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Multiple facets of biodiversity drive the diversity–stability relationship

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A substantial body of evidence has demonstrated that biodiversity stabilizes ecosystem functioning over time in grassland ecosystems. However, the relative importance of different facets of biodiversity underlying the diversity–stability relationship remains unclear. Here we use data from 39 grassland biodiversity experiments and structural equation modelling to investigate the roles of species richness, phylogenetic diversity and both the diversity and community-weighted mean of functional traits representing the 'fast–slow' leaf economics spectrum in driving the diversity–stability relationship. We found that high species richness and phylogenetic diversity stabilize biomass production via enhanced asynchrony in the performance of co-occurring species. Contrary to expectations, low phylogenetic diversity enhances ecosystem stability directly, albeit weakly. While the diversity of fast–slow functional traits has a weak effect on ecosystem stability, communities dominated by slow species enhance ecosystem stability by increasing mean biomass production relative to the standard deviation of biomass over time. Our in-depth, integrative assessment of factors influencing the diversity–stability relationship demonstrates a more multicausal relationship than has been previously acknowledged.

The relationship between the biodiversity and the stability of ecosystems has long been a fundamental subject of ecological research[1–4]. More recently, this research topic has gained new impetus due to concerns about the consequences of global environmental change and biodiversity loss, both of which threaten the stability of ecosystem functions and the ecosystem services they underpin[5–8]. Much of this work has examined the relationship between plant species diversity and biomass production, often in

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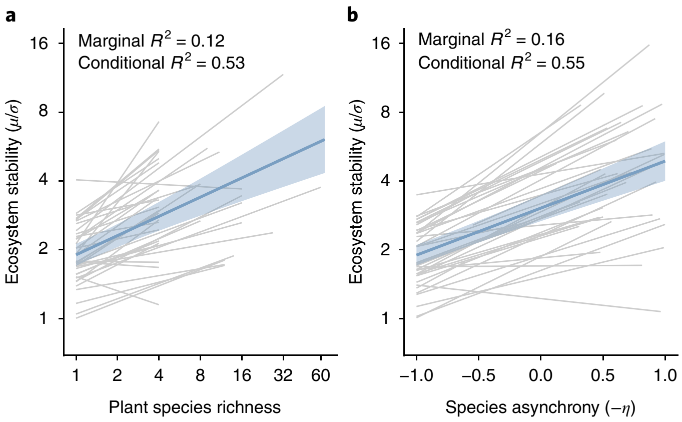

Fig. 1 | Relationships among ecosystem stability, plant species richness and species asynchrony across experimental grasslands. a, **b**, Plant species richness (**a**) and species asynchrony (**b**) effects on ecosystem stability of aboveground biomass production across 39 experimental grassland studies.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

grasslands. Both theoretical and empirical research has consistently demonstrated that the primary productivity of species-rich communities shows lower variation over time than that of less diverse communities, a finding that has been attributed to a wide range of non-exclusive mechanisms[9–16].

Temporal stability (or invariability) of ecosystem functioning is an integrative measure of the responses of populations and communities to each other and to environmental variation[17]. While there are many means of measuring stability[8,18], temporal stability of primary biomass production is typically defined as mean biomass divided by its temporal standard deviation (μ/σ[19]) and it is this invariability measure that we use throughout this paper. Thus, the higher stability of species-rich ecosystems is related to several properties including their greater biomass, higher resistance (biomass shows little deviation from average levels during perturbations) and/or resilience (biomass returns to average levels rapidly after perturbations)[3,20,21]. Furthermore, numerous statistical mechanisms have been proposed as drivers of stability and tested empirically[11,13,14]. Of these, perhaps the primary mechanism through which diversity stabilizes biomass production is species asynchrony[13,14,22,23], which describes the extent to which species-level productivity is correlated within a community over time. Asynchrony, where decreases in the productivity of some species are compensated by increases in the productivity of other species, can promote ecosystem stability as a consequence of interspecific interactions[14,24], negative frequency dependence, for example due to pathogen outbreaks[25,26] and/or the greater likelihood that diverse communities contain a wider range of species' responses to environmental conditions[13,27]. Accordingly, it is likely that multiple and correlated facets of biodiversity[28] underpin species asynchrony, including taxonomic diversity[29], functional diversity[30,31] and phylogenetic diversity[32], which collectively may influence ecosystem stability[33–35]. We hypothesize that the relationship between biodiversity and ecosystem stability is mediated by four classes of biological drivers and that these operate both directly, for instance by affecting biomass production, and indirectly, via species asynchrony.

The first class of biological drivers is functional composition, which may stabilize biomass production in grasslands because growth-related traits strongly influence the production, persistence and stability of plant biomass[36]. While plants differ greatly in their trait values and strategies, a large proportion of global plant trait variation is correlated along a single leaf economics axis that distinguishes between exploitative species that are capable of rapid resource uptake, growth and tissue turnover (hereafter 'fast' species) and conservative species with slower rates of growth, resource uptake and tissue turnover (hereafter 'slow' species)[37,38]. The former typically possess high specific leaf area (SLA), low leaf dry matter content (LDMC) and high leaf nitrogen concentrations (N), the latter the opposite[38–40]. There is growing evidence that variation in functional composition along this 'fast–slow' leaf economics spectrum influences ecosystem stability. For example, communities dominated by species with high LDMC values have been found to increase ecosystem stability in experimental and semi-natural grassland communities[41]. As high ecosystem resistance may limit the capacity for high resilience to be expressed by preventing perturbations from affecting baseline conditions, we may therefore expect that communities dominated by species with slow leaf economics ('slow communities') will be more stable than those dominated by species with fast leaf economics ('fast communities')[42]. However, the net effect of fast–slow functional composition on ecosystem stability across multiple communities may be low because the opposing effects of fast communities, which should be more resilient, and slow communities, which should be more resistant, may cancel each other out.

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

The third class of biological drivers that we propose as underlying the diversity–stability relationship are those associated with phylogenetic diversity. Generally, phylogenetic diversity can be seen as representing the diversity of phylogenetically conserved functional traits, which may constitute a broader set of traits than is typically included in functional diversity measures. Traits that reflect a shared co-evolutionary history of biotic interactions often show a high degree of phylogenetic conservatism[43], such as symbiotic N_2 fixation and mycorrhizal tendency[33,44]. Closely related species are also known to share pathogens or immune responses via their shared co-evolutionary history[45,46]. Importantly, phylogenetic diversity has been shown to positively affect ecosystem stability in grasslands in most analyses[32,33,35], but not all[29]. We therefore hypothesize that greater phylogenetic diversity will stabilize biomass production over time by increasing (measured and unmeasured) trait diversity and by diluting the effects of pathogen outbreaks and herbivore attacks, which are strong regulators of biomass production in grasslands[46].

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

While there is empirical evidence, typically from single sites, that each of the aforementioned biological drivers contributes to the overall relationship between diversity and stability, they probably operate concurrently and their relative importance and interrelationships have not been investigated. Here, we make a general,

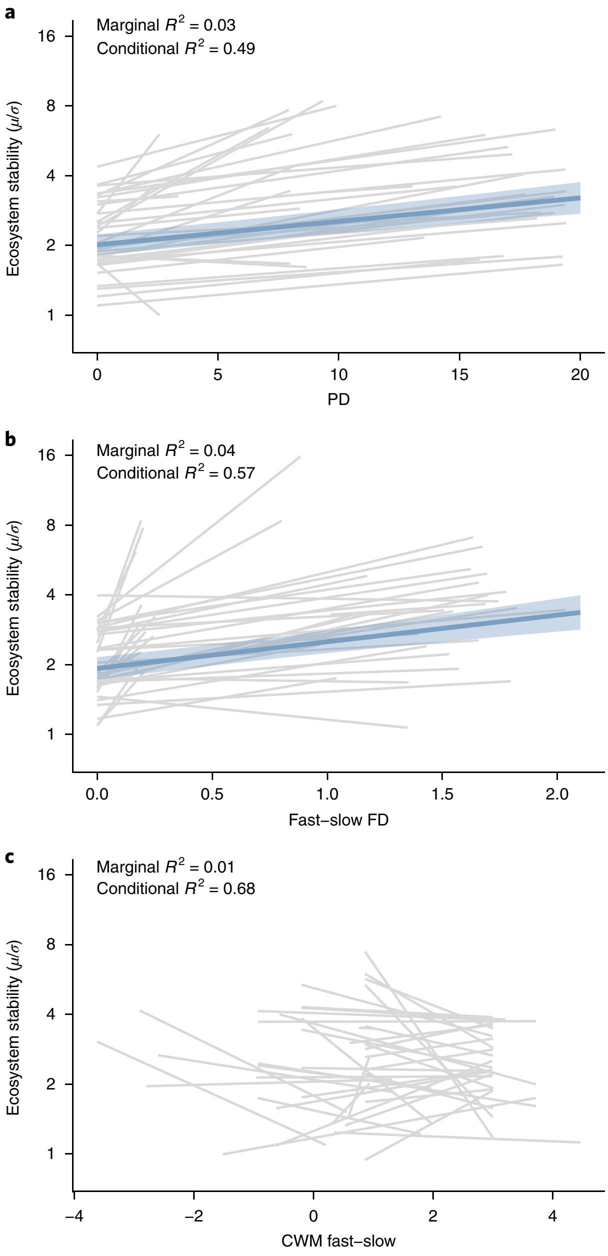

Fig. 2 | Relationships among ecosystem stability, phylogenetic and fast–slow functional diversity, and the community-weighted mean of fast–slow traits across experimental grasslands. a,b,c, Phylogenetic (**a**; PD) and fast–slow functional diversity (**b**; fast–slow FD) and community-weighted mean of fast–slow traits (**c**; CWM fast–slow) effects on ecosystem stability of aboveground biomass production across 39 experimental grassland studies. Phylogenetic diversity is abundance-weighted mean nearest taxon distance and fast–slow FD is abundance-weighted functional dispersion of fast–slow traits. CWM fast–slow is the first axis of a principal component analysis of community-weighted means of key leaf functional traits associated with 'fast' and 'slow' ecological strategies: specific leaf area (SLA), leaf matter dry content (LMDC) and leaf N and P concentrations. Low values of the fast–slow spectrum correspond to communities dominated by 'slow' species, that is, low SLA and leaf N and P and high LDMC; and high values correspond to communities dominated by 'fast' species, that is, high SLA and leaf N and P and low LDMC. Lines are mixed-effects model fits for each study (light grey lines) or across all studies (black lines; $P \leq 0.05$). Marginal and conditional R^2 represent model variation explained by fixed effects and the combination of fixed and random effects, respectively. Light blue bands represent 95% confidence intervals.

integrative assessment of the contribution of different facets of biodiversity in driving biodiversity–stability relationships. This was achieved by performing a meta-level analysis using data from 39 grassland biodiversity–ecosystem function experiments distributed across North America and Europe. Direct and indirect effects of the biological drivers were assessed using structural equation models (SEM), which represented the relationships described above (Supplementary Figs. 1 and 2), and which control for covariation among the different facets of biodiversity[29,35]. We hypothesized that: (1) greater plant species richness, diversity in traits that capture the fast–slow leaf economics spectrum, and phylogenetic diversity will increase ecosystem stability by increasing asynchrony and that (2) species-rich communities with high fast–slow functional diversity and phylogenetic diversity, and those dominated by species with slow leaf economics, will increase ecosystem stability directly as they increase the temporal mean of biomass production, a component of stability, via classical diversity–function mechanisms, such as complementarity and selection effects[24,53].

Results

Our analysis shows positive bivariate relationships between stability, asynchrony and several biodiversity facets: species richness, phylogenetic diversity (calculated as mean nearest taxon distance (MNTD); see Methods), fast–slow functional diversity (calculated using traits associated with the fast–slow leaf economics spectrum), and that these are significant and generally consistent across experiments (Figs. 1 and 2). These drivers explained low amounts of variation in ecosystem stability (Supplementary Table 1, marginal R^2), with a larger proportion being explained by the random effects (Supplementary Tables 1 and 2, conditional R^2). In contrast, although phylogenetic diversity and fast–slow functional diversity were positively related to ecosystem stability, there was no consistent effect of the community-weighted mean of fast–slow traits on ecosystem stability ($P > 0.10$; Fig. 2c). However, the effect of the community-weighted mean of fast–slow traits was highly variable across all experimental sites; at certain experimental sites dominance by species with slow traits stabilized productivity (Fig. 2c), while fast species stabilized production at others.

These relationships were investigated in more depth with our structural equation model, which provides strong evidence that asynchrony is a key mechanism mediating the biodiversity–stability relationship and that asynchrony is driven by multiple facets of biodiversity (Fig. 3). Overall, the data fit our model well (Fisher's $C = 7.51$, d.f. = 12, $P = 0.82$; $K = 34$, $n = 1{,}699$). Fixed effects explained 20% of variation in ecosystem stability (marginal R^2), which increased to 59% (conditional R^2) when accounting for fixed and random effects. In total, plant species richness, phylogenetic diversity, fast–slow functional diversity and mean and inter-annual variation in water availability explained 52% of variation in species asynchrony (marginal R^2), which increased to 79% when random effects were accounted for (conditional R^2).

The strongest pathway of influence on ecosystem stability was from plant species richness via species asynchrony (standardized path coefficient of indirect effect = 0.21). This effect was larger and more consistent across experimental sites than the direct effect of species richness (standardized path coefficient of direct effect = 0.03, $P = 0.60$), thus suggesting that much of the effect of plant species richness on ecosystem stability is explained by species asynchrony. Phylogenetic diversity also had strong yet opposing effects on ecosystem stability. It indirectly increased ecosystem stability via asynchrony (standardized path coefficient of indirect effect = 0.12), while the direct pathway between phylogenetic diversity and ecosystem stability was negative (standardized path coefficient of direct effect = −0.10; $P < 0.001$). This negative effect was weaker than the positive indirect effect via species asynchrony, thus explaining the overall positive relationship between phylogenetic

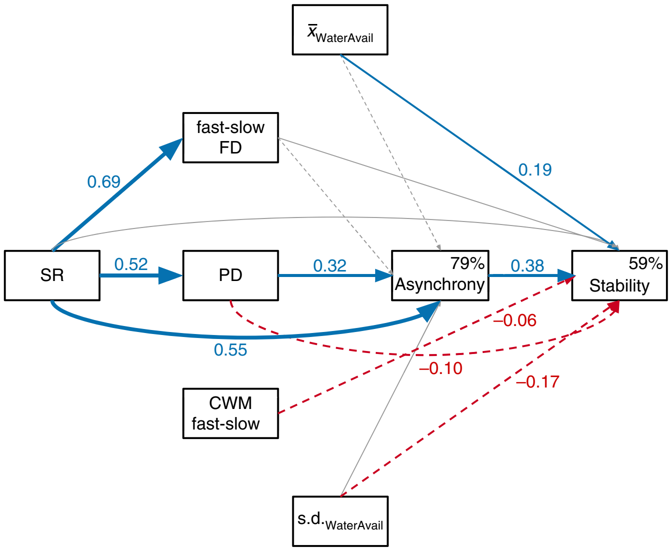

Fig. 3 | Direct and indirect effects of multiple facets of biodiversity on ecosystem stability across experimental grasslands. Structural equation model (SEM) exploring the effects of plant species richness, fast–slow functional diversity (fast–slow FD; abundance-weighted functional dispersion), phylogenetic diversity (abundance-weighted mean nearest taxon distance), functional composition (CWM fast–slow), mean ($\bar{x}_{\text{WaterAvail}}$) and inter-annual variation in water availability (s.d.$_{\text{WaterAvail}}$) on species asynchrony and ecosystem stability of aboveground biomass production across 39 experimental grassland studies. The model fit the data well (Fisher's $C=7.51$, d.f. = 12, $P=0.82$; $K=34$, $n=1{,}699$). Boxes represent measured variables and arrows represent relationships among variables. Solid blue and dashed red arrows represent significant ($P\leq 0.05$) positive and negative standardized path coefficients, respectively, and grey arrows represent non-significant standardized path coefficients. Standardized path coefficients are given next to each (significant) path; widths of significant paths are scaled by standardized path coefficients. Conditional R^2 (based on both fixed and random effects) for asynchrony and ecosystem stability is reported in the corresponding box.

diversity and ecosystem stability, along with covariance with species richness (Fig. 2a).

The community-weighted mean of fast–slow traits had a direct negative effect on ecosystem stability, meaning that communities dominated by slow species were more stable than those dominated by fast species (Fig. 3). Contrary to our expectations, the SEM revealed that fast–slow functional diversity did not directly or indirectly (via asynchrony) stabilize ecosystem productivity ($P>0.05$). Furthermore, these weak effects of fast–slow functional diversity on ecosystem stability were also generally robust to the use of an alternative measure of fast–slow functional diversity, functional richness (Supplementary Fig. 3). Finally, we assessed potentially important effects of climate and found that mean and inter-annual variation in water availability had significant, yet opposite effects on ecosystem stability and no significant effects on species asynchrony (Fig. 3).

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

Species richness promoted ecosystem stability by increasing mean aboveground biomass production but also increasing its variability, while the direct effect of phylogenetic diversity on ecosystem stability operated via negative effects on the standard deviation of biomass. Furthermore, these analyses revealed that the weak negative effect of the community-weighted mean of fast–slow traits on ecosystem stability masked contrasting effects on the components of the invariability measure; communities dominated by species with fast trait values decreased mean biomass (standardized path coefficient of direct effect = −0.12) to a greater extent than they decreased standard deviation of biomass (standardized path coefficient of direct effect = −0.08). Asynchrony increased ecosystem stability by reducing the standard deviation of biomass. Finally, inter-annual variation in water availability had strong yet variable effects on the standard deviation of biomass (standardized path coefficient of direct effect = 0.17, $P=0.08$), while those of mean water availability on mean aboveground biomass production were weak. These relationships were generally robust to the use of different combinations of phylogenetic and functional diversity indices and detrended ecosystem stability (Supplementary Figs. 4–8).

As most studies available for inclusion in our analyses collected data for less than four years (33 of 39 studies), we performed sensitivity analyses to test whether our results differed between short- and long-term studies. We found that bivariate relationships between stability and individual facets of biodiversity had similar results between short- and long-term studies, as indicated by non-significant interactions between study duration and each facet of biodiversity (Supplementary Table 3). In an SEM using only data from long-term studies (six studies > 4 years, $n=454$ plots), we found that our overall conclusions were not affected by study duration but that certain paths became stronger, with notable increases in the effects of fast–slow functional diversity (Supplementary Fig. 9). In long-term studies, fast–slow functional diversity had both a direct positive effect on ecosystem stability and a negative effect operating on asynchrony (Supplementary Fig. 9). The strength of the effects of the community-weighted mean of fast–slow traits on ecosystem stability also increased, with fast communities having a direct negative effect on ecosystem stability (Supplementary Fig. 9). Further sensitivity analyses showed that trait identity affected path strength and direction (Supplementary Figs. 10–13). Of the four individual traits making up the fast–slow leaf economics spectrum (Supplementary Fig. 15), the community-weighted means of leaf P and leaf N had direct positive and negative effects on ecosystem stability, respectively, while the effects of the community-weighted means of LDMC and SLA on ecosystem stability were not statistically significant.

Discussion

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

The strongest and most consistent driver of stability across the 39 experiments examined in our study (Supplementary Table 4) was that of species richness, operating via species asynchrony. This probably reflects niche differences among species that affect their relative performance over time in a temporally variable environment[22,54–56]. However, these niche differences were not captured by the functional diversity of fast–slow leaf traits or phylogenetic diversity.

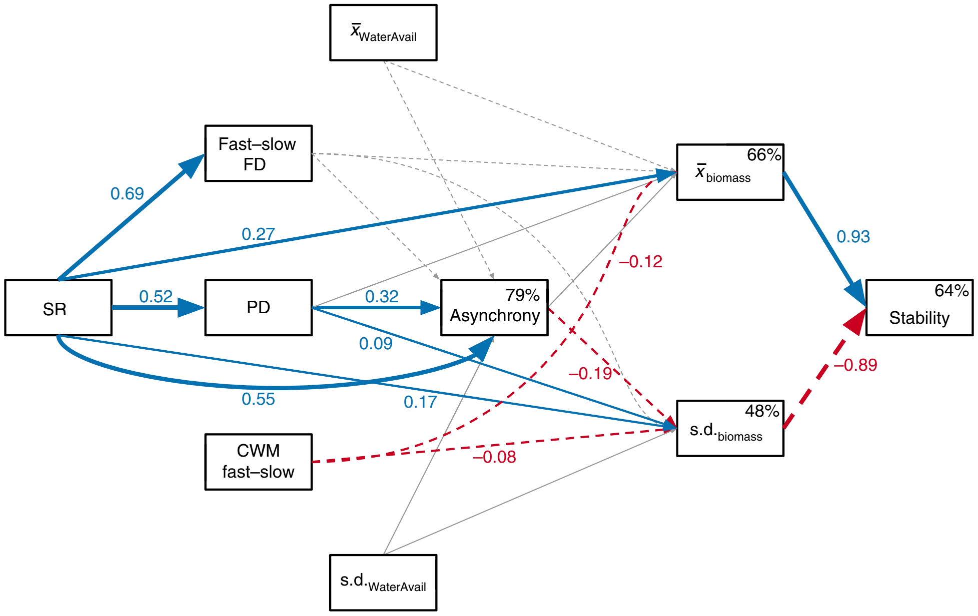

Fig. 4 | Direct and indirect effects of multiple facets of biodiversity on mean and variation in aboveground biomass production across experimental grasslands. Structural equation model (SEM) exploring the effects of plant species richness, fast–slow functional diversity (fast–slow FD; abundance-weighted functional dispersion), phylogenetic diversity (abundance-weighted mean nearest taxon distance), functional composition (CWM fast–slow), mean ($\bar{x}_{\text{WaterAvail}}$) and inter-annual variation in water availability (s.d.$_{\text{WaterAvail}}$) on species asynchrony, mean ($\bar{x}_{\text{biomass}}$) and variation in (s.d.$_{\text{biomass}}$) aboveground biomass production and ecosystem stability of aboveground biomass production across 39 experimental grassland studies. The model fit the data well (Fisher's $C = 22.19$, d.f. = 22, $P = 0.45$; $K = 49$, $n = 1{,}699$). Boxes represent measured variables and arrows represent relationships among variables. Solid blue and dashed red arrows represent significant ($P \leq 0.05$) positive and negative standardized path coefficients, respectively, and grey arrows represent non-significant standardized path coefficients. Standardized path coefficients are given next to each (significant) path; widths of significant paths are scaled by standardized path coefficients. Conditional R^2 (based on both fixed and random effects) for asynchrony, $\bar{x}_{\text{biomass}}$, s.d.$_{\text{biomass}}$ and ecosystem stability is reported in the corresponding box.

Instead, the species richness-asynchrony-stability relationship may be driven by unmeasured traits that are not phylogenetically conserved. Such traits may be related to rooting strategies, photosynthetic pathways, non-structural carbohydrate concentrations and properties related to phenology, demographic storage and regeneration[48,49,51,57–59]. Data for some of these traits are relatively sparse[60] and the collection of such information should be a priority in addressing the current question and those related to other aspects of ecosystem stability, such as resistance and resilience[61].

Species richness also affected ecosystem stability directly. We found that species richness stabilizes biomass production via its stronger effects on mean biomass production over time than effects operating via the standard deviation, which is in line with previous studies[14,29]. As with the effects of species richness on asynchrony, we suggest that these effects may be explained by effects of species richness on complementarity and selection[24,53] that are unrelated to the functional diversity of fast–slow leaf traits or phylogenetic diversity.

The next most important driver of diversity–stability relationships was phylogenetic diversity. Interestingly, phylogenetic diversity influences ecosystem stability via two different pathways, one positive and operating indirectly via species asynchrony, and one negative and operating directly. The indirect asynchrony pathway was the stronger of the two, resulting in a positive overall effect and is probably due to a range of phylogenetically conserved traits. As herbivores and pathogens often have a narrow and phylogenetically conserved host range[45,46], herbivore attacks and disease outbreaks can be weaker in communities of distantly related species and thus affect only a small proportion of community biomass. In contrast, phylogenetically clustered communities will experience strong and simultaneous reductions in biomass production as pests and pathogens spread across the community. The weaker direct negative effect operated via standard deviation in biomass. This path may reflect experimental communities that are dominated by more inherently stable and phylogenetically clustered plant functional groups, such as grasses[62,63]. Furthermore, our analysis illustrates that the effects of phylogenetic diversity on ecosystem stability are sensitive to the phylogenetic diversity metric used[35]. Consistent with a previous study[29], but in contrast with those presented in Figs. 3 and 4, SEMs using mean pairwise distance (MPD) showed weak direct and indirect effects of phylogenetic diversity on ecosystem stability, probably due to its strong, positive correlation with plant species richness (Supplementary Figs. 3 and 4 Supplementary Appendix 2). We suggest that the stronger effects of MNTD reflect the fact that it better represents the tendency for pathogens and herbivores, which play a major role in driving grassland productivity[25,64], to have a phylogenetically narrow host range[45,46].

Evidence for the fast–slow leaf economics spectrum affecting ecosystem stability as an overall strategy (community-weighted mean) was weak across the full dataset. However, this relationship masked contrasting effects of fast traits, which reduced mean aboveground biomass production while reducing its standard deviation. The net result was that communities dominated by species with fast trait values were marginally less stable than those dominated by species with slow trait values. Furthermore, individual site-level relationships between the community-weighted mean of fast–slow traits and ecosystem stability were often very strong, but extremely variable across sites. These findings suggest that the relationship between the fast–slow leaf economics spectrum and ecosystem stability is heavily dependent on site-specific factors, which could include study duration, environmental conditions and the 'matching' of appropriate functional strategies to a site. For example, fast traits may confer ecosystem stability at sites subject to repeated disturbances due to their ability to allow fast recovery, while slow traits may confer ecosystem stability in the face of chronic environmental stresses, such as low nutrient availability or water availability, for example the Texan dry grasslands included in our study[65,66]. Site-level information detailing disturbance regimes and the constancy of soil water availability and nutrient supply at a finer temporal resolution may clarify in which environmental conditions particular plant strategies stabilize (or destabilize) biomass production[67].

The effect of fast–slow functional diversity and the community-weighted mean of fast–slow traits became markedly stronger when only long-term (>4 year) studies were considered. We hypothesize that this is due to the strengthening of biodiversity effects on mean community biomass production over time[68]. Furthermore, the hypothesized effects of fast and slow traits on resilience and resistance have a greater chance of detection because extreme events, such as drought, are more likely to occur in long-term studies[21]. However, such patterns may also be driven by ecological differences in the sites where long- and short-term studies were conducted, as long-term sites tended to include more communities dominated by slow species (Supplementary Fig. 14).

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

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

Methods

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

For each plot within the experiments, we quantified ecosystem stability as the inverse of the coefficient of variation of aboveground plant biomass (μ/σ[19]), which is the ratio of the mean to the standard deviation of annual aboveground plant biomass over time. Ecosystem stability was determined with and without detrending, as recent studies have shown directional changes in aboveground plant biomass with time[52,68]. Ecosystem stability was detrended by regressing aboveground plant biomass against experimental year and calculating the standard deviation of the residuals of each regression[9]. For each plot, detrended ecosystem stability was calculated as mean aboveground plant biomass divided by the detrended standard deviation. All main analyses were performed using ecosystem stability with (Figs. 1–4) and without detrending (Supplementary Figs. 5–8). As results were qualitatively similar, we present results for ecosystem stability without detrending in the main text and for detrended ecosystem stability in Supplementary Information.

Following a previous publication[14], species synchrony (η) was quantified as the average correlation across species between the biomass of each species and the total biomass of all other species in a plot:

$$\eta = (1/n) \sum_i \operatorname{corr}\left(Y_i, \sum j \neq i \; Y_j\right) \tag{1}$$

where Y_i is the biomass of species i in a plot containing n species. Because asynchrony implies negative synchrony, we multiplied η by -1. Thus, species asynchrony ($-\eta$) ranges from -1, where species' aboveground plant biomass is maximally synchronous, to 1, where species' aboveground plant biomass is maximally asynchronous. Further, $-\eta$ is independent of the number of species and their individual variances[14], which contrasts with species asynchrony as calculated previously[80].

We selected four leaf traits associated with the fast–slow leaf economics spectrum[37], specific leaf area (SLA; $\mathrm{mm^2\,mg^{-1}}$), leaf dry matter content (LDMC; $\mathrm{g\,g^{-1}}$), foliar N (%) and foliar P (%). These data were obtained from the TRY database[81] (Supplementary Appendix 1) and additional studies in our database that measured traits[82–85]. Trait values were converted to standardized units and those considered unlikely to be correct (z-score > 4[81]) were excluded. Values were then averaged by trait data contributor and then by species. Genus-level means were used when species-level data were not available; species-level data for SLA, LDMC, leaf N and leaf P were available for 98%, 83%, 92% and 62% of species, respectively. Combining species- and genus-level values, our final trait data set included SLA, LDMC and foliar N values for more than 96% of the species and leaf P values for 93% of the species. While absolute values of species-level traits may differ between locally collected data and databases, which may influence our ability to detect biodiversity effects[86], inter-specific variation is usually greater than intra-specific variation (particularly for organ-level traits) and species ranking is conserved for commonly used traits across data sources[87,88].

Fast–slow functional composition and diversity. We used the first axis of a principal component analysis (PCA) of community-weighted means of SLA, LDMC, leaf N and leaf P to represent the fast–slow leaf economics spectrum (hereafter 'community-weighted mean (CWM) of fast–slow traits'[38]). PCA was performed using the *PCA* function in 'FactoMineR'[89]. The first PCA captured 60.4% of variation among the four traits (Supplementary Fig. 15) and represents the fast–slow leaf economics spectrum of communities, from those dominated by slow species with low SLA and leaf N and P and high LDMC to those dominated by fast species with high SLA and leaf N and P and low LDMC.

We calculated functional diversity in traits associated with the fast–slow leaf economics spectrum (hereafter 'fast–slow functional diversity') as either abundance-weighted functional dispersion or functional richness to represent complementarity among co-occurring species and volume of trait space, respectively, using the 'FD' package[90]. Results for both measures of fast–slow functional diversity were qualitatively similar. Therefore, we present results for functional dispersion in the main text and for functional richness in Supplementary Information. Functional composition and functional diversity were calculated annually for each plot and then averaged across years.

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

Climate. As empirical and theoretical studies have shown strong impacts of mean and inter-annual variation in water availability on productivity in grasslands[67,69,70], we included site-level climate data to explain across-site variation in ecosystem stability and species asynchrony. To capture the joint effects[96] of precipitation and temperature on experimental plant communities during each study, we calculated a water availability index as the ratio of annual precipitation to potential evapotranspiration[97] using data from CRU TS 4.0.1[98] (Supplementary Table 4). For each study, we calculated the mean and the standard deviation of water availability.

Data analysis. To explore bivariate relationships between each of our hypothesized drivers and ecosystem stability, we fitted separate linear mixed-effects models (independently of SEMs) that tested for the effects of plant species richness, phylogenetic diversity, fast–slow functional diversity, the community-weighted mean of fast–slow traits and species asynchrony on ecosystem stability. Multiple random effect structures were tested for each model, first using a basic structure defined by the experimental design of all studies where study was treated as a random intercept and species richness as a random slope. We also tested for interactions of predictor variables with plant species richness and included them as random slopes when supported by model selection. We used AICc to select the most parsimonious random effects structure. AICc is a second-order bias correction to Akaike's information criterion for small sample sizes[99]. Models were fitted using the 'nlme' package and model assumptions were checked by visually inspecting residual plots for homogeneity and quantile-quantile plots for normality. Intra-class correlation (ICC) was calculated to compare variability within a study to variability across studies.

Because many studies collected data for less than four years, we also tested whether our results differed between short- and long-term studies. We did so by adding a two-way interaction between a predictor variable and study duration and study duration as a main effect to the models in Supplementary Table 1, where study duration was a binary variable with a value of one for studies that collected data for more than four years and a value of zero for all other studies. For all models, we found similar results between short- and long-term studies, as interactions between each facet of biodiversity and study duration were not statistically significant (Supplementary Table 3).

To test the relative importance of the different mechanisms represented by the community-weighted mean of fast–slow traits, fast–slow functional diversity, phylogenetic diversity, climate and asynchrony in driving temporal stability, we fitted piecewise structural equation models[100] (SEM) using 'piecewiseSEM'. Testing for relationships with resistance and resilience (as in a previous study[21]) was not possible because of the unequal distribution of extreme climate events across sites, which prevented fitting a general SEM. We formulated a hypothetical causal model (Supplementary Fig. 1) based on a priori knowledge of grassland ecosystems and used this to test the fit of the model to the data. We also included direct paths from species richness, fast–slow functional diversity and phylogenetic diversity to ecosystem stability to represent biological drivers that influence ecosystem stability, for example via complementarity effects on the temporal mean of biomass production[24,53]. Finally, we included direct paths from mean and inter-annual variation in water availability to ecosystem stability. We included direct paths from species richness to fast–slow functional diversity and phylogenetic diversity because variation in these variables can be directly attributed to the experimental manipulation of species richness in all studies[33].

All initial models contained partial bivariate correlations between fast–slow functional diversity and phylogenetic diversity[35]. Additional partial bivariate correlations were added to the initial model if they significantly improved model fit using modification indices ($P < 0.05$). To test the sensitivity of our model to functional and phylogenetic diversity indices, the duration of the time series and the choice of traits, we fitted additional models for each combination of functional and phylogenetic diversity indices, using only data from long-term experiments (>4 years), and for each functional trait separately. Finally, we fit another SEM to see if stabilizing effects on biomass production operated via the two components of the invariability measure, mean and standard deviation of biomass production (Supplementary Fig. 2). In this model, we added direct paths from species richness, phylogenetic diversity, fast–slow functional diversity and species asynchrony to the mean and standard deviation of biomass and from mean water availability to mean biomass and from inter-annual variation in water availability to standard deviation of biomass production. Model fit was assessed using Fisher's C statistic ($P > 0.10$). SEMs were fit using linear mixed-effects models where study was treated as a random factor and species richness as a random slope. Random effect structures allowed the intercepts and slopes to vary among studies. In all analyses, plant species richness, ecosystem stability and mean water availability were $\log_2$ transformed to meet normality assumptions. Model assumptions of normality were inspected visually. As many of the variables included in our SEM were correlated (see Supplementary Appendix 2), we estimated variance inflation. This demonstrated that multi-collinearity did not affect parameter estimates (VIF < 3). All analyses were performed using R 3.4.4[101].

Reporting Summary. Further information on experimental design is available in the Nature Research Reporting Summary linked to this article.

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

Data availability. Data supporting the findings of this study are available from the corresponding author upon request.

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Authorship contributions

D.C., N.E. and F.I. conceived the project. D.C., P.M., N.E., W.D.P., Y.H., C.R., F.I., A.E., J.N.G., J.H., A.J., N.L., S.T.M., J.v.R., A.W. and M.D.S. further developed the project in a workshop. N.E., C.R., F.I., M.B., C.Be., G.B., N.B., C.By., B.E.L.C., J.A.C., J.H.C.C., J.M.C., E.D.L., A.H., A.J., J.Ka., J.Kr., V.L., V.M., V.O., H.W.P., P.B.R., J.v.R., B.S., N.A.S., D.T., A.W. and B.W. contributed experimental and functional trait data. D.C. compiled data. D.C. analysed data with significant input from P.M., N.E., W.D.P. and Y.H. D.C. and P.M. wrote the first draft of the manuscript and all co-authors contributed substantially to revisions.

Competing interests

The authors declare no competing interests.

Additional information

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n/a	Confirmed	
☐	☒	The exact sample size (n) for each experimental group/condition, given as a discrete number and unit of measurement
☐	☒	An indication of whether measurements were taken from distinct samples or whether the same sample was measured repeatedly
☐	☒	The statistical test(s) used AND whether they are one- or two-sided *Only common tests should be described solely by name; describe more complex techniques in the Methods section.*
☐	☒	A description of all covariates tested
☐	☒	A description of any assumptions or corrections, such as tests of normality and adjustment for multiple comparisons
☐	☒	A full description of the statistics including central tendency (e.g. means) or other basic estimates (e.g. regression coefficient) AND variation (e.g. standard deviation) or associated estimates of uncertainty (e.g. confidence intervals)
☐	☒	For null hypothesis testing, the test statistic (e.g. F, t, r) with confidence intervals, effect sizes, degrees of freedom and P value noted *Give P values as exact values whenever suitable.*
☒	☐	For Bayesian analysis, information on the choice of priors and Markov chain Monte Carlo settings
☐	☒	For hierarchical and complex designs, identification of the appropriate level for tests and full reporting of outcomes
☒	☐	Estimates of effect sizes (e.g. Cohen's d, Pearson's r), indicating how they were calculated
☐	☒	Clearly defined error bars *State explicitly what error bars represent (e.g. SD, SE, CI)*

Our web collection on statistics for biologists may be useful.

Software and code

Policy information about availability of computer code

Data collection: not applicable

Data analysis: R version 3.4.4

For manuscripts utilizing custom algorithms or software that are central to the research but not yet described in published literature, software must be made available to editors/reviewers upon request. We strongly encourage code deposition in a community repository (e.g. GitHub). See the Nature Research guidelines for submitting code & software for further information.

Data

Policy information about availability of data

All manuscripts must include a data availability statement. This statement should provide the following information, where applicable:

- Accession codes, unique identifiers, or web links for publicly available datasets
- A list of figures that have associated raw data
- A description of any restrictions on data availability

Data supporting the findings of this study are available from the authors upon request.

Field-specific reporting

Please select the best fit for your research. If you are not sure, read the appropriate sections before making your selection.

☐ Life sciences ☐ Behavioural & social sciences ☒ Ecological, evolutionary & environmental sciences

For a reference copy of the document with all sections, see nature.com/authors/policies/ReportingSummary-flat.pdf

Ecological, evolutionary & environmental sciences study design

All studies must disclose on these points even when the disclosure is negative.

Study description	Hierarchical design with multiple levels of plant species richness per experiment. Thirty nine experimental grassland ecosystems and 1699 plots.
Research sample	All experiments contributing data manipulated plant species diversity in a grassland experiment and had collected primary plant biomass annually for at least three years. With at least three years (or timepoints) of data, we are able to estimate ecosystem stability, which is the primary response variable in our study.
Sampling strategy	We performed an extensive search of the literature and contacted colleagues that worked on similar questions. Our dataset (which includes published and unpublished studies), is the most comprehensive one assembled to date with raw data (i.e. not effect sizes).
Data collection	Not applicable. All raw data was sent to corresponding author and harmonized across datasets for analysis.
Timing and spatial scale	For each experiment, we used primary plant biomass collected annually as a proxy for grassland productivity. The length of each study varied considerably, most lasted at least three years but at least six studies lasted more than four. Most studies conducted their experiments using 1m x 1m plots.
Data exclusions	We excluded functional trait data if individual observations were considered likely to be erroneous (using a protocol established by the database managers).
Reproducibility	Not applicable. In some ways, we use data from 39 experiments with sufficiently similar experimental designs to test reproducibility.
Randomization	Many studies allocated the location of plots randomly, and also determined the composition of multi-species communities randomly.
Blinding	Blinding was not relevant to our study because it is a meta-level study and we expected for there to be a positive relationship between plant species richness and ecosystem stability. We used structural equation modeling to test additional hypotheses about additional co-variates simultaneously and reported these tests in our manuscript.

Did the study involve field work? ☐ Yes ☒ No

Reporting for specific materials, systems and methods

Materials & experimental systems

n/a	Involved in the study
☒	☐ Unique biological materials
☒	☐ Antibodies
☒	☐ Eukaryotic cell lines
☒	☐ Palaeontology
☒	☐ Animals and other organisms
☒	☐ Human research participants

Methods

n/a	Involved in the study
☒	☐ ChIP-seq
☒	☐ Flow cytometry
☒	☐ MRI-based neuroimaging