Title: Multiple facets of biodiversity drive the diversity-stability relationship

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Abstract

A significant body of evidence has demonstrated that biodiversity stabilizes ecosystem functioning in grassland ecosystems. However, the relative importance of the biological drivers underlying these relationships remains unclear. Here we utilized data from 39 biodiversity experiments and a structural equation modeling approach to investigate the roles of phylogenetic diversity, functional diversity and community-level averages of ‘fast-slow’ traits, species richness, and asynchrony in driving the diversity-stability relationship. The structural equation model explained 78% of variation in asynchrony and 58% in ecosystem stability and showed that high species richness and phylogenetic diversity stabilized biomass production via asynchrony and, surprisingly, that low phylogenetic diversity enhanced ecosystem stability directly. The effects of functional diversity and fast-slow traits on ecosystem stability were weak and highly variable across sites, respectively. These results demonstrate that biodiversity influences ecosystem stability via multiple pathways, thus suggesting a more complex role of biodiversity in mediating ecosystem stability than previously recognized.

Introduction

The relationship between the diversity of ecosystems and their stability has long been a fundamental subject of fundamental ecological research (May 1973; McNaughton 1978; Ives & Carpenter 2007), and this research topic has gained new impetus due to global environmental change and biodiversity loss, both of which threaten the stability of ecosystem functions and the ecosystem services they underpin (Balvanera *et al.* 2006; Hautier *et al.* 2015; Isbell *et al.* 2015b; Donohue *et al.* 2016). A substantial body of theoretical and empirical work on this question has focused on the relationship between plant species diversity and biomass production, and this has consistently demonstrated that the productivity of species-rich systems shows less variation over time (e.g., Jiang & Pu 2009; Hector *et al.* 2010; Campbell *et al.* 2011; de Mazancourt *et al.* 2013; Gross *et al.* 2014).

Stability (or invariability) of ecosystem functioning is an integrative measure of short- and long-term responses of populations and communities to environmental variation (Oliver *et al.* 2015). As a result, higher stability of species-rich ecosystems can be attributed to their higher resistance (*i.e.*, biomass shows little deviation from normal during perturbations) and/or resilience (*i.e.*, biomass returns to normal rapidly after perturbations; Tilman & Downing 1994; Van Ruijven & Berendse 2010; Isbell *et al.* 2015a). To date, a considerable number of mechanisms – not necessarily mutually exclusive - have been proposed as the cause of these patterns, primarily asynchrony in species responses to environmental variation, insurance effects, overyielding, and statistical averaging (Doak *et al.* 1998; Yachi & Loreau 1999; Lehman & Tilman 2000; Loreau & Mazancourt 2008; de Mazancourt *et al.* 2013) and tested empirically (*e.g.*, Isbell *et al.* 2009; Hector *et al.* 2010; Roscher *et al.* 2011; de Mazancourt *et al.* 2013; Gross *et al.* 2014; Hautier *et al.* 2014). Here, we explore a suite of potential biodiversity-dependent mechanisms that influence stability. We hypothesize that the relationship between biodiversity and ecosystem stability is mediated by a range of biological drivers and that we can identify the signal of these mechanisms using community-level properties: functional composition and functional and phylogenetic diversity.

Functional composition may play a key role in stabilizing biomass production in grasslands because growth-related traits strongly influence the production and persistence of plant biomass (Díaz & Cabido 2001). While plants differ greatly in their trait values and strategies, a large proportion of global plant trait variation is correlated along a single axis which distinguishes between ‘fast’ or exploitative species that are capable of rapid resource uptake, growth, and tissue turnover and ‘slow’ or conservative species with slower rates of growth, resource uptake, and tissue turnover (Wright *et al.* 2004; Reich 2014). The former typically possess high specific leaf area (SLA), low leaf dry matter content (LDMC), and high leaf nitrogen (N), the latter the opposite (Grime 1977; Reich 2014; Díaz *et al.* 2016). There is growing evidence that variation in functional composition along the fast-slow spectrum has cascading effects on ecosystem stability. For example, high LDMC values have been found to increase ecosystem stability in experimental and semi-natural grassland communities (Polley *et al.* 2013; Májeková *et al.* 2014). We therefore expect that communities dominated by slow species will be more stable than those dominated by fast species. The net effect of functional composition on ecosystem stability, however, 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 plant ecological strategies, quantified as trait diversity, may explain ecosystem stability because higher trait variability should increase temporal niche complementarity, thus reducing variation of productivity over time (“functional insurance” ; Díaz & Cabido 2001). That is, functionally diverse communities maintain biomass production over time because they contain an array of fast and slow species that vary in their ability to compete for and utilise growth-limiting resources, such as water, nutrients, and light (Flynn *et al.* 2011; Roscher *et al.* 2012; Spasojevic & Suding 2012; Fischer *et al.* 2016). As fast species are likely to recover rapidly following disturbance (resilience) and slow species will be able to tolerate environmental stresses and perturbations (resistance ; Grime 1977; Reich 2014), we hypothesize that functionally diverse communities will exhibit both resistance and 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. Broadly speaking, phylogenetic diversity can be seen as representing the diversity of phylogenetically conserved functional traits. Traits which reflect a shared co-evolutionary history of biotic interactions often show a high degree of phylogenetic conservatism (Gomez *et al.* 2010), such as mycorrhizal tendency and N fixation (Flynn *et al.* 2011; Reinhart *et al.* 2012). Phylogenetically similar species are also known to share pathogens or immune responses via their shared co-evolutionary history (Gilbert *et al.* 2012; Parker *et al.* 2015). Importantly, there is strong evidence showing that phylogenetic diversity has a consistently positive effect on ecosystem stability in grasslands (Flynn *et al.* 2011; Cadotte *et al.* 2012; Cadotte 2015). We therefore hypothesize that greater phylogenetic diversity will stabilize biomass production over time by increasing (measured and unmeasured) trait diversity and diluting the effects of pathogen outbreaks and herbivore attacks.

Plant species richness may affect ecosystem stability via multiple pathways that are independent of functional and phylogenetic diversity. There is evidence for a range of trait-based mechanisms not related to the fast-slow spectrum via which diversity may confer ecosystem stability, such as persistent seedbanks (Pérez-Harguindeguy *et al.* 2013), aerenchyma production that maintains gas exchange (Wright *et al.* 2016), and regrowth from belowground storage organs (Hoover *et al.* 2014) or carbohydrate reserves (McDowell *et al.* 2008), that confer resilience. There are also properties that enhance resistance, such as drought tolerance (Bartlett *et al.* 2012; Craine *et al.* 2013). Furthermore, diversity may also confer ecosystem stability through traits that enable community-level production in the face of environmental variability, such as variation in rooting depth (Weigelt *et al.* 2008) and phenology (Fargione & Tilman 2005). Plant species richness can also directly affect ecosystem stability by modifying environmental conditions. For example, the higher productivity of species-rich communities is associated with more rapid rates of soil organic matter accumulation (Fornara & Tilman 2008; Cong *et al.* 2014; Lange *et al.* 2015) and soil aggregate formation (Gould *et al.* 2016), which result in a more aerobic, mesic soil environment in which plant growth is more constant. We expect that these pathways will be represented statistically by residual effects of species richness on ecosystem stability (Fig. S1).

Multiple biological drivers (described above) may simultaneously affect ecosystem stability by increasing species asynchrony. Asynchrony, which describes the extent to which species-level productivity is correlated within a community over time, has been identified in a growing number of theoretical and empirical studies as a key mechanism underlying diversity-stability relationships (e.g., Yachi & Loreau 1999; de Mazancourt *et al.* 2013; Gross *et al.* 2014; Hautier *et al.* 2014). Asynchrony, where decreases in the productivity of some species are compensated by increases in the productivity of other species, causes ecosystem stability to increase due to interspecific interactions (e.g., Lehman & Tilman 2000; Gross *et al.* 2014), negative frequency dependence, e.g. due to pathogen outbreaks (Maron *et al.* 2011; Schnitzer *et al.* 2011), and/or the greater likelihood that diverse communities contain a wider range of species' responses to environmental conditions (de Mazancourt *et al.* 2013; Tredennick *et al.* 2017). With the notable exception of species richness, biodiversity-dependent mechanisms have rarely been used to explain the effects of asynchrony (but see Roscher *et al.* 2011). We hypothesize that multiple facets of biodiversity □ species richness and functional and phylogenetic diversity will enhance asynchrony by increasing variation in traits that confer resistance and resilience (Mori *et al.* 2013; Aubin *et al.* 2016).

While there is empirical evidence that each of the aforementioned biological drivers contribute to the overall relationship between diversity and stability, the relative importance of these drivers has not been investigated across a range of grassland ecosystems. Here we assessed for the first time the simultaneous contribution of multiple aspects of biodiversity in driving biodiversity-stability relationships by performing a meta-level analysis using data from 39 grassland biodiversity-ecosystem function experiments distributed across North America and Europe. The biological drivers were decoupled using structural equation models, which represented the interrelations described above (Fig. S1). We hypothesized that: *i*) greater plant species richness, functional diversity, and phylogenetic diversity will increase ecosystem stability by increasing asynchrony and *ii*) species-rich communities and those dominated by slow species will increase ecosystem stability directly. We show that high species richness and phylogenetic diversity stabilize biomass production via asynchrony and, surprisingly, that low phylogenetic diversity increases ecosystem stability directly.

Methods

Data preparation

We created a database by combining data from biodiversity experiments that manipulated plant species richness in grasslands and measured community- and species-level aboveground plant biomass for at least three years using 39 studies across North America and Europe from Isbell *et al.* (2015a) and Craven *et al.* (2016) (Table S1). In total, our dataset comprises observations from 1,692 plots and 165 plant species, which were standardized using the Taxonomic Name Resolution Service (http://trns.iplantcollaborative.org ; Boyle *et al.* 2013).

For each plot within these experiments, we quantified ecosystem stability (or ecosystem invariability) as the inverse of the coefficient of variation (μ/σ ; e.g., Isbell *et al.* 2015a), which is the ratio of the mean to the standard deviation of aboveground plant biomass over time. Asynchrony (η) was quantified following Gross *et al.* (2014) as the average correlation across species between the biomass of each species and the total biomass of all other species in a plot:

$\eta = (1/n)\ \Sigma_i \text{ corr } (Y_i, \Sigma\ j \neq i\ Y_j)$, (Eq.1)

where Y_i is the biomass of species *i* in a plot containing *n* species. This measure of asynchrony ranges from -1, where species' aboveground plant biomass is maximally asynchronous, to 1, where species' aboveground plant biomass is maximally synchronized. Further, η is independent of the number of species and individual species' variances (Gross *et al.* 2014).

We selected four 'fast-slow' leaf traits associated with the leaf economic spectrum (Wright *et al.* 2004; Díaz *et al.* 2016)(Wright *et al.* 2004; Díaz *et al.* 2016), specific leaf area (SLA; $mm^2\ mg^{-1}$), leaf dry matter content (LDMC; $g\ g^{-1}$) , foliar N (%), and foliar P (%) and obtained data from the TRY database (Kattge *et al.* 2011) and additional studies that measured traits in our data set (Grime *et al.* 2007; Wacker *et al.* 2009; Roscher *et al.* 2012; Daneshgar *et al.* 2013; Jane A. Catford, unpublished data). Trait values were converted to the same units and outliers were excluded (standard deviation > 4). Values were then averaged by 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.

Functional diversity and composition

We calculated functional diversity in ‘fast-slow’ traits as either functional dispersion (FD; abundance weighted) or functional richness (FRic; not weighted by abundance) to represent complementarity among co-occurring species and volume of trait space, respectively, using the ‘FD’ package (Laliberté & Legendre 2010). Results for both measures of functional diversity were qualitatively similar. Therefore, we present results for functional dispersion in the main text and for functional richness in Supplementary Materials.

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 spectrum, where ‘slow’ communities have high community-level averages in trait values that are correlated with slow rates of resource acquisition and growth, and ‘fast’ communities have high community-level averages in trait values that correspond to high rates of resource acquisition and growth (Reich 2014; Salguero-Gómez *et al.* 2016). The first PCA captured 60.4% of variation among the four traits (Figure S2) and represents the ‘fast-slow’ 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. Trait measures were calculated annually for each plot and then averaged across years.

Phylogenetic diversity

We used the molecular phylogeny from Zanne *et al.* (2014) 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* ; Pearse *et al.* 2015). We then calculated abundance-weighted phylogenetic diversity as mean nearest taxon distance (eMNTD ; Webb *et al.* 2002; Pearse *et al.* 2014). eMNTD captures competitive differences among species in previous studies (Godoy *et al.* 2014) and the sharing of specialized pathogens tends to be confined to closely related species (Gilbert *et al.* 2012; Parker *et al.* 2015). eMNTD, therefore, is a good metric to test our hypotheses about the mechanisms that explain variation in species asynchrony and ecosystem stability.

Climate

As previous studies have reported strong impacts of inter-annual variation in weather conditions on plant productivity over time (Huxman *et al.* 2004; Sala *et al.* 2012), we included site-level climate data in order to explain across-site variation in ecosystem stability. To describe environmental conditions during each study in a consistent manner across sites, we calculated mean annual precipitation (MAP), mean annual temperature (MAT), inter-annual variation in precipitation (coefficient of variation of MAP), and inter-annual variation in temperature (coefficient of variation of MAT) using data from CRU TS 3.2.3 (Harris *et al.* 2014). We tested for the individual effects of each climatic variable on mean temporal stability using a linear regression model and found that inter-annual variation in precipitation best explained variation in mean temporal stability (ΔAICc = 3.68). This variable was therefore selected for use in later analyses.

Data analysis

To explore the bi-variate relationships between each of our hypothesized drivers and ecosystem stability, we first fitted separate linear mixed-effects models that tested for the effects of plant species richness, asynchrony, phylogenetic diversity, functional diversity, and the fast-slow spectrum on ecosystem stability. Multiple random effect structures were tested for each model; random effects were included for a study factor and interactions of study with plant species richness and other predictor variables. Random effect structures allowed the intercepts and slopes to vary among studies if their retention was supported by model selection. We used AICc, a second-order bias correction to Akaike's information criterion for small sample sizes, to select the most parsimonious model (Burnham & Anderson 2003). Models were fit 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 the variability within a study to variability across studies.

To estimate the direction and strength of relationships between plant species richness, functional and phylogenetic diversity, the fast-slow spectrum, and asynchrony, Pearson’s correlation coefficients and sampling variance were calculated for each study. Using the ‘metafor’ package, mean effect sizes of the relationships among the aforementioned variables were estimated using random effects models and restricted maximum likelihood (Viechtbauer 2010). The Knapp-Hartung adjustment was used to account for the uncertainty in the estimation of residual heterogeneity (Knapp & Hartung 2003).

To test the relative importance of the fast-slow spectrum, functional and phylogenetic diversity, climate, and asynchrony in driving temporal stability, we fit piecewise structural equation models (SEM ; Lefcheck 2016) using ‘piecewiseSEM’. Testing the aforementioned effects on resistance and resilience (as in Isbell *et al.* 2015a) 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 (Fig. S1) based on a priori knowledge of the system, which we used to test the fit of the model to the data. This model mirrors the relationships. We also included direct paths from species richness, functional and phylogenetic diversity to ecosystem stability to represent other potential biodiversity-dependent mechanisms that influence ecosystem stability. Finally, we included a direct path from inter-annual variation in precipitation to ecosystem stability. We included direct paths from species richness to functional and phylogenetic diversity and the fast-slow spectrum because variation in these variables can be directly attributed to the experimental manipulation of species richness in all studies (Flynn *et al.* 2011). All initial models contained correlated errors between functional diversity, phylogenetic diversity, and the fast-slow spectrum. Paths were added to the initial model if they significantly improved model fit using modification indices ($P < 0.05$). This resulted in the addition of a direct path between phylogenetic diversity and ecosystem stability in the final model. Model fit was assessed using Fisher's C statistic ($P > 0.10$). SEMs were fitted using linear mixed-effects models where study was treated as a random group factor and species richness as a random slope. In all analyses, plant species richness and ecosystem stability were $\log_2$ transformed. Model assumptions of normality and homogeneity of variance were inspected visually and collinearity was assessed by estimating variance inflation (VIF < 2 ; Zuur *et al.* 2010). All analyses were performed using R 3.3.1 (R Core Team 2016).

Results

Our analysis confirms that species richness, phylogenetic and functional diversity, and asynchrony each demonstrated a significant and positive relationship with ecosystem stability that was generally consistent across experiments (Figs. 1 and 2). Individual fixed effects of these drivers explained low amounts of variation in ecosystem stability (Table 1, marginal R^2), with a larger proportion being explained by the random effects (Tables 1 and S3, conditional R^2). In contrast, there was not a consistent effect of the fast-slow spectrum on ecosystem stability ($P > 0.10$; Fig. 2c). While there was evidence that communities dominated by 'slow' species stabilized productivity to a greater extent than those dominated by 'fast' species at certain experimental sites (Fig. 2c) and vice-versa, the high intra-class correlation for this model (Tables 1 and S3) indicates that the CWM fast-slow effect was highly variable across all experimental sites.

Across experimental sites, all measures of diversity were significantly positively correlated with one another (r = 0.67 – 0.94; Fig. S2, Table S2). CWM of the fast-slow spectrum also varied significantly in response to species richness and functional richness. With increasing species and functional richness, communities became increasingly dominated by ‘fast’ species (Fig. S2, Table S2). With increasing species richness, phylogenetic diversity and functional diversity, and asynchrony increased significantly (Fig. S2, Table S2).

Our structural equation model provided clear evidence that asynchrony is a key mechanism mediating the biodiversity-stability relationships and that it is is driven by multiple aspects of biodiversity (Fig. 3). Overall, the data fit our model well (Fisher’s C = 11.84, df = 12, P =0.51; AICc = 72.96, K = 30, n = 1,692). Fixed effects explained 19% of variation in ecosystem stability (marginal R^2), which increased to 58% (conditional R^2) when accounting for fixed and random effects. In total, species richness, phylogenetic and functional diversity, and the fast-slow spectrum explained 53% of variation in asynchrony (marginal R^2), which increased to 78% when random effects were accounted for (conditional R^2).

The strongest pathway of influence on ecosystem stability was from plant species richness via asynchrony (standardized indirect effect = 0.21). This effect was larger and more consistent across experimental sites than the marginally significant direct effect of species richness (standardized path coefficient of direct effect = 0.08, P = 0.099). This suggests that much of the effects of plant species richness on stability are explained by asynchrony. Phylogenetic diversity also had strong yet opposing effects on ecosystem stability. Phylogenetic diversity indirectly increased ecosystem stability via its effect on asynchrony (standardized path coefficient of indirect effect = 0.12). Conversely, the unexpected post hoc direct pathway between phylogenetic diversity and stability was negative (standardized path coefficient of direct effect = - 0.10; P < 0.001) but weaker, thus explaining the overall positive relationship between phylogenetic diversity and ecosystem stability (Fig. 2a). Interannual variation in precipitation also had strong, direct, and negative effect on ecosystem stability. Independent of factors related to biodiversity, less variable environmental conditions stabilized plant productivity. Contrary to our expectations, the SEM revealed that neither the functional diversity nor mean of fast-slow leaf traits consistently stabilized (or destabilized) ecosystem productivity ($P > 0.05$). This lack of relationship held when an alternative measure of of functional diversity, functional richness, was used (Fig. S4).

Discussion

The results support our overall hypothesis that multiple components of biodiversity mediate the diversity-stability relationship, principally via their effects on asynchrony. However, the relative importance of certain biological drivers, e.g. functional diversity and fast-slow leaf traits, varied substantially across studies.

The strongest and most consistent driver of stability in the 39 experiments of our study was that of species richness, operating via asynchrony. This is likely to reflect functional niche differences among species that affect their relative performance over time in a temporally variable environment (Yachi & Loreau 1999; Allan *et al.* 2011; Isbell *et al.* 2011; Turnbull *et al.* 2016). However, these niche differences were not captured by our measures of functional (fast-slow) diversity. Instead, the species richness-asynchrony-stability relationship points to a role of traits unrelated to the fast-slow spectrum that stabilize stabilize productivity. Such traits may include rooting strategies, photosynthetic pathways, and regeneration traits (e.g., Edwards *et al.* 2010; Hoover *et al.* 2014; Schroeder-Georg i *et al.* 2016). Data for such traits is relatively sparse (Iversen *et al.* 2017) and the collection of such information should be a priority in addressing the current question and those related to the components of temporal stability, i.e. resistance and resilience (e.g., Mori *et al.* 2013; Aubin *et al.* 2016).

Species richness also affected ecosystem stability directly, albeit via a weak path that was marginally statistically significant (P = 0.099). We suggest that these effects operated via the greater accumulation of soil organic matter and nutrient stocks in diverse communities (Fornara & Tilman 2008; Oelmann *et al.* 2011; Cong *et al.* 2014), which may be further enhanced by positive effects of diversity on the abundance of soil macro- and micro-organisms, such as earthworms and mycorrhiza, that improve the physical structure of soils (Van Der Heijden *et al.* 2006; Eisenhauer *et al.* 2010, 2012). Further, greater root biomass – which also increases with species richness (e.g., Fornara & Tilman 2008; Mueller *et al.* 2012) – has been found to stabilize ecosystem productivity (Tilman *et al.* 2006) by enhancing nutrient storage and carbohydrate reserves. It is unlikely that these positive feedback effects between plant species richness and environmental conditions operate via asynchrony.

The next most important driver of diversity-stability relationships was phylogenetic diversity. Interestingly, phylogenetic diversity affected ecosystem stability via two different pathways, one positive and operating via asynchrony and one negative and operating directly. The hypothesized indirect pathway was the stronger of these, resulting in a weakly positive overall effect (Fig. 2a) and is likely to be due to a range of phylogenetically conserved traits. Those traits may contain pathogen and herbivore outbreaks to just a few species and therefore a small proportion of community biomass. The direct negative effect was not hypothesized. We suggest that this may reflect a habitat filtering effect possibly related to climatic variability, where a subset of closely related species are better suited to typical site conditions making them more consistently productive over time (Bai *et* *al.* 2004). This path may also reflect experimental communities that are dominated by more inherently stable plant functional groups, such as grasses (Hoover *et al.* 2015; Shi *et al.* 2016).

Evidence for fast-slow leaf traits affecting ecosystem stability, as either an overall strategy (CWM) or in terms of their functional diversity, was weak. Individual site-level relationships between the CWM of fast-slow traits and stability were often very strong, but extremely variable across sites, ranging from strongly positive to strongly negative and resulting in an overall weak effect. This suggests that the relationship between the fast-slow spectrum and ecosystem stability is heavily dependent upon 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 aridity, e.g. the dry grasslands of the experimental sites in Texas included in our study (Wilsey & Polley 2004; Wilsey *et al.* 2009). However, we did not detect significant interactions between CWM of the fast-slow spectrum and the multiple descriptors of climate on ecosystem stability (results not presented). Site-level information detailing disturbance regimes and the constancy of soil water availability and nutrient supply may clarify in which environmental conditions particular plant strategies stabilize (or destabilize) biomass production.

The final driver of ecosystem stability in our models was climate. Inter-annual variation in climate conditions – but not mean annual climate conditions – negatively affected ecosystem stability. This is likely to represent the strong annual variation in the timing and intensity of aboveground biomass production in such environments, e.g. inter-annual variation in the timing and intensity of seasonal rains, and provides evidence that inter-annual variation in climate may be a key fundamental driver of ecosystem stability. As mentioned above, a better characterization of site conditions may provide a more complete understanding of the drivers of ecosystem stability (Ives & Carpenter 2007). Furthermore, initial investigations indicate a powerful interactive role between environmental conditions and biotic community properties (e.g., Xu *et al.* 2015; Yang *et al.* 2017), as abiotic and management factors not only control diversity and productivity but also influence the capacity for diversity to stabilize ecosystem function (Hautier *et al.* 2014; Craven *et al.* 2016). This means that in 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. With respect to this, our results indicate that the promotion of certain components of diversity (e.g. phylogenetic diversity) would play a greater role than others (e.g. functional diversity of fast-slow traits) in promoting the stability of fodder production. However, the effect of such management on other ecosystem functions and services and their ecosystem stability (e.g. productivity) would also need to be considered (Donohue *et al.* 2016). Threshold-based measures of stability (Oliver *et al.* 2015) may also be more relevant to such applications than the variability measures employed here, as a threshold-based view of ecosystem stability allows under- and overproduction to be viewed differently.

In conclusion, our study is the first to relate multiple components of biodiversity to ecosystem stability and to estimate their relative importance in driving the diversity-stability relationship. Doing this showed that the role of biodiversity in stabilizing grassland biomass productivity operated via numerous pathways, and therefore that it is more complex and nuanced than has been previously demonstrated. By accounting for multiple drivers of stability, we were also able explain a large amount of variation in both synchrony (conditional R^2 = 78 %) and ecosystem stability (conditional $R^2 = 58$ %). In an era of increased climate instability (Goodess 2013; Stott 2016), it is important to gain a greater understanding of each of these component processes so that the functional benefits of biodiversity may be effectively conserved and promoted.

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