversity (Fig. 3). Overall, the data fit our model well (Fisher's  $C = 7.51$ ,  $df = 12$ ,  $P =$   
280  $0.82$ ;  $K = 34$ ,  $n = 1,699$ ). Fixed effects explained 20% of variation in ecosystem stability  
281 (marginal  $R^2$ ), which increased to 59% (conditional  $R^2$ ) when accounting for fixed and  
282 random effects. In total, plant species richness, phylogenetic diversity, fast-slow functional

283 diversity, and mean and inter-annual variation in water availability explained 52% of  
284 variation in species asynchrony (marginal  $R^2$ ), which increased to 79% when random effects  
285 were accounted for (conditional  $R^2$ ).

286

287 The strongest pathway of influence on ecosystem stability was from plant species richness  
288 via species asynchrony (standardized path coefficient of indirect effect = 0.21). This effect  
289 was larger and more consistent across experimental sites than the direct effect of species  
290 richness (standardized path coefficient of direct effect = 0.03,  $P = 0.60$ ), thus suggesting that  
291 much of the effect of plant species richness on ecosystem stability is explained by species  
292 asynchrony. Phylogenetic diversity also had strong yet opposing effects on ecosystem  
293 stability. It indirectly increased ecosystem stability via asynchrony (standardized path  
294 coefficient of indirect effect = 0.12), while the direct pathway between phylogenetic diversity  
295 and ecosystem stability was negative (standardized path coefficient of direct effect = - 0.10;  $P$   
296 < 0.001). This negative effect was weaker than the positive indirect effect via species  
297 asynchrony, thus explaining the overall positive relationship between phylogenetic diversity  
298 and ecosystem stability, along with covariance with species richness (Fig. 2a).

299

300 The community-weighted mean of fast-slow traits had a direct negative effect on ecosystem  
301 stability, meaning that communities dominated by slow species were more stable than those  
302 dominated by fast species (Fig. 3). Contrary to our expectations, the SEM revealed that fast-  
303 slow functional diversity did not directly or indirectly (via asynchrony) stabilize ecosystem  
304 productivity ( $P > 0.05$ ). Furthermore, these weak effects of fast-slow functional diversity on  
305 ecosystem stability were also generally robust to the use of an alternative measure of fast-  
306 slow functional diversity, functional richness (Supplementary Fig. 3). Finally, we assessed  
307 potentially important effects of climate and found that mean and inter-annual variation in

308 water availability had significant, yet opposite effects on ecosystem stability and no  
309 significant effects on species asynchrony (Fig. 3).

310

311 Further analyses provided added insight into mechanisms underlying the biodiversity-  
312 stability relationship. By including the two components of the invariability measure in a  
313 separate SEM, i.e., mean and standard deviation of biomass production, we found that species  
314 richness and the community-weighted mean of fast-slow traits stabilized mean aboveground  
315 biomass production while asynchrony decreased inter-annual variation in biomass (Fig. 4;  
316 Fisher's  $C = 22.19$ ,  $df = 22$ ,  $P = 0.45$ ;  $K = 49$ ,  $n = 1,699$ ). Fixed effects explained 52% of  
317 variation in ecosystem stability (marginal  $R^2$ ), which increased to 64% (conditional  $R^2$ ) when  
318 also accounting for random effects. Multiple facets of biodiversity and climate only explained  
319 15% and 8% of variation in mean and standard deviation of biomass production (marginal  
320  $R^2$ ), respectively. When also accounting for across-site variation (conditional  $R^2$ ), explained  
321 variation increased to 66% for mean aboveground biomass production and 48% for the  
322 standard deviation of biomass.

323

324 Species richness promoted ecosystem stability by increasing mean aboveground biomass  
325 production but also increasing its variability, while the direct effect of phylogenetic diversity  
326 on ecosystem stability operated via negative effects on the standard deviation of biomass.

327 Furthermore, these analyses revealed that the weak negative effect of the community-  
328 weighted mean of fast-slow traits on ecosystem stability masked contrasting effects on the  
329 components of the invariability measure; communities dominated by species with fast trait  
330 values decreased mean biomass (standardized path coefficient of direct effect = -0.12) to a  
331 greater extent than they decreased standard deviation of biomass (standardized path  
332 coefficient of direct effect = -0.08). Asynchrony increased ecosystem stability by reducing

333 the standard deviation of biomass. Finally, inter-annual variation in water availability had  
334 strong yet variable effects on the standard deviation of biomass (standardized path coefficient  
335 of direct effect = 0.17,  $P = 0.08$ ), while those of mean water availability on mean  
336 aboveground biomass production were weak. These relationships were generally robust to the  
337 use of different combinations of phylogenetic and functional diversity indices and detrended  
338 ecosystem stability (Supplementary Figs. 4-8).

339

340 As most studies available for inclusion in our analyses collected data for less than four years  
341 (33 of 39 studies), we performed sensitivity analyses to test whether our results differed  
342 between short- and long-term studies. We found that bivariate relationships between stability  
343 and individual facets of biodiversity had similar results between short- and long-term studies,  
344 as indicated by non-significant interactions between study duration and each facet of  
345 biodiversity (Supplementary Table 3). In an SEM using only data from long-term studies (six  
346 studies >4 years,  $n = 454$  plots), we found that our overall conclusions were not affected by  
347 study duration but that certain paths became stronger, with notable increases in the effects of  
348 fast-slow functional diversity (Supplementary Fig. 9). In long-term studies, fast-slow  
349 functional diversity had both a direct positive effect on ecosystem stability and a negative  
350 effect operating on asynchrony (Supplementary Fig. 9). The strength of the effects of the  
351 community-weighted mean of fast-slow traits on ecosystem stability also increased, with fast  
352 communities having a direct negative effect on ecosystem stability (Supplementary Fig. 9).  
353 Further sensitivity analyses showed that trait identity affected path strength and direction  
354 (Supplementary Figs. 10-13). Of the four individual traits making up the fast-slow leaf  
355 economics spectrum, the community-weighted means of leaf P and leaf N had direct positive  
356 and negative effects on ecosystem stability, respectively, while the effects of the community-  
357 weighted means of LDMC and SLA on ecosystem stability were not statistically significant.

358

359 **Discussion**

360

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

365

366 The strongest and most consistent driver of stability across the 39 experiments examined in  
367 our study was that of species richness, operating via species asynchrony. This likely reflects  
368 niche differences among species that affect their relative performance over time in a  
369 temporally variable environment<sup>22,54-56</sup>. However, these niche differences were not captured  
370 by the functional diversity of fast-slow leaf traits or phylogenetic diversity. Instead, the  
371 species richness-asynchrony-stability relationship may be driven by unmeasured traits that  
372 are not phylogenetically conserved. Such traits may be related to rooting strategies,  
373 photosynthetic pathways, non-structural carbohydrate concentrations, and properties related  
374 to phenology, demographic storage and regeneration<sup>48,49,51,57-59</sup>. Data for some of these traits  
375 is relatively sparse<sup>60</sup> and the collection of such information should be a priority in addressing  
376 the current question and those related to other aspects of ecosystem stability, i.e. resistance  
377 and resilience<sup>61</sup>.

378

379 Species richness also affected ecosystem stability directly. We found that species richness  
380 stabilizes biomass production via its stronger effects on mean biomass production over time  
381 than effects operating via the standard deviation, which is in line with previous studies<sup>14,29</sup>.  
382 As with the effects of species richness on asynchrony, we suggest that these effects may be  
383 explained by effects of species richness on complementarity and selection<sup>24,53</sup> that are

384 unrelated to the functional diversity of fast-slow leaf traits or phylogenetic diversity.  
385  
386 The next most important driver of diversity-stability relationships was phylogenetic diversity.  
387 Interestingly, phylogenetic diversity influences ecosystem stability via two different  
388 pathways, one positive and operating indirectly via species asynchrony, and one negative and  
389 operating directly. The indirect asynchrony pathway was the stronger of the two, resulting in  
390 a positive overall effect and is likely due to a range of phylogenetically conserved traits. As  
391 herbivores and pathogens often have a narrow and phylogenetically conserved host range<sup>45,46</sup>,  
392 herbivore attacks and disease outbreaks can be weaker in communities of distantly related  
393 species and thus affect only a small proportion of community biomass. In contrast,  
394 phylogenetically clustered communities will experience strong and simultaneous reductions  
395 in biomass production as pests and pathogens spread across the community. The weaker  
396 direct negative effect operated via standard deviation in biomass. This path may reflect  
397 experimental communities that are dominated by more inherently stable and phylogenetically  
398 clustered plant functional groups, such as grasses<sup>62,63</sup>. Furthermore, our analysis illustrates  
399 that the effects of phylogenetic diversity on ecosystem stability are sensitive to the  
400 phylogenetic diversity metric used<sup>35</sup>. Consistent with<sup>29</sup>, but in contrast with those presented  
401 in Figs. 3 and 4, SEMs using mean pairwise distance (MPD) showed weak direct and indirect  
402 effects of phylogenetic diversity on ecosystem stability, probably due to its strong, positive  
403 correlation with plant species richness (Supplementary Figs. 3 & 4, Supplementary Appendix  
404 2). We suggest that the stronger effects of MNTD reflect the fact that it better represents the  
405 tendency for pathogens and herbivores, which play a major role in driving grassland  
406 productivity<sup>25,64</sup>, to have a phylogenetically narrow host range<sup>45,46</sup>.  
407  
408 Evidence for the fast-slow leaf economics spectrum affecting ecosystem stability as an

409 overall strategy (community-weighted mean) was weak across the full dataset. However, this  
410 relationship masked contrasting effects of fast traits, which reduced mean aboveground  
411 biomass production while reducing its standard deviation. The net result was that  
412 communities dominated by species with fast trait values were marginally less stable than  
413 those dominated by species with slow trait values. Furthermore, individual site-level  
414 relationships between the community-weighted mean of fast-slow traits and ecosystem  
415 stability were often very strong, but extremely variable across sites. These findings suggest  
416 that the relationship between the fast-slow leaf economics spectrum and ecosystem stability is  
417 heavily dependent upon site-specific factors, which could include study duration,  
418 environmental conditions, and the ‘matching’ of appropriate functional strategies to a site.  
419 For example, fast traits may confer ecosystem stability at sites subject to repeated  
420 disturbances due to their ability to allow fast recovery, while slow traits may confer  
421 ecosystem stability in the face of chronic environmental stresses, such as low nutrient  
422 availability or water availability, e.g. the Texan dry grasslands included in our study<sup>65,66</sup>. Site-  
423 level information detailing disturbance regimes and the constancy of soil water availability  
424 and nutrient supply at a finer temporal resolution may clarify in which environmental  
425 conditions particular plant strategies stabilize (or destabilize) biomass production<sup>67</sup>.  
426  
427 The effect of fast-slow functional diversity and the community-weighted mean of fast-slow  
428 traits became markedly stronger when only long-term (i.e. >4 year) studies were considered.  
429 We hypothesize that this is due to the strengthening of biodiversity effects on mean  
430 community biomass production over time<sup>68</sup>. Furthermore, the hypothesized effects of fast and  
431 slow traits on resilience and resistance have a greater chance of detection because extreme  
432 events, e.g. drought, are more likely to occur in long-term studies<sup>21</sup>. However, such patterns  
433 may also be driven by ecological differences in the sites where long- and short-term studies



434 were conducted, as long-term sites tended to include more communities dominated by slow  
435 species (Supplementary Fig. 14).

436

437 The final driver of ecosystem stability in our models was climate. Mean and inter-annual  
438 variation in water availability had equally strong, yet opposing effects on ecosystem stability,  
439 which were manifested largely via the standard deviation of aboveground biomass production  
440 over time. This is likely to represent the strong annual variation in the timing and intensity of  
441 aboveground biomass production in seasonal environments, e.g. inter-annual variation in  
442 temperature and the timing and intensity of rains, and provides evidence that inter-annual  
443 climatic variability may be a key driver of ecosystem stability<sup>67,69,70</sup>. As mentioned above, a  
444 better characterization of site conditions may provide a more complete understanding of the  
445 drivers of ecosystem stability<sup>4</sup>. Furthermore, other studies have indicated a powerful  
446 interactive role between environmental conditions and biotic community properties<sup>71,72</sup>, as  
447 abiotic and management factors not only control diversity and productivity, but also influence  
448 the capacity for diversity to stabilize ecosystem function by altering the mechanisms that  
449 regulate diversity, such as asynchrony and resource-use complementarity<sup>23,67,73</sup>. This means  
450 that under natural conditions changes in diversity are not the ultimate cause of ecosystem  
451 stability, but are an intermediate property of ecosystem response to global change drivers that  
452 might also influence ecosystem stability via other pathways. A greater understanding of these  
453 interactions and how they operate in natural ecosystems is required to improve both our  
454 fundamental understanding of ecosystem stability and to integrate knowledge of diversity-  
455 stability relationship into agroecosystem management<sup>74</sup>. To do this, further studies that  
456 incorporate both global change drivers, and the measurement and manipulation of diversity  
457 are required<sup>75,76</sup>. Threshold-based measures of stability<sup>17</sup> may also be more relevant to  
458 agroecological research than the variability measures employed here, as such measures allow

459 under- and overproduction to be considered differently.

460

461 In conclusion, our study makes a general, multi-site assessment of how multiple facets of  
462 biodiversity, e.g. taxonomic, functional, and phylogenetic diversity, influence diversity-  
463 stability relationships. By integrating multiple factors that are hypothesized to control  
464 diversity-stability relationships in a single analysis, we were able to identify several  
465 important pathways, including those related to phylogenetic diversity and the fast-slow leaf  
466 economics spectrum, through which plant community properties affect the stability of  
467 grassland biomass productivity. Furthermore, the meta-level approach here allows us to  
468 assess which of these relationships are general and strong, and which are context dependent.  
469 In an era of increased climatic variability<sup>77,78</sup> and biodiversity change, it is important to gain a  
470 deeper understanding of each of these component processes so that the functional benefits of  
471 biodiversity may be effectively conserved and promoted.

472

## 473 **Methods**

### 474 **Data preparation**

475 We assembled a database by combining data from biodiversity experiments that manipulated  
476 plant species richness in grasslands and measured community- and species-level aboveground  
477 plant biomass annually for at least three years. In total, we used data from 39 studies across  
478 North America and Europe (Supplementary Table 4) from<sup>21</sup> and<sup>73</sup>. Our dataset comprises  
479 observations from 1,699 plots and 165 plant species, which were standardized using the  
480 Taxonomic Name Resolution Service (<http://trns.iplantcollaborative.org><sup>79</sup>).

481

482 For each plot within the experiments, we quantified ecosystem stability as the inverse of the  
483 coefficient of variation of aboveground plant biomass ( $\mu/\sigma^{19}$ ), which is the ratio of the mean

484 to the standard deviation of annual aboveground plant biomass over time. Ecosystem stability  
485 was determined with and without detrending, as recent studies have shown directional  
486 changes in aboveground plant biomass with time<sup>52,68</sup>. Ecosystem stability was detrended by  
487 regressing aboveground plant biomass against experimental year and calculating the standard  
488 deviation of the residuals of each regression<sup>9</sup>. For each plot, detrended ecosystem stability  
489 was calculated as mean aboveground plant biomass divided by the detrended standard  
490 deviation. All main analyses were performed using ecosystem stability with (Figs. 1-4) and  
491 without detrending (Supplementary Figs. 5-8). As results were qualitatively similar, we  
492 present results for ecosystem stability without detrending in the main text and for detrended  
493 ecosystem stability in Supplementary Information .

494

495 Following<sup>14</sup>, species synchrony ( $\eta$ ) was quantified as the average correlation across species  
496 between the biomass of each species and the total biomass of all other species in a plot:

$$497 \eta = (1/n) \sum_i \text{corr} (Y_i, \sum_{j \neq i} Y_j) , \quad (1)$$

498 where  $Y_i$  is the biomass of species  $i$  in a plot containing  $n$  species. Because asynchrony  
499 implies negative synchrony, we multiplied  $\eta$  by -1. Thus, species asynchrony ( $-\eta$ ) ranges  
500 from -1, where species' aboveground plant biomass is maximally synchronous, to 1, where  
501 species' aboveground plant biomass is maximally asynchronous. Further,  $-\eta$  is independent of  
502 the number of species and their individual variances<sup>14</sup>, which contrasts with species  
503 asynchrony as calculated by<sup>80</sup>.

504

505 We selected four leaf traits associated with the fast-slow leaf economics spectrum<sup>37</sup>, specific  
506 leaf area (SLA;  $\text{mm}^2 \text{mg}^{-1}$ ), leaf dry matter content (LDMC;  $\text{g g}^{-1}$ ), foliar N (%), and foliar P  
507 (%). These data were obtained from the TRY database<sup>81</sup> (Supplementary Appendix 1) and  
508 additional studies in our database that measured traits<sup>82-85</sup>. Trait values were converted to

509 standardized units and those considered unlikely to be correct ( $z$ -score  $> 4$ <sup>81</sup>) were excluded.  
510 Values were then averaged by trait data contributor and then by species. Genus-level means  
511 were used when species-level data were not available; species-level data for SLA, LDMC,  
512 leaf N, and leaf P were available for 98%, 83 %, 92 %, and 62 % of species, respectively.  
513 Combining species- and genus-level values, our final trait data set included SLA, LDMC, and  
514 foliar N values for more than 96% of the species and leaf P values for 93% of the species.  
515 While absolute values of species-level traits may differ between locally collected data and  
516 databases, which may influence our ability to detect biodiversity effects<sup>86</sup>, inter-specific  
517 variation is usually greater than intra-specific variation (particularly for organ-level traits)  
518 and species ranking is conserved for commonly used traits across data sources<sup>87,88</sup>.

519

#### 520 **Fast-slow functional composition and diversity**

521 We used the first axis of a principal component analysis (PCA) of community-weighted  
522 means of SLA, LDMC, leaf N, and leaf P to represent the fast-slow leaf economics spectrum  
523 (hereafter ‘community-weighted mean (CWM) of fast-slow traits’<sup>38</sup>). PCA was performed  
524 using the *PCA* function in ‘FactoMineR’<sup>89</sup>. The first PCA captured 60.4% of variation among  
525 the four traits (Supplementary Fig. 15) and represents the fast-slow leaf economics spectrum  
526 of communities, from those dominated by slow species with low SLA and leaf N and P and  
527 high LDMC to those dominated by fast species with high SLA and leaf N and P and low  
528 LDMC.

529

530 We calculated functional diversity in traits associated with the fast-slow leaf economics  
531 spectrum (hereafter ‘fast-slow functional diversity’) as either abundance-weighted functional  
532 dispersion or functional richness to represent complementarity among co-occurring species  
533 and volume of trait space, respectively, using the ‘FD’ package<sup>90</sup>. Results for both measures

534 of fast-slow functional diversity were qualitatively similar. Therefore, we present results for  
535 functional dispersion in the main text and for functional richness in Supplementary  
536 Information. Functional composition and functional diversity were calculated annually for  
537 each plot and then averaged across years.

538

### 539 **Phylogenetic diversity**

540 We used the molecular phylogeny from <sup>91,92</sup> as a backbone to build a phylogeny of all species  
541 within the experiments, conservatively binding species into the backbone using dating  
542 information from congeners in the tree (using *congeneric.merge*<sup>93</sup>). We then calculated  
543 abundance-weighted phylogenetic diversity as mean nearest taxon distance (MNTD<sup>94</sup>) and  
544 mean pairwise distance (MPD) annually for each plot and then calculated the average across  
545 years. MNTD has captured competitive differences among species in previous studies<sup>95</sup> and  
546 the sharing of specialized pathogens tends to be confined to closely related species<sup>45,46</sup>.  
547 MNTD, therefore, is a good metric to test our hypotheses about the mechanisms that explain  
548 variation in species asynchrony and ecosystem stability. Furthermore, there was a strong,  
549 positive correlation between MPD and plant species richness ( $r = 0.86$ ; Supplementary  
550 Appendix 2). We therefore present results for MNTD in the main text and for MPD in  
551 Supplementary Information.

552

### 553 **Climate**

554 As empirical and theoretical studies have shown strong impacts of mean and inter-annual  
555 variation in water availability on productivity in grasslands<sup>67,69,70</sup>, we included site-level  
556 climate data to explain across-site variation in ecosystem stability and species asynchrony. To  
557 capture the joint effects<sup>96</sup> of precipitation and temperature on experimental plant communities  
558 during each study, we calculated a water availability index as the ratio of annual precipitation

559 to potential evapotranspiration<sup>97</sup> using data from CRU TS 4.0.1<sup>98</sup> (Supplementary Table 4).

560 For each study, we calculated mean and the standard deviation of water availability.

561

## 562 **Data analysis**

563 To explore bivariate relationships between each of our hypothesized drivers and ecosystem

564 stability, we fit separate linear mixed-effects models (independently of SEMs) that tested for

565 the effects of plant species richness, phylogenetic diversity, fast-slow functional diversity,

566 community-weighted mean of fast-slow traits, and species asynchrony on ecosystem stability.

567 Multiple random effect structures were tested for each model, first using a basic structure

568 defined by the experimental design of all studies where study was treated as a random

569 intercept and species richness as a random slope. We also tested for interactions of predictor

570 variables with plant species richness and included them as random slopes when supported by

571 model selection. We used AICc to select the most parsimonious random effects structure.

572 AICc is a second-order bias correction to Akaike's information criterion for small sample

573 sizes<sup>99</sup>. Models were fit using the 'nlme' package and model assumptions were checked by

574 visually inspecting residual plots for homogeneity and quantile-quantile plots for normality.

575 Intra-class correlation (ICC) was calculated to compare variability within a study to

576 variability across studies.

577

578 Because many studies collected data for less than four years, we also tested whether our

579 results differed between short- and long-term studies. We did so by adding a two-way

580 interaction between a predictor variable and study duration and study duration as a main

581 effect to the models in Supplementary Table 1, where study duration was a binary variable

582 with a value of one for studies that collected data for more than four years and a value of zero

583 for all other studies. For all models, we found similar results between short- and long-term

584 studies, as interactions between each facet of biodiversity and study duration were not  
585 statistically significant (Supplementary Table 3).

586

587 To test the relative importance of the different mechanisms represented by the community-  
588 weighted mean of fast-slow traits, fast-slow functional diversity, phylogenetic diversity,  
589 climate, and asynchrony in driving temporal stability, we fit piecewise structural equation  
590 models<sup>100</sup> (SEM) using ‘piecewiseSEM’. Testing for relationships with resistance and  
591 resilience (as in <sup>21</sup>) was not possible because of the unequal distribution of extreme climate  
592 events across sites, which prevented fitting a general SEM. We formulated a hypothetical  
593 causal model (Supplementary Fig. 1) based on *a priori* knowledge of grassland ecosystems  
594 and used this to test the fit of the model to the data. We also included direct paths from  
595 species richness, fast-slow functional diversity, and phylogenetic diversity to ecosystem  
596 stability to represent biological drivers that influence ecosystem stability, e.g. via  
597 complementarity effects on the temporal mean of biomass production<sup>24,53</sup>. Finally, we  
598 included direct paths from mean and inter-annual variation in water availability to ecosystem  
599 stability. We included direct paths from species richness to fast-slow functional diversity and  
600 phylogenetic diversity because variation in these variables can be directly attributed to the  
601 experimental manipulation of species richness in all studies<sup>33</sup>.

602

603 All initial models contained partial bivariate correlations between fast-slow functional  
604 diversity and phylogenetic diversity<sup>35</sup>. Additional partial bivariate correlations were added to  
605 the initial model if they significantly improved model fit using modification indices ( $P <$   
606  $0.05$ ). To test the sensitivity of our model to functional and phylogenetic diversity indices, the  
607 duration of the time series, and the choice of traits, we fit additional models for each  
608 combination of functional and phylogenetic diversity indices, using only data from long-term

609 experiments (>4 years), and for each functional trait separately. Finally, we fit another SEM  
610 to see if stabilizing effects on biomass production operated via the two components of the  
611 invariability measure, mean and standard deviation of biomass production (Supplementary  
612 Fig. 2). In this model, we added direct paths from species richness, phylogenetic diversity,  
613 fast-slow functional diversity, and species asynchrony to the mean and standard deviation of  
614 biomass and from mean water availability to mean biomass and from inter-annual variation in  
615 water availability to standard deviation of biomass production. Model fit was assessed using  
616 Fisher's C statistic ( $P > 0.10$ ). SEMs were fit using linear mixed-effects models where study  
617 was treated as a random factor and species richness as a random slope. Random effect  
618 structures allowed the intercepts and slopes to vary among studies. In all analyses, plant  
619 species richness, ecosystem stability, and mean water availability were  $\log_2$  transformed to  
620 meet normality assumptions. Model assumptions of normality were inspected visually. As  
621 many of the variables included in our SEM were correlated (see Supplementary Appendix 2),  
622 we estimated variance inflation. This demonstrated that multi-collinearity did not affect  
623 parameter estimates ( $VIF < 3$ ). All analyses were performed using R 3.4.4<sup>101</sup>.

624

625 **Data availability.** Data supporting the findings of this study are available from the authors  
626 upon request.

627

628 **Code availability.** R code of all analyses is available via GitHub ([https://github.com/idiv-](https://github.com/idiv-biodiversity/StabilityII)  
629 [biodiversity/StabilityII](https://github.com/idiv-biodiversity/StabilityII)).

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631

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660 **Authorship contributions**

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662 DC, NE, and FI conceived the project, DC, PM, NE, WDP, YH, CR, FI, AE, JNG, JH, AJ,

663 NL, STM, JvR, AW, and MDS further developed the project in a workshop; NE, CR, FI, MB,

664 CB, GB, NB, CB, BELC, JAC, JHCC, JMC, EDL, AH, AJ, JK, JK, VL, VM, VO, HWP,

665 PBR, JvR, BS, NAS, DT, AW, and BW contributed experimental and functional trait data;

666 DC compiled data; DC analyzed data with significant input from PM, NE, WDP, and YH.

667 DC and PM wrote the first draft of the manuscript and all co-authors contributed substantially

668 to revisions.

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671 **Competing interests**

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697 **Figure Legends**

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699 **Figure 1.** Plant species richness (**a**) and species asynchrony (**b**) effects on ecosystem  
700 stability of aboveground biomass production across 39 experimental grassland studies. Lines  
701 are mixed-effects model fits for each study (light gray lines) or across all studies (black lines;  
702  $P \leq 0.05$ ). Synchrony ranges from -1 to 1, where -1 represents maximum synchrony and +1  
703 maximum asynchrony. Marginal and conditional  $R^2$  represent model variation explained by  
704 fixed effects and the combination of fixed and random effects, respectively. Light blue bands  
705 represent 95% confidence intervals.

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708 **Figure 2.** Phylogenetic (**a**; PD) and fast-slow functional diversity (**b**; Fast-Slow FD) and  
709 community-weighted mean of fast-slow traits (**c**; CWM Fast-Slow) effects on ecosystem  
710 stability of aboveground biomass production across 39 experimental grassland studies.  
711 Phylogenetic diversity is abundance-weighted mean nearest taxon distance (MNTD) and  
712 Fast-Slow FD is abundance-weighted functional dispersion of fast-slow traits. CWM Fast-  
713 Slow is the first axis of a principal component analysis of community-weighted means of key  
714 leaf functional traits associated with ‘fast’ and ‘slow’ ecological strategies: specific leaf area  
715 (SLA), leaf matter dry content (LDMC), and leaf N and P concentrations. Low values of the  
716 fast-slow spectrum correspond to communities dominated by ‘slow’ species, i.e. low SLA  
717 and leaf N and P and high LDMC and high values to communities dominated ‘fast’ species,  
718 i.e. high SLA and leaf N and P and low LDMC. Lines are mixed-effects model fits for each  
719 study (light gray lines) or across all studies (black lines;  $P \leq 0.05$ ). Marginal and conditional  
720  $R^2$  represent model variation explained by fixed effects and the combination of fixed and  
721 random effects, respectively. Light blue bands represents 95% confidence intervals.

722

723 **Figure 3.** Structural equation model (SEM) exploring the effects of plant species richness,  
724 fast-slow functional diversity (Fast-Slow FD; abundance-weighted functional dispersion),  
725 phylogenetic diversity (abundance-weighted mean nearest taxon distance), functional  
726 composition (CWM Fast-Slow), mean ( $\bar{x}_{\text{WaterAvail}}$ ) and inter-annual variation in water  
727 availability ( $\text{sd}_{\text{WaterAvail}}$ ) on species asynchrony and ecosystem stability of aboveground  
728 biomass production across 39 experimental grassland studies. The model fit the data well  
729 (Fisher’s  $C = 7.51$ ,  $df = 12$ ,  $P = 0.82$ ;  $K = 34$ ,  $n = 1,699$ ). Boxes represent measured variables  
730 and arrows represent relationships among variables. Solid blue and dashed red arrows  
731 represent significant ( $P \leq 0.05$ ), positive and negative standardized path coefficients,  
732 respectively, and gray arrows represent non-significant standardized path coefficients.  
733 Standardized path coefficients are given next to each (significant) path; widths of significant  
734 paths are scaled by standardized path coefficients. Conditional  $R^2$  (based on both fixed and  
735 random effects) for asynchrony and ecosystem stability is reported in the corresponding box.

736

737 **Figure 4.** Structural equation model (SEM) exploring the effects of plant species richness,  
738 fast-slow functional diversity (Fast-Slow FD; abundance-weighted functional dispersion),  
739 phylogenetic diversity (abundance-weighted mean nearest taxon distance), functional  
740 composition (CWM Fast-Slow), mean ( $\bar{x}_{\text{WaterAvail}}$ ) and inter-annual variation in water  
741 availability ( $\text{sd}_{\text{WaterAvail}}$ ) on species asynchrony, mean ( $\bar{x}_{\text{biomass}}$ ) and variation in ( $\text{sd}_{\text{biomass}}$ )  
742 aboveground biomass production and ecosystem stability of aboveground biomass production  
743 across 39 experimental grassland studies. The model fit the data well (Fisher’s  $C = 22.19$ ,  $df$   
744  $= 22$ ,  $P = 0.45$ ;  $K = 49$ ,  $n = 1,699$ ). Boxes represent measured variables and arrows represent  
745 relationships among variables. Solid blue and dashed red arrows represent significant ( $P \leq$   
746  $0.05$ ), positive and negative standardized path coefficients, respectively, and gray arrows

747 represent non-significant standardized path coefficients. Standardized path coefficient are  
748 given next to each (significant) path; widths of significant paths are scaled by standardized  
749 path coefficients. Conditional  $R^2$  (based on both fixed and random effects) for asynchrony,  
750  $\bar{x}_{\text{biomass}}$ ,  $sd_{\text{biomass}}$ , and ecosystem stability is reported in the corresponding box.  
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