



Swansea University
Prifysgol Abertawe



Cronfa - Swansea University Open Access Repository

This is an author produced version of a paper published in:
Nature Ecology & Evolution

Cronfa URL for this paper:
<http://cronfa.swan.ac.uk/Record/cronfa43762>

Paper:

Craven, D., Eisenhauer, N., Pearse, W., Hautier, Y., Isbell, F., Roscher, C., Bahn, M., Beierkuhnlein, C., Bönisch, G., et. al. (2018). Multiple facets of biodiversity drive the diversity–stability relationship. *Nature Ecology & Evolution*
<http://dx.doi.org/10.1038/s41559-018-0647-7>

This item is brought to you by Swansea University. Any person downloading material is agreeing to abide by the terms of the repository licence. Copies of full text items may be used or reproduced in any format or medium, without prior permission for personal research or study, educational or non-commercial purposes only. The copyright for any work remains with the original author unless otherwise specified. The full-text must not be sold in any format or medium without the formal permission of the copyright holder.

Permission for multiple reproductions should be obtained from the original author.

Authors are personally responsible for adhering to copyright and publisher restrictions when uploading content to the repository.

<http://www.swansea.ac.uk/library/researchsupport/ris-support/>

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

2

3

4 **Authors**

5

6 Dylan Craven^{1,2,3,4*}, Nico Eisenhauer^{1,2}, William D. Pearse⁵, Yann Hautier⁶, Forest Isbell
7⁷, Christiane Roscher^{8,1}, Michael Bahn⁹, Carl Beierkuhnlein¹⁰, Gerhard Bönisch¹¹, Nina
8 Buchmann¹², Chaeho Byun¹³, Jane A. Catford¹⁴, Bruno E.L. Cerabolini¹⁵, J. Hans C.
9 Cornelissen¹⁶, Joseph M. Craine¹⁷, Enrica De Luca¹⁸, Anne Ebeling¹⁹, John N. Griffin²⁰,
10 Andy Hector²¹, Jes Hines^{1,2}, Anke Jentsch²², Jens Kattge^{1,11}, Jürgen Kreyling²³, Vojtech
11 Lanta^{24,25}, Nathan Lemoine²⁶, Sebastian T. Meyer²⁷, Vanessa Minden^{28,29}, Vladimir
12 Onipchenko³⁰, H. Wayne Polley³¹, Peter B. Reich^{32,33}, Jasper van Ruijven³⁴, Brandon
13 Schamp³⁵, Melinda D. Smith²⁶, Nadejda A. Soudzilovskaia³⁶, David Tilman⁷, Alexandra
14 Weigelt^{1,2}, Brian Wilsey³⁷, Peter Manning³⁸

15

16 **Author Affiliations**

17

18 1 German Centre for Integrative Biodiversity Research (iDiv) Halle-Jena-Leipzig, 04103
19 Leipzig, Germany

20 2 Institute of Biology, Leipzig University, 04103 Leipzig, Germany

21 3 Department of Community Ecology, Helmholtz Centre for Environmental Research – UFZ,
22 06120 Halle (Saale), Germany

23 4 Biodiversity, Macroecology & Biogeography, Faculty of Forest Sciences and Forest
24 Ecology, University of Göttingen, 37077 Göttingen, Germany

25 5 Department of Biology, Utah State University, Logan, UT 84322, USA

26 6 Ecology and Biodiversity Group, Department of Biology, Utrecht University, Utrecht, CH
27 3584, The Netherlands

28 7 Department of Ecology, Evolution and Behavior, University of Minnesota, Saint Paul, MN,
29 USA

30 8 Department of Physiological Diversity, Helmholtz Centre for Environmental Research –
31 UFZ, 04103 Leipzig, Germany

32 9 Institute of Ecology, University of Innsbruck, 6020 Innsbruck, Austria

33 10 Department of Biogeography, BayCEER, University of Bayreuth, 95440 Bayreuth,
34 Germany

35 11 Max Planck Institute for Biogeochemistry, 07754 Jena, Germany

36 12 Institute of Agricultural Sciences, ETH Zurich, Zurich, Switzerland

37 13 School of Civil and Environmental Engineering, Yonsei University, Seoul 03722, Korea
38 14 Biological Sciences, University of Southampton, Southampton, SO17 1BJ, UK
39 15 Department of Theoretical and Applied Science, University of Insubria, Varese I-21100,
40 Italy
41 16 Systems Ecology, Department of Ecological Science, Vrije Universiteit, 1081 HV
42 Amsterdam, The Netherlands
43 17 Jonah Ventures, Manhattan, KS 66502, USA
44 18 Institute of Evolutionary Biology and Environmental Studies, University of Zurich, 8057
45 Zurich, Switzerland
46 19 Institute of Ecology, University of Jena, 07743 Jena, Germany
47 20 Department of Biosciences, College of Science, Swansea University, Swansea, Wales, UK
48 21 Department of Plant Sciences, University of Oxford, Oxford, OX1 3RB, UK
49 22 Department of Disturbance Ecology, BayCEER, University of Bayreuth, 95440 Bayreuth,
50 Germany
51 23 Experimental Plant Ecology, Institute of Botany and Landscape Ecology, Greifswald
52 University, 17487 Greifswald, Germany
53 24 Department of Botany, Faculty of Science, University of South Bohemia, 37005 České
54 Budějovice, Czech Republic
55 25 Department of Functional Ecology, Institute of Botany CAS, 37901 Třeboň, Czech
56 Republic
57 26 Department of Biology, Graduate Degree Program in Ecology, Colorado State University,
58 Fort Collins, CO, USA
59 27 Department of Ecology and Ecosystem Management, School of Life Sciences
60 Weihenstephan, Technical University of Munich, 85354 Freising, Germany
61 28 Department of Biology, Ecology and Biodiversity, Vrije Universiteit Brussel, 1050
62 Brussels, Belgium
63 29 Institute of Ecology and Environmental Sciences, Landscape Ecology Group, University
64 of Oldenburg, 26111 Oldenburg, Germany
65 30 Faculty of Biology, Department of Geobotany, Moscow State University, Moscow, Russia
66 31 USDA, Agricultural Research Service, Grassland, Soil & Water Research Laboratory,
67 Temple, Texas 76502, USA
68 32 Department of Forest Resources, University of Minnesota, St. Paul, MN 55108, USA
69 33 Hawkesbury Institute for the Environment, Western Sydney University, Penrith, New
70 South Wales 2751, Australia
71 34 Plant Ecology and Nature Conservation Group, Wageningen University, 6700 AA
72 Wageningen, The Netherlands
73 35 Dept. of Biology, Algoma University, Sault Ste. Marie, Ontario, Canada, P6A 2G4
74 36 Environmental Biology Department, Institute of Environmental Sciences, CML, Leiden
75 University, 2333 CC Leiden, The Netherlands
76

77 37 Department of Ecology, Evolution and Organismal Biology, Iowa State University, Ames,
78 IA, USA

79 38 Senckenberg Biodiversity and Climate Research Centre (SBIK-F), 60325 Frankfurt,
80 Germany

81

82

83

84 * **Contact information:**

85

86 Biodiversity, Macroecology & Biogeography, Faculty of Forest Sciences and Forest Ecology,

87 University of Göttingen

88 Büsgenweg 1, 37077

89 Göttingen, Germany

90

91 e-mail: dylan.craven@aya.yale.edu

92

93

94

95

96

97

98

99

100

101

102

103

104

105

106

107

108

109

110

111

112

113

114

115

116

117

118

119

120

121

122

123

124

125

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.**

142
143
144
145
146
147
148
149
150
151
152
153
154
155

156

157

158 The relationship between the biodiversity and the stability of ecosystems has long been a
159 fundamental subject of ecological research¹⁻⁴. More recently, this research topic has gained
160 new impetus due to concerns about the consequences of global environmental change and
161 biodiversity loss, both of which threaten the stability of ecosystem functions and the
162 ecosystem services they underpin⁵⁻⁸. 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 mechanisms⁹⁻¹⁶.

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 variation¹⁷.
171 While there are many means of measuring stability^{8,18}, temporal stability of primary biomass
172 production is typically defined as mean biomass divided by its temporal standard deviation
173 (μ/σ ¹⁹), 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)^{3,20,21}. Furthermore, numerous statistical mechanisms have been proposed
178 as drivers of stability and tested empirically^{11,13,14}. Of these, perhaps the primary mechanism
179 through which diversity stabilizes biomass production is species asynchrony^{13,14,22,23}, 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^{14,24}, negative frequency dependence, e.g. due to
184 pathogen outbreaks^{25,26}, and/or the greater likelihood that diverse communities contain a
185 wider range of species' responses to environmental conditions^{13,27}. Accordingly, it is likely
186 that multiple and correlated facets of biodiversity²⁸ underpin species asynchrony, including
187 taxonomic diversity²⁹, functional diversity^{30,31}, and phylogenetic diversity³², which
188 collectively may influence ecosystem stability³³⁻³⁵. 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 biomass³⁶. 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^{37,38}). 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 opposite³⁸⁻⁴⁰. 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 communities⁴¹. 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')⁴². 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^{38,39}), 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 conservatism⁴³, such as symbiotic N₂ fixation and
228 mycorrhizal tendency^{33,44}. Closely related species are also known to share pathogens or
229 immune responses via their shared co-evolutionary history^{45,46}. Importantly, phylogenetic
230 diversity has been shown to positively affect ecosystem stability in grasslands in most
231 analyses^{32,33,35}, but not all²⁹. 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 grasslands⁴⁶.

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 seedbanks⁴⁷, regrowth from
239 belowground storage organs⁴⁸, carbohydrate reserves⁴⁹, variation in rooting depth⁵⁰, and
240 phenology⁵¹. We expect that these effects will indirectly enhance ecosystem stability via
241 increased asynchrony¹³ and directly via greater mean biomass production over time^{29,52}.

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^{29,35}. 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^{24,53}.

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^{22,54-56}. 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^{48,49,51,57-59}. Data for some of these traits
375 is relatively sparse⁶⁰ 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 resilience⁶¹.

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^{14,29}.
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^{24,53} 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^{45,46},
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^{62,63}. Furthermore, our analysis illustrates
399 that the effects of phylogenetic diversity on ecosystem stability are sensitive to the
400 phylogenetic diversity metric used³⁵. Consistent with²⁹, 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^{25,64}, to have a phylogenetically narrow host range^{45,46}.
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^{65,66}. 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 production⁶⁷.
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 time⁶⁸. 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 studies²¹. 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^{67,69,70}. As mentioned above, a
444 better characterization of site conditions may provide a more complete understanding of the
445 drivers of ecosystem stability⁴. Furthermore, other studies have indicated a powerful
446 interactive role between environmental conditions and biotic community properties^{71,72}, 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^{23,67,73}. 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 management⁷⁴. To do this, further studies that
456 incorporate both global change drivers, and the measurement and manipulation of diversity
457 are required^{75,76}. Threshold-based measures of stability¹⁷ 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^{77,78} 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) from²¹ and⁷³. 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>⁷⁹).

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 (μ/σ^{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^{52,68}. Ecosystem stability was detrended by
487 regressing aboveground plant biomass against experimental year and calculating the standard
488 deviation of the residuals of each regression⁹. 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 Following¹⁴, species synchrony (η) 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 η 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 variances¹⁴, which contrasts with species
503 asynchrony as calculated by⁸⁰.

504

505 We selected four leaf traits associated with the fast-slow leaf economics spectrum³⁷, specific
506 leaf area (SLA; $\text{mm}^2 \text{mg}^{-1}$), leaf dry matter content (LDMC; g g^{-1}), foliar N (%), and foliar P
507 (%). These data were obtained from the TRY database⁸¹ (Supplementary Appendix 1) and
508 additional studies in our database that measured traits⁸²⁻⁸⁵. Trait values were converted to

509 standardized units and those considered unlikely to be correct (z -score > 4 ⁸¹) 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 effects⁸⁶, 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^{87,88}.

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’³⁸). PCA was performed
524 using the *PCA* function in ‘FactoMineR’⁸⁹. 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’ package⁹⁰. 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 ^{91,92} 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*⁹³). We then calculated
543 abundance-weighted phylogenetic diversity as mean nearest taxon distance (MNTD⁹⁴) 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 studies⁹⁵ and
546 the sharing of specialized pathogens tends to be confined to closely related species^{45,46}.
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^{67,69,70}, we included site-level
556 climate data to explain across-site variation in ecosystem stability and species asynchrony. To
557 capture the joint effects⁹⁶ 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 evapotranspiration⁹⁷ using data from CRU TS 4.0.1⁹⁸ (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 sizes⁹⁹. 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 models¹⁰⁰ (SEM) using ‘piecewiseSEM’. Testing for relationships with resistance and
591 resilience (as in ²¹) 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^{24,53}. 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 studies³³.

602

603 All initial models contained partial bivariate correlations between fast-slow functional
604 diversity and phylogenetic diversity³⁵. 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 3.4.4¹⁰¹.

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)).

630

631

632

633

1. May, R. M. *Stability and complexity in model ecosystems*. **6**, (Princeton University Press, 1973).
2. McNaughton, S. J. Stability and diversity of ecological communities. *Nature* **274**, 251–253 (1978).
3. Tilman, D. & Downing, J. A. Biodiversity and stability in grasslands. *Nature* **367**, 363–365 (1994).
4. Ives, A. R. & Carpenter, S. R. Stability and Diversity of Ecosystems. *Science* **317**, 58–62 (2007).
5. Balvanera, P. *et al.* Quantifying the evidence for biodiversity effects on ecosystem functioning and services. *Ecol. Lett.* **9**, 1146–1156 (2006).
6. Hautier, Y. *et al.* Anthropogenic environmental changes affect ecosystem stability via biodiversity. *Science* **348**, 336–340 (2015).
7. Isbell, F., Tilman, D., Polasky, S. & Loreau, M. The biodiversity-dependent ecosystem service debt. *Ecol. Lett.* **18**, 119–134 (2015).
8. Donohue, I. *et al.* Navigating the complexity of ecological stability. *Ecol. Lett.* **19**, 1172–1185 (2016).
9. Tilman, D., Reich, P. B. & Knops, J. M. H. Biodiversity and ecosystem stability in a decade-long grassland experiment. *Nature* **441**, 629–632 (2006).
10. Jiang, L. & Pu, Z. Different effects of species diversity on temporal stability in single-trophic and multitrophic communities. *Am. Nat.* **174**, 651–659 (2009).
11. Hector, A. *et al.* General stabilizing effects of plant diversity on grassland productivity through population asynchrony and overyielding. *Ecology* **91**, 2213–2220 (2010).
12. Campbell, V., Murphy, G. & Romanuk, T. N. Experimental design and the outcome and interpretation of diversity–stability relations. *Oikos* **120**, 399–408 (2011).
13. de Mazancourt, C. *et al.* Predicting ecosystem stability from community composition and biodiversity. *Ecol. Lett.* **16**, 617–625 (2013).
14. Gross, K. *et al.* Species Richness and the Temporal Stability of Biomass Production: A

- New Analysis of Recent Biodiversity Experiments. *Am. Nat.* **183**, 1–12 (2014).
15. Aussenac, R. *et al.* Intraspecific variability in growth response to environmental fluctuations modulates the stabilizing effect of species diversity on forest growth. *J. Ecol.* **105**, 1010–1020 (2017).
 16. del Rio, M. *et al.* Species interactions increase the temporal stability of community productivity in *Pinus sylvestris*–*Fagus sylvatica* mixtures across Europe. *J. Ecol.* **105**, 1032–1043 (2017).
 17. Oliver, T. H. *et al.* Biodiversity and Resilience of Ecosystem Functions. *Trends Ecol. Evol.* **30**, 673–684 (2015).
 18. Arnoldi, J.-F., Loreau, M. & Haegeman, B. Resilience, reactivity and variability: a mathematical comparison of ecological stability measures. *J. Theor. Biol.* **389**, 47–59 (2016).
 19. Tilman, D. The ecological consequences of changes in biodiversity: a search for general principles. *Ecology* **80**, 1455–1474 (1999).
 20. Van Ruijven, J. & Berendse, F. Diversity enhances community recovery, but not resistance, after drought. *J. Ecol.* **98**, 81–86 (2010).
 21. Isbell, F. *et al.* Biodiversity increases the resistance of ecosystem productivity to climate extremes. *Nature* **526**, 574–577 (2015).
 22. Yachi, S. & Loreau, M. Biodiversity and ecosystem productivity in a fluctuating environment: The insurance hypothesis. *Proc. Natl. Acad. Sci.* **96**, 1463–1468 (1999).
 23. Hautier, Y. *et al.* Eutrophication weakens stabilizing effects of diversity in natural grasslands. *Nature* **508**, 521–525 (2014).
 24. Lehman, C. L. & Tilman, D. Biodiversity, Stability, and Productivity in Competitive Communities. *Am. Nat.* **156**, 534–552 (2000).
 25. Maron, J. L., Marler, M., Klironomos, J. N. & Cleveland, C. C. Soil fungal pathogens and the relationship between plant diversity and productivity. *Ecol. Lett.* **14**, 36–41 (2011).
 26. Schnitzer, S. A. *et al.* Soil microbes drive the classic plant diversity–productivity pattern. *Ecology* **92**, 296–303 (2011).

27. Tredennick, A. T., de Mazancourt, C., Loreau, M. & Adler, P. B. Environmental responses, not species interactions, determine synchrony of dominant species in semiarid grasslands. *Ecology* **98**, 971–981 (2017).
28. Naeem, S. *et al.* Biodiversity as a multidimensional construct: a review, framework and case study of herbivory's impact on plant biodiversity. *Proc R Soc B* **283**, 20153005 (2016).
29. Venail, P. *et al.* Species richness, but not phylogenetic diversity, influences community biomass production and temporal stability in a re-examination of 16 grassland biodiversity studies. *Funct. Ecol.* **29**, 615–626 (2015).
30. Roscher, C. *et al.* Identifying population- and community-level mechanisms of diversity–stability relationships in experimental grasslands. *J. Ecol.* **99**, 1460–1469 (2011).
31. 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. *Ecology* **99**, 360–371 (2018).
32. Cadotte, M. W., Dinnage, R. & Tilman, D. Phylogenetic diversity promotes ecosystem stability. *Ecology* **93**, S223–S233 (2012).
33. Flynn, D. F. B., Mirotnick, N., Jain, M., Palmer, M. I. & Naeem, S. Functional and phylogenetic diversity as predictors of biodiversity–ecosystem–function relationships. *Ecology* **92**, 1573–1581 (2011).
34. Spasojevic, M. J. & Suding, K. N. Inferring community assembly mechanisms from functional diversity patterns: the importance of multiple assembly processes. *J. Ecol.* **100**, 652–661 (2012).
35. Cadotte, M. W. Phylogenetic diversity and productivity: gauging interpretations from experiments that do not manipulate phylogenetic diversity. *Funct. Ecol.* **29**, 1603–1606 (2015).
36. Díaz, S. & Cabido, M. Vive la différence: plant functional diversity matters to ecosystem processes. *Trend Ecol. Evol.* **16**, 646–655 (2001).
37. Wright, I. J. *et al.* The worldwide leaf economics spectrum. *Nature* **428**, 821–827

- (2004).
38. Reich, P. B. The world-wide ‘fast–slow’ plant economics spectrum: a traits manifesto. *J. Ecol.* **102**, 275–301 (2014).
 39. Grime, J. P. Evidence for the existence of three primary strategies in plants and its relevance to ecological and evolutionary theory. *Am. Nat.* **111**, 1169–1194 (1977).
 40. Díaz, S. *et al.* The global spectrum of plant form and function. *Nature* **529**, 167–171 (2016).
 41. Polley, H. W., Isbell, F. I. & Wilsey, B. J. Plant functional traits improve diversity-based predictions of temporal stability of grassland productivity. *Oikos* **122**, 1275–1282 (2013).
 42. Májeková, M., de Bello, F., Doležal, J. & Lepš, J. Plant functional traits as determinants of population stability. *Ecology* **95**, 2369–2374 (2014).
 43. Gomez, J. M., Verdu, M. & Perfectti, F. Ecological interactions are evolutionarily conserved across the entire tree of life. *Nature* **465**, 918–921 (2010).
 44. Reinhart, K. O., Wilson, G. W. T. & Rinella, M. J. Predicting plant responses to mycorrhizae: integrating evolutionary history and plant traits. *Ecol. Lett.* **15**, 689–695 (2012).
 45. Gilbert, G. S., Magarey, R., Suiter, K. & Webb, C. O. Evolutionary tools for phytosanitary risk analysis: phylogenetic signal as a predictor of host range of plant pests and pathogens. *Evol. Appl.* **5**, 869–878 (2012).
 46. Parker, I. M. *et al.* Phylogenetic structure and host abundance drive disease pressure in communities. *Nature* **520**, 542–544 (2015).
 47. Pérez-Harguindeguy, N. *et al.* New handbook for standardised measurement of plant functional traits worldwide. *Aust. J. Bot.* **61**, 167–234 (2013).
 48. Hoover, D. L., Knapp, A. K. & Smith, M. D. Resistance and resilience of a grassland ecosystem to climate extremes. *Ecology* **95**, 2646–2656 (2014).
 49. O’Brien, M. J., Leuzinger, S., Philipson, C. D., Tay, J. & Hector, A. Drought survival of tropical tree seedlings enhanced by non-structural carbohydrate levels. *Nat. Clim Change* **4**, 710–714 (2014).

50. Weigelt, A., Schumacher, J., Roscher, C. & Schmid, B. Does biodiversity increase spatial stability in plant community biomass? *Ecol. Lett.* **11**, 338–347 (2008).
51. Fargione, J. & Tilman, D. Niche differences in phenology and rooting depth promote coexistence with a dominant C4 bunchgrass. *Oecologia* **143**, 598–606 (2005).
52. Reich, P. B. *et al.* Impact of Biodiversity Loss Escalate Through Time As Redundancy Fades. *Science* **336**, 589–592 (2012).
53. Loreau, M. & Hector, A. Partitioning selection and complementarity in biodiversity experiments. *Nature* **412**, 72–76 (2001).
54. Allan, E. *et al.* More diverse plant communities have higher functioning over time due to turnover in complementary dominant species. *Proc. Natl. Acad. Sci.* **108**, 17034–17039 (2011).
55. Isbell, F. *et al.* High plant diversity is needed to maintain ecosystem services. *Nature* **477**, 199–202 (2011).
56. Turnbull, L. A., Isbell, F., Purves, D. W., Loreau, M. & Hector, A. Understanding the value of plant diversity for ecosystem functioning through niche theory. *Proc. R. Soc. Lond. B Biol. Sci.* **283**, (2016).
57. Edwards, E. J., Osborne, C. P., Strömberg, C. A. E. & Smith, S. A. The Origins of C4 Grasslands: Integrating Evolutionary and Ecosystem Science. *Science* **328**, 587–591 (2010).
58. Bartlett, M. K., Scoffoni, C. & Sack, L. The determinants of leaf turgor loss point and prediction of drought tolerance of species and biomes: a global meta-analysis. *Ecol. Lett.* **15**, 393–405 (2012).
59. Schroeder & Georgi, T. *et al.* From pots to plots: hierarchical trait-based prediction of plant performance in a mesic grassland. *J. Ecol.* **104**, 206–218 (2016).
60. Iversen, C. M. *et al.* A global Fine-Root Ecology Database to address below-ground challenges in plant ecology. *New Phytol.* **215**, 15–26 (2017).
61. Aubin, I. *et al.* 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. *Environ. Rev.* **24**, 164–186 (2016).

62. Hoover, D. L., Duniway, M. C. & Belnap, J. Pulse-drought atop press-drought: unexpected plant responses and implications for dryland ecosystems. *Oecologia* **179**, 1211–1221 (2015).
63. Shi, Z. *et al.* Dual mechanisms regulate ecosystem stability under decade-long warming and hay harvest. *Nat. Commun.* **7**, 11973 (2016).
64. Mitchell, C. E., Tilman, D. & Groth, J. V. Effects of Grassland Plant Species Diversity, Abundance, and Composition on Foliar Fungal Disease. *Ecology* **83**, 1713–1726 (2002).
65. Wilsey, B. J. & Polley, H. W. Realistically Low Species Evenness Does Not Alter Grassland Species-Richness-Productivity Relationships. *Ecology* **85**, 2693–2700 (2004).
66. Wilsey, B. J., Teaschner, T. B., Daneshgar, P. P., Isbell, F. I. & Polley, H. W. Biodiversity maintenance mechanisms differ between native and novel exotic-dominated communities. *Ecol. Lett.* **12**, 432–442 (2009).
67. Hallett, L. M. *et al.* Biotic mechanisms of community stability shift along a precipitation gradient. *Ecology* **95**, 1693–1700 (2014).
68. Guerrero-Ramírez, N. R. *et al.* Diversity-dependent temporal divergence of ecosystem functioning in experimental ecosystems. *Nat. Ecol. Evol.* **1** (2017). doi:10.1038/s41559-017-0325-1
69. Craine, J. M. *et al.* Timing of climate variability and grassland productivity. *Proc. Natl. Acad. Sci.* **109**, 3401–3405 (2012).
70. Stuart-Haëntjens, E. *et al.* Mean annual precipitation predicts primary production resistance and resilience to extreme drought. *Sci. Total Environ.* **636**, 360–366 (2018).
71. Xu, Z. *et al.* Environmental changes drive the temporal stability of semi-arid natural grasslands through altering species asynchrony. *J. Ecol.* **103**, 1308–1316 (2015).
72. Yang, Z. *et al.* Daytime warming lowers community temporal stability by reducing the abundance of dominant, stable species. *Glob. Change Biol.* **23**, 154–163 (2017).
73. Craven, D. *et al.* Plant diversity effects on grassland productivity are robust to both nutrient enrichment and drought. *Philos. Trans. R. Soc. Lond. B Biol. Sci.* **371**, (2016).
74. Isbell, F. *et al.* Linking the influence and dependence of people on biodiversity across scales. *Nature* **546**, 65–72 (2017).

75. Borer, E. T. *et al.* Finding generality in ecology: a model for globally distributed experiments. *Methods Ecol. Evol.* **5**, 65–73 (2014).
76. Eisenhauer Nico *et al.* Biodiversity–ecosystem function experiments reveal the mechanisms underlying the consequences of biodiversity change in real world ecosystems. *J. Veg. Sci.* **27**, 1061–1070 (2016).
77. Goodess, C. M. How is the frequency, location and severity of extreme events likely to change up to 2060? *Environ. Sci. Policy* **27, Supplement 1**, S4–S14 (2013).
78. Stott, P. How climate change affects extreme weather events. *Science* **352**, 1517–1518 (2016).
79. Boyle, B. *et al.* The taxonomic name resolution service: an online tool for automated standardization of plant names. *BMC Bioinformatics* **14**, 16 (2013).
80. Loreau, M. & Mazancourt, C. de. Species synchrony and its drivers: neutral and nonneutral community dynamics in fluctuating environments. *Am. Nat.* **172**, E48–E66 (2008).
81. Kattge, J. *et al.* TRY - a global database of plant traits. *Glob. Change Biol.* **17**, 2905–2935 (2011).
82. Grime, J. P. Plant strategy theories: a comment on Craine (2005). *J. Ecol.* **95**, 227–230 (2007).
83. Wacker, L., Baudois, O., Eichenberger-Glinz, S. & Schmid, B. Diversity effects in early- and mid-successional species pools along a nitrogen gradient. *Ecology* **90**, 637–48 (2009).
84. Roscher, C. *et al.* Using Plant Functional Traits to Explain Diversity–Productivity Relationships. *PLoS ONE* **7**, e36760 (2012).
85. Daneshgar, P. P., Polley, H. W. & Wilsey, B. J. Simple plant traits explain functional group diversity decline in novel grassland communities of Texas. *Plant Ecol.* **214**, 231–241 (2013).
86. Roscher Christiane *et al.* Origin context of trait data matters for predictions of community performance in a grassland biodiversity experiment. *Ecology* **99**, 1214–1226 (2018).

87. Kazakou, E. *et al.* Are trait-based species rankings consistent across data sets and spatial scales? *J. Veg. Sci.* **25**, 235–247 (2014).
88. Siefert, A. *et al.* A global meta-analysis of the relative extent of intraspecific trait variation in plant communities. *Ecol. Lett.* **18**, 1406–1419 (2015).
89. Lê, S., Josse, J., Husson, F. & others. FactoMineR: an R package for multivariate analysis. *J. Stat. Softw.* **25**, 1–18 (2008).
90. Laliberté, E. & Legendre, P. A distance-based framework for measuring functional diversity from multiple traits. *Ecology* **91**, 299–305 (2010).
91. Zanne, A. E. *et al.* Three keys to the radiation of angiosperms into freezing environments. *Nature* **506**, 89 (2014).
92. Zanne, A. *et al.* *Data from: Three keys to the radiation of angiosperms into freezing environments.* (Dryad Digital Repository, 2013). doi:10.5061/dryad.63q27.2
93. Pearse, W. D. *et al.* pez: phylogenetics for the environmental sciences. *Bioinformatics* **31**, 2888–2890 (2015).
94. Webb, C. O., Ackerly, D. D., McPeck, M. A. & Donoghue, M. J. Phylogenies and Community Ecology. *Annu. Rev. Ecol. Syst.* **33**, 475–505 (2002).
95. Godoy, O., Kraft, N. J. B. & Levine, J. M. Phylogenetic relatedness and the determinants of competitive outcomes. *Ecol. Lett.* **17**, 836–844 (2014).
96. Valencia Enrique *et al.* Functional diversity enhances the resistance of ecosystem multifunctionality to aridity in Mediterranean drylands. *New Phytol.* **206**, 660–671 (2015).
97. Middleton, N. J. & Thomas, D. S. *World Atlas of Desertification.* (United Nations Environment Programme / Edward Arnold, 1992).
98. Harris, I.C. & Jones, P.D. CRU TS4.01: Climatic Research Unit (CRU) Time-Series (TS) version 4.01 of high-resolution gridded data of month-by-month variation in climate (Jan. 1901- Dec. 2016). *Cent. Environ. Data Anal.*
99. Burnham, K. & Anderson, D. *Model Selection and Multimodel Inference: a practical information-theoretic approach.* (Springer Science & Business Media, 2003).
100. Lefcheck, J. S. piecewiseSEM: Piecewise structural equation modelling in r for ecology,

evolution, and systematics. *Methods Ecol. Evol.* **7**, 573–579 (2016).

101. R Core Team. *R: A Language and Environment for Statistical Computing*. (R
Foundation for Statistical Computing, 2018).

636

637

638

639 **Acknowledgements**

640 This paper is a product of the sSTABILITY group funded by sDiv (www.idiv.de/stability), the
641 Synthesis Centre of the German Centre for Integrative Biodiversity Research (iDiv) Halle-
642 Jena-Leipzig (DFG FZT 118). The Jena Experiment is funded by the Deutsche
643 Forschungsgemeinschaft (DFG, German Research Foundation; FOR 1451) and the Swiss
644 National Science Foundation. The Cedar Creek biodiversity experiments were supported by
645 awards from the Andrew Mellon Foundation, the U.S. National Science Foundation (NSF)
646 Long-Term Ecological Research (DEB-9411972, DEB-0080382, DEB-0620652, and DEB-
647 1234162), Biocomplexity Coupled Biogeochemical Cycles (DEB-0322057), Long-Term
648 Research in Environmental Biology (DEB-0716587, DEB-1242531), and Ecosystem
649 Sciences (NSF DEB- 1120064) Programs; as well as the U.S. Department of Energy
650 Programs for Ecosystem Research (DE-FG02-96ER62291), and National Institute for
651 Climatic Change Research (DE-FC02-06ER64158). The Texas MEND study was funded by
652 US-NSF DEB-0639417 and USDA-NIFA-2014-67003-22067. The study has been supported
653 by the TRY initiative on plant traits (<http://www.try-db.org>). TRY is currently supported by
654 DIVERSITAS/Future Earth and the German Centre for Integrative Biodiversity Research
655 (iDiv) Halle-Jena-Leipzig. V.O. received financial support from the Russian Science
656 Foundation (#14-50-00029). The authors would also like to thank Jon Lefcheck for his help
657 in revising the structural equation model.

658

659

660 **Authorship contributions**

661

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.

669

670

671 **Competing interests**

672 The authors have no competing interests.

673

674 **Correspondence**

675 Correspondence and requests for materials should be addressed to DC

676 (dylan.craven@aya.yale.edu).

677

678

679

680

681

682

683

684

685

686

687

688

689

690

691

692

693

694

695

696

697 **Figure Legends**

698

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.

706

707

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}_{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}_{biomass} , sd_{biomass} , and ecosystem stability is reported in the corresponding box.
751
752
753







