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SYNTHESIS

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# Consistently positive effect of species diversity on ecosystem, but not population, temporal stability

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## Abstract

Despite much recent progress, our understanding of diversity–stability relationships across different study systems remains incomplete. In particular, recent theory clarified that within-species population stability and among-species asynchronous population dynamics combine to determine ecosystem temporal stability, but their relative importance in modulating diversity-ecosystem temporal stability relationships in different ecosystems remains unclear. We addressed this issue with a meta-analysis of empirical studies of ecosystem and population temporal stability in relation to species diversity across a range of taxa and ecosystems. We show that ecosystem temporal stability tended to increase with species diversity, regardless of study systems. Increasing diversity promoted asynchrony, which, in turn, contributed to increased ecosystem stability. The positive diversity–ecosystem stability relationship persisted even after accounting for the influences of environmental covariates (e.g., precipitation and nutrient input). By contrast, species diversity tended to reduce population temporal stability in terrestrial systems but increase population temporal stability in aquatic systems, suggesting that asynchronous dynamics among species are essential for stabilizing diverse terrestrial ecosystems. We conclude that there is compelling empirical evidence for a general positive relationship between species diversity and ecosystem-level temporal stability, but the contrasting diversity–population temporal stability relationships between terrestrial and aquatic systems call for more investigations into their underlying mechanisms.

KEYWORDS
asynchrony, biodiversity, ecosystem functions, meta-analysis, stability

## INTRODUCTION

Are ecosystems with more species more stable (i.e., less variable over time) in the functions that they provide? This question has intrigued ecologists for decades (Margalef, 1963; McNaughton, 1968; Odum, 1969; King & Pimm, 1983). Building on previous conceptual development (Elton, 1958; MacArthur, 1955; Margalef, 1963; Odum, 1969), McNaughton (1977) hypothesized that species diversity would stabilize ecosystem functions, while also suggesting the increasing degree of asynchronous population dynamics among species (hereafter asynchrony; note that asynchrony is a different concept than compensatory dynamics (*sensu* Gonzalez & Loreau, 2009), although the two are often used interchangeably) in more diverse communities as the underlying mechanism. Empirical tests of this hypothesis had been few until the 1990 s, when ecologists began to use controlled experiments to explore how ongoing biodiversity loss influences the functioning of ecosystems, including their stability. Since then, with some notable exceptions (e.g., Bezemer & Van Der Putten, 2007; Sasaki & Lauenroth, 2011), an increasing number of empirical studies have reported results in line with McNaughton's hypothesis (e.g., Hector et al., 2010; Tilman et al., 2006). In parallel, theoretical explorations also supported positive relationships between species diversity and ecosystem temporal stability, while identifying asynchrony as a potentially important stabilizing mechanism (Ives et al., 1999; Loreau & De Mazancourt, 2013; Yachi & Loreau, 1999). Nevertheless, a general understanding of diversity-ecosystem temporal stability relationships and associated mechanisms across different types of ecological systems is still lacking. Here, we synthesize findings of existing empirical studies of the relationships between species diversity and temporal stability of ecosystem functions and populations via quantitative meta-analyses.

Our meta-analyses emphasize the framework that population stability of species embedded in an ecological community and asynchronous population dynamics among these co-occurring species combine to determine the temporal stability of aggregated ecosystem properties (Figure 1). Partitioning the stability of aggregated ecosystem properties into population-level stability and asynchrony facilitates the understanding of the roles of biotic processes in regulating ecosystem stability, including those directly influencing population stability (Thibaut & Connolly, 2013). Under this framework, the relationship between species diversity and ecosystem stability would depend on how species diversity influences population stability and asynchrony (Figure 1). In situations where average population stability declines with diversity, which has been frequently reported in grassland biodiversity experiments (e.g., Hector et al., 2010; Roscher et al., 2011; Tilman et al., 2006), increasing asynchrony must overcome lower population stability to confer great ecosystem-level stability in more diverse communities (Figure 1a). This scenario corresponds to the theoretical prediction that species diversity may stabilize ecosystem properties while having a destabilizing effect on population dynamics (Ives et al., 1999; Lehman & Tilman, 2000; May, 1974). On the other hand, ecosystem stability could decline with species diversity (e.g., Polley et al., 2007; Sasaki & Lauenroth, 2011), if reduced population stability in more diverse communities overwhelms asynchrony (Figure 1b). Under situations where average population stability increases with diversity, which has been frequently reported in aquatic

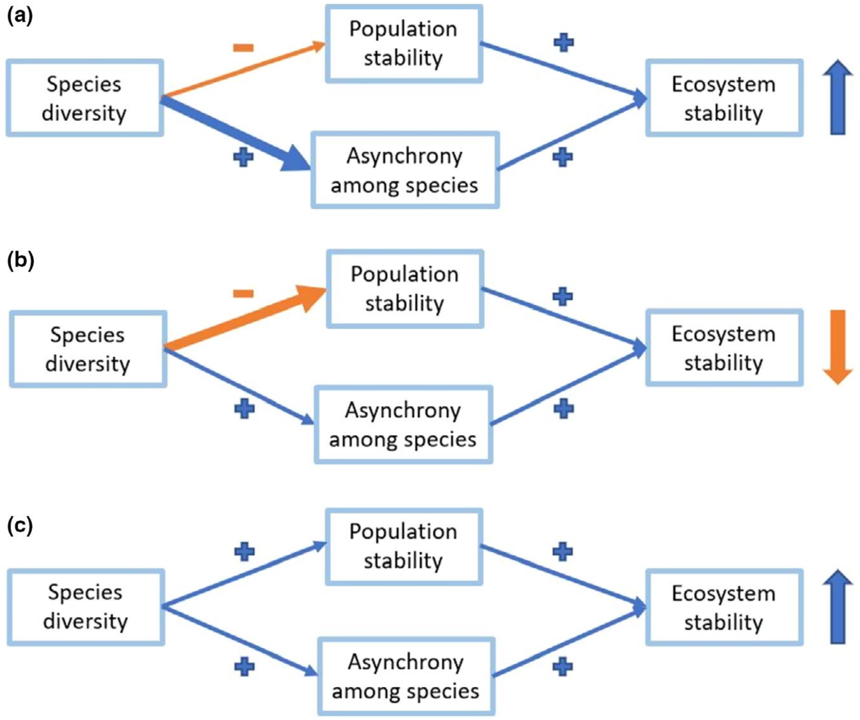

**FIGURE 1** A conceptual diagram illustrating scenarios where species diversity influences ecosystem temporal stability via changing within-species population temporal stability and among-species asynchrony. In panel (a), increasing diversity reduces population stability and promotes asynchrony, but the increase in asynchrony more than compensates for the decline in population stability, resulting in greater ecosystem stability. The results of many terrestrial biodiversity studies are consistent with this scenario. In panel (b), increasing diversity also reduces population stability and promotes asynchrony, but the decline in population stability overwhelms the increase in asynchrony, resulting in reduced ecosystem stability. In panel (c), increasing diversity promotes both population stability and asynchrony, resulting in greater ecosystem stability. The results of many aquatic biodiversity studies are consistent with this scenario. Note that other scenarios where species diversity reduces asynchrony, which have rarely been reported in the literature, are not considered here for simplicity

biodiversity studies (e.g., Downing et al., 2014; Romanuk et al., 2006), asynchrony may combine with increased population stability to promote the stability of more diverse ecosystems (Figure 1c). These different scenarios necessitate the need to examine population stability and asynchrony together to understand their contributions to ecosystem stability. Recent meta-level diversity-stability studies, however, have focused on either asynchrony (Craven et al., 2018; Valencia et al., 2020) or population stability (Houlahan et al., 2018) in relation to ecosystem stability. Moreover, despite the perceived importance of asynchrony for stabilizing ecosystem properties, empirical evidence for its prevalence in ecological communities is equivocal (Gonzalez & Loreau, 2009; Houlahan et al., 2007; Valencia et al., 2020; Vasseur et al., 2014), calling for further investigations on this topic. The accumulating number of recent studies allows us to assess whether asynchrony tends to increase with species diversity and whether ecosystem stability tends to increase with asynchrony.

Another important goal of our meta-analysis is to discern if diversity–stability relationships differ between different ecological systems, a topic that was initially explored more than a decade ago (Jiang & Pu, 2009) but not addressed by more recent meta-level studies (Craven et al., 2018; Gross et al., 2014; Houlahan et al., 2018; van der Plas, 2019; Valencia et al., 2020). In a previous meta-analysis, Jiang and Pu (2009) found that species diversity tended to stabilize both population and ecosystem dynamics in multitrophic (all studies being aquatic) systems but did not affect population or ecosystem stability in single-trophic (all but one study being terrestrial) systems. This result, if robust, would suggest potentially different stability-regulating mechanisms between multitrophic/aquatic and single-trophic/terrestrial systems, possibly reflecting the structural and functional differences between aquatic and terrestrial communities (e.g., Shurin et al., 2002, 2006). This preliminary result also suggests that asynchrony may not increase sufficiently with species diversity to stabilize diverse single-trophic/terrestrial communities, which appears consistent with the recent finding of Valencia et al., (2020) that positive relationships between asynchrony and species diversity tend to be rare in natural and semi-natural terrestrial plant communities. However, the generality of these findings needs to be re-evaluated as the analysis of Jiang and Pu (2009) was based on a limited number of studies, and the result of Valencia et al., (2020), which focused on terrestrial plant communities, seems to vary with the metrics used to quantify asynchrony. Our meta-analysis revisits this important topic, asking whether diversity–stability relationships differ between multitrophic/aquatic and single-trophic/terrestrial systems.

A third goal of our meta-analysis is to assess if species diversity remains a significant predictor of ecosystem stability, after considering abiotic variables that also have the potential to influence ecosystem dynamics. Species diversity is among a host of ecological factors that may influence the stability of an ecosystem. For example, precipitation regimes (Hallett et al., 2014) and increased nitrogen deposition (Hautier et al., 2014, 2015) are known to alter ecosystem stability. However, it is largely unknown whether influences from these abiotic forces would confound our interpretation of the effect of species diversity on ecosystem stability. Given Earth's ecosystems are increasingly subjected to anthropogenic environmental changes (Fischer & Knutti, 2015; Reay et al., 2008; Walther et al., 2002), it is imperative to find out whether species diversity still plays a significant role in regulating ecosystem stability after accounting for these environmental covariates. The increased availability of studies that have investigated diversity–stability relationships under different abiotic environmental conditions provided us the opportunity to answer this question.

# MATERIAL AND METHODS

## Literature search and data set compilation

Our meta-analysis followed the Preferred Reporting Items for Systematic Reviews and Meta-Analyses (PRISMA) Statement (Moher et al., 2009; http://www.prisma-statement.org/) as the guideline for data collection, selection, analysis and reporting. The literature selection procedure was provided as a PRISMA flow diagram (Appendix S1: Figure S1). Studies were collected by searching the Web of Science database, using the keyword combination: (*diversity OR *richness) AND (temporal stability OR variability). Our search returned 18,786 records published on or before December 2020 (our cut-off date for this meta-analysis). We screened the titles and abstracts of all retrieved papers to determine whether the studies met our criteria for inclusion: (1) the study considered one or more dimensions of biodiversity, including species, functional and phylogenetic diversity; (2) the study reported temporal stability of ecosystem functions (mostly community biomass or abundance) and/or temporal stability of populations across at least two diversity levels; and (3) the study documented the relationships between species diversity and ecosystem/population temporal stability as correlation coefficients between the two variables, or other statistics that can be readily transformed into correlation coefficients (e.g., $F$ values with one degree of freedom). Further screening excluded reviews, commentaries, modelling papers and studies that did not report empirical data or reported duplicate data from other studies. We also manually examined reference lists of the electronically retrieved studies that met our criteria and studies considered in relevant reviews (i.e., Campbell et al., 2011; Gross et al., 2014; Jiang & Pu, 2009; van der Plas, 2019) to further expand our database. Finally, we obtained the open-access data from the multisite Agrodiversity experiment conducted in Europe and Canada (Kirwan et al., 2014) and calculated the correlation coefficients between plant species diversity and ecosystem/population stability for the experimental sites for which plant biomass data over three consecutive years were available.

Our final data set consisted of 74 studies that examined the relationship between species diversity (specifically species richness) and the temporal stability of ecosystem functions, contributing 147 data entries at the ecosystem level, and 23 studies that examined the relationship between species diversity and population temporal stability, contributing 65 data entries at the population level (Appendix S1: Table S1; Appendix S2). These studies are globally distributed (Appendix S1: Figure S2). A few studies investigated the relationships between other dimensions of biodiversity, including phylogenetic (four studies) and functional (six studies) diversity and ecosystem temporal stability (Appendix S1: Table S2). Many of these studies reported temporal variability, quantified as the coefficient of variation (CV), rather than stability; for the studies that reported stability as the inverse of CV of which the original data were available, we transformed the data into CV to be included in our meta-analysis. These studies covered a range of organisms, including plants, algae, phytoplankton, zooplankton, protozoans, insects, fish, bacteria and fungi. Ecosystem functions reported in these studies included community biomass production (111 estimates), abundance (33 estimates), parasitism rate (two estimates) and pollinator visit (one estimate). These studies were categorized in three different ways to explore possible heterogeneity among groups: (1) the type of investigational approach (experimental vs. observational), (2) ecosystem type (terrestrial vs. aquatic) and (3) trophic complexity (single vs. multitrophic). Experimental studies were defined as those in which species diversity was directly manipulated, whereas observational studies as those in which species diversity gradients were established via natural assembly or through manipulation of resource (e.g., nitrogen) availability. Single-trophic systems are those in which trophic interactions were absent or minimal.

We compiled a list of studies that examined the relationship between species diversity and asynchrony (Appendix S1: Table S3), all quantified as community-wide species asynchrony (Loreau & de Mazancourt, 2008) of biomass (26 entries) or abundance (3 entries), and the relationship between asynchrony and ecosystem temporal stability (51 entries). Community-wide species asynchrony was calculated as $1-\sigma^2/\left(\sum_{i=1}^{S}\sigma_i\right)^2$, where $\sigma^2$is is the variance of community biomass/abundance and $\sigma_i$ is the standard deviation of species $i$ biomass/abundance in a community with $S$ species (Loreau & de Mazancourt, 2008). Most of these studies reported species asynchrony; in cases where species synchrony was reported, it was transformed into asynchrony.

To find out if species diversity still affects ecosystem stability after accounting for environmental covariates, we assembled a total of 14 studies that have investigated diversity–stability relationships under different abiotic environmental conditions. The environmental conditions considered included nutrient enrichment, stream hydrology, soil tillage, precipitation and temperature. For seven studies (contributing eight entries), we were able to obtain data that statistically accounted for the effects of environmental covariates on temporal stability. Specifically, the semi-partial correlation coefficients between species diversity and ecosystem stability were obtained by first regressing ecosystem stability against the environmental covariate and then regressing the residual against species diversity. For eight studies (contributing nine entries), we were able to calculate partial correlation coefficients between species diversity and ecosystem stability to account for the possibility that species diversity itself may also be influenced by the environmental covariate. For those studies that directly manipulated environmental conditions (seven entries), we compared the direction and strength (correlation coefficients) of diversity–stability relationships under ambient (unmanipulated) versus manipulated environmental conditions.

## Meta-analysis

We used Fisher's $z$-transformed correlation coefficient (Pearson's $r$) between species diversity and temporal stability as the effect size (Rosenthal, 1991). WebPlotDigitizer 4.3 (available at https://automeris.io/WebPlotDigitizer/) was used to extract data from figures when relevant data were only graphically available. The individual effect size was calculated as

$$z=\frac{1}{2}\ln\left(\frac{1+r}{1-r}\right),(1)$$

where $r$ is the correlation coefficient between species diversity and temporal variability. Note that a negative effect size in Eqn (1), indicative of a negative diversity–variability relationship, would imply a positive diversity–stability relationship. To avoid confusion, we reversed the signs of all effect size values calculated from correlation coefficients between diversity and temporal variability, such that a positive effect size indicates a positive diversity–stability relationship.

We conducted separate meta-analyses for diversity–ecosystem stability relationships, diversity–population stability relationships, diversity–asynchrony relationships and asynchrony–ecosystem stability relationships. The effect sizes were analysed using random-effects models (Gurevitch et al., 2001; Gurevitch & Hedges, 1999) that incorporate effect size variations among studies. We considered effect sizes as significant if their 95% confidence intervals did not intercept zero (Borenstein et al., 2009).

Cochran's $Q$ statistic (Cochran, 1954) was used to assess the heterogeneity in effect sizes across studies and between groups (e.g., type of study, ecosystem type, trophic complexity). As the species diversity gradient (Campbell et al., 2011), minimum species diversity values and experimental duration may influence diversity–stability relationships, we used random-effects meta-regressions to assess whether these study characteristics affected the effect size of the diversity–stability relationship. Experimental duration (days) was log10-transformed to improve data normality.

We presented cumulative forest plots of diversity–stability relationships to assess whether and how these relationships changed over time. Publication bias was assessed using funnel plots, Egger's regression test for funnel plot asymmetry (Egger et al., 1997), and Rosenthal's Fail-Safe $N$ test (Rosenthal, 1979). All meta-analyses were performed using R (R Development Core Team, 2018) with the 'metafor' (Viechtbauer, 2010) and 'meta' packages (Schwarzer, 2007).

# RESULTS

## Diversity–stability relationships

Our meta-analysis of species diversity–ecosystem temporal stability relationships revealed a positive overall mean effect size that differed significantly from zero (Figure 2a), indicating that ecosystem temporal stability tends to increase with species diversity. This positive pattern persisted after studies were categorized into experimental and observational studies (between-group heterogeneity $Q_B$ =0.424, $p$ = 0.515; Figure 2a), aquatic and terrestrial studies ($Q_B$ =0.080, $p$ = 0.777; Figure 2a), or single and multitrophic studies ($Q_B$ =0.091, $p$ = 0.763; Figure 2a). This positive diversity–ecosystem stability relationship was also robust to variation in the type of ecosystem function considered ($Q_B$ =1.215, $p$ = 0.750; Appendix S1: Figure S3), the range of species diversity gradient ($p$ = 0.911; Appendix S1: Figure S4a), the minimum level of species diversity ($p$ = 0.309; Appendix S1: Figure S4b), and experimental duration ($p$ = 0.928; Appendix S1: Figure S4c). The cumulative forest plot revealed that the species diversity–ecosystem stability relationship became more positive over time (Figure S5). The effect sizes of functional/phylogenetic diversity and ecosystem stability relationships were similarly positive (Appendix S1: Figure S6).

In contrast to the ecosystem-level results, our meta-analysis of species diversity–population temporal stability relationships showed that the overall mean effect size did not significantly differ from zero (Figure 2b). Mean effect size, however, varied among the study systems we considered. Specifically, mean effect size was significantly positive in observational studies but negative in experimental studies, significantly positive in aquatic studies but negative in terrestrial studies, and significantly positive in multi-trophic studies but negative in single-trophic studies (Figure 2b), indicating that population temporal stability increased with species diversity in observational/aquatic/multitrophic studies, but declined with species diversity in experimental/terrestrial/single-trophic studies. Mean effect size was significantly greater in observational than experimental studies ($Q_B$ =9.565, $p$ = 0.002), in aquatic than terrestrial studies ($Q_B$ =9.592, $p$ = 0.002), and in multitrophic than single-trophic studies ($Q_B$ =8.305, $p$ = 0.004). The cumulative forest plot showed that the diversity–population stability relationship became less positive over time (Appendix S1: Figure S7).

## The species diversity–asynchrony and asynchrony–stability relationships

We found a significant positive relationship between species diversity and community-wide species

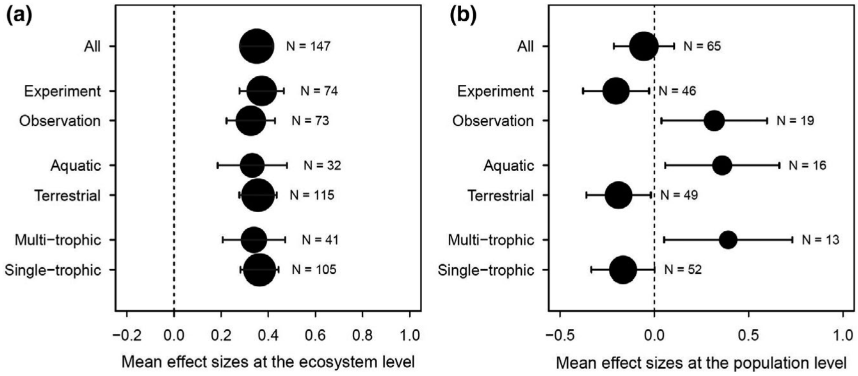

**FIGURE 2** The relationships between species diversity and temporal stability. (a) Mean effect sizes [±95% confidence intervals (CIs)] of the relationships between species diversity and ecosystem-level temporal stability. (b) Mean effect sizes (±95% CIs) of the relationships between species diversity and population-level temporal stability. Positive values indicate that temporal stability increases with diversity. Studies were categorized into experimental versus observational, terrestrial versus aquatic and single-trophic versus multitrophic systems. The size of the symbol is proportional to the sample size (i.e., the number of data entries) in each category. $N$ denotes sample size. The vertical dotted line indicates where the mean effect size equals 0

asynchrony, except for aquatic and multitrophic systems for which the number of studies was small ($N = 2$ in both groups) and effect sizes did not differ from zero (Figure 3a). We also found a significant positive relationship between species asynchrony and ecosystem temporal stability, a pattern that held for all categories of studies (Figure 3b).

### Diversity–stability relationships after accounting for environmental covariates

Analyses of studies in which the effects of environmental covariates on ecosystem stability were statistically accounted for, using either semi-partial or partial correlation coefficients as effect sizes, showed that the mean effect size of the diversity–stability relationship remained positive (Figure 4a and b). The adjusted mean effect size did not differ from the mean effect size obtained before accounting for the effect of environmental covariates ($p = 0.074$ for Figure 4a; $p = 0.778$ for Figure 4b). A similar pattern was found when comparing studies conducted under manipulated versus ambient environmental conditions (Figure 4c; $p = 0.132$).

### Publication bias

No significant publication bias was detected in our meta-analysis of the relationships between species richness and ecosystem temporal stability, either visually with the funnel plot (Appendix S1: Figure S8a) or statistically with Egger's regression test ($z = 1.291$, $p = 0.197$) and Rosenthal's *Fail-Safe N* test (Fail-Safe number =14,568). Publication bias was also not detected in the meta-analysis of species diversity–population stability relationships (Appendix S1: Figure S8b; $z = 1.775$, $p = 0.076$; Fail-Safe number =737).

## DISCUSSION

Our meta-analyses produced several notable findings. First, we found a consistently positive relationship between species diversity and ecosystem temporal stability, pointing to the important stabilizing role of species diversity for ecosystem properties. Second, the relationship between species diversity and population temporal stability varied across study systems, being positive in aquatic/multitrophic and negative in terrestrial/single-trophic systems. Third, we found that the degree of asynchrony strengthened as species diversity increased, contributing to increased ecosystem stability in more diverse communities. Finally, the positive diversity–ecosystem temporal stability relationships remained even after adjusting for the potentially confounding effects of environmental covariates, reinforcing the robustness of our findings.

The consistently positive diversity–ecosystem temporal stability relationships identified by our meta-analysis, which included a substantially larger number of studies than previous meta-analyses (Campbell et al., 2011; Gross et al., 2014; Houlahan et al., 2018; Jiang & Pu, 2009), provided arguably the strongest evidence for species diversity stabilizing the functioning of ecosystems. Our meta-analysis covers a broad range of taxa and ecosystems, complementing recent meta-level analyses that used linear mixed models to delineate diversity-stability relationships in terrestrial plant communities (Craven et al., 2018; Houlahan et al., 2018; Valencia et al., 2020). Note that some of our findings differ in important ways from those of previous meta-analyses. For example, although Jiang and Pu (2009) reported positive diversity–ecosystem stability relationships in multitrophic, but not single-trophic communities, our results showed that trophic complexity did not alter diversity–ecosystem stability relationships, which were consistently positive in both multitrophic and single-trophic communities. This

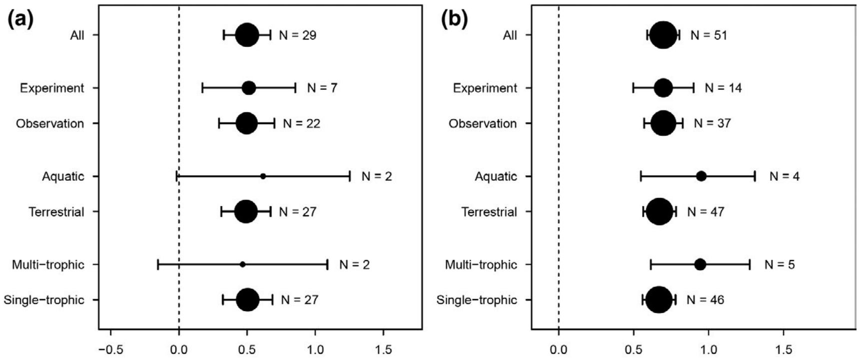

**FIGURE 3** The relationships between species diversity, community-wide species asynchrony, and ecosystem temporal stability. (a) Mean effect sizes [±95% confidence intervals (CIs)] of the relationships between species diversity and asynchrony. (b) Mean effect sizes (±95% CIs) of the relationships between asynchrony and ecosystem stability. Positive values indicate that asynchrony increases with diversity (panel a) and that ecosystem stability increases with asynchrony (panel b). Studies were categorized into experimental versus observational, terrestrial versus aquatic and single-trophic versus multitrophic systems. The size of the symbol is proportional to the sample size in each category. *N* denotes sample size. The vertical dashed line indicates where effect size equals 0

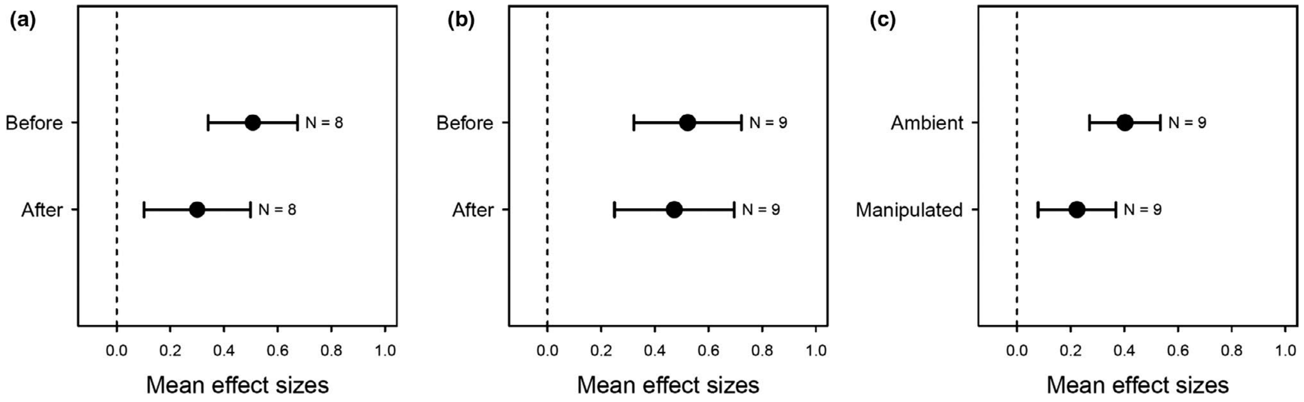

**FIGURE 4** The diversity–stability relationships before and after accounting for environmental covariates. (a) Mean effect sizes [±95% confidence intervals (CIs)] of the relationships between species diversity and ecosystem temporal stability before and after the influence of environmental covariates on temporal stability was statistically accounted for. (b) Mean effect sizes (±95% CIs) of the relationships between species diversity and ecosystem temporal stability before and after the influence of environmental covariates on both species diversity and temporal stability were statistically accounted for. (c) Mean effect sizes (±95% CIs) of the relationships between species diversity and ecosystem temporal stability under ambient and altered environmental conditions. The size of the symbol is proportional to the sample size in each category. *N* denotes the sample size. The vertical dashed line indicates where effect size equals 0

discrepancy presumably arose from the greater statistical power (ρ = 1.00 for single-trophic studies) of our meta-analysis, in which the number of single-trophic studies (*N* = 105) more than tripled that in Jiang and Pu (2009; *N* = 27; ρ = 0.378 for single-trophic studies), demonstrating the importance of adequate sample sizes (i.e., the number of data entries in the data set) for identifying general ecological patterns via meta-analysis.

In addition to species diversity, other dimensions of biodiversity, such as functional (e.g., Carrara et al., 2015; Craven et al., 2018; Roscher et al., 2011) and phylogenetic (e.g., Cadotte et al., 2012; Craven et al., 2018; Mazzochini et al., 2019; Pu et al., 2014) diversity, are known to influence ecosystem temporal stability. Our meta-analysis also revealed significant positive relationships between functional/phylogenetic diversity and ecosystem temporal stability (Appendix S1: Figure S6). These results thus lend support to the idea that functional diversity, which captures variation in functional traits that govern species responses to environmental changes and biotic interactions, and phylogenetic diversity, which accounts for species evolutionary histories and serves as a proxy of diversity of phylogenetically conserved traits, could be useful predictors of ecosystem stability (Cadotte et al., 2012; Craven et al., 2018). Our results are also consistent with those of Craven et al., (2018), who reported that species, functional, and phylogenetic diversity all contributed to stabilizing plant biomass production across 39 grassland biodiversity experiments. Note that our meta-analysis considered only published studies that have examined the relationships between functional/phylogenetic diversity and ecosystem temporal stability, providing a separate test of these relationships from Craven et al., (2018). However, given the small number of relevant studies included in our analysis, this aspect of our findings should be treated as preliminary. More studies relating multiple dimensions of biodiversity to ecological stability, including meta-level analyses of existing data (e.g., Craven et al., 2018), are needed to further understand the role of biodiversity in regulating ecological stability across various ecological systems.

Contrasting with the consistently positive effect of species diversity on ecosystem temporal stability, we found that species diversity stabilized population dynamics in observational/aquatic/multitrophic studies, but destabilized population dynamics in experimental/terrestrial/single-trophic studies. The latter result supports theoretical predictions of negative diversity–population stability relationships in competitive systems (Ives et al., 1999; Lehman & Tilman, 2000), but differs notably from the lack of diversity effect on population stability in experimental/terrestrial/single-trophic studies reported previously (Jiang & Pu, 2009), a discrepancy that may also be explained by increased statistical power (ρ = 0.616, compared with ρ = 0.459 in Jiang & Pu, 2009) of our meta-analysis. It is worth noting that in our meta-analysis most experimental studies as well as most studies classified as single-trophic are terrestrial, whereas most observational studies as well as most studies classified as multitrophic are aquatic. Therefore, the effects of the investigational approach, trophic complexity and ecosystem type cannot be clearly differentiated. Here, we focus on the comparison between terrestrial and aquatic systems, as the ecosystem type largely determined trophic complexity and investigational approaches in diversity–stability studies. Ecological communities are typically characterized by many weak trophic interactions and few strong trophic interactions (Wootton & Emmerson, 2005). One important difference between terrestrial and aquatic systems is, however, that trophic interactions (specifically herbivore-plant interactions) tend to be stronger in water than on land, reflecting differences in the size and stoichiometry of producers (plants vs. phytoplankton) between the two habitats (Shurin et al., 2002, 2006). Positive diversity–population stability relationships in aquatic communities may have emerged because weak trophic interactions, which are known to dampen unstable population dynamics associated with strong trophic interactions (Jiang et al., 2009; McCann et al., 1998; O'Gorman & Emmerson, 2009), are more frequent and thus play a more important stabilizing role in more diverse aquatic communities. By contrast, the stabilizing effect of weak trophic interactions may not be as effective in terrestrial communities, where strong, destabilizing trophic interactions comparable in magnitude with those in aquatic communities are generally lacking (Shurin et al., 2002, 2006).

Given that the stability of aggregated ecosystem properties is determined by the population stability of individual species and asynchrony between species, the contrasting effects of species diversity on population stability in terrestrial and aquatic studies point to important differences in how diversity stabilizes ecosystem properties between the two habitats. Within the terrestrial environment, asynchrony must increase sufficiently with diversity to counteract the negative effect of diversity on population stability, conferring greater stability to more diverse ecosystems (Figure 1a). Asynchrony should therefore constitute an essential stabilizing mechanism for diverse terrestrial ecosystems. Within the aquatic environment, by contrast, increases in population stability and asynchrony may both contribute to the greater stability of more diverse ecosystems (Figure 1c). In other words, whereas in terrestrial ecosystems the stabilizing effects of biodiversity must be mediated by its positive effect on asynchrony (Figure 1a), in aquatic ecosystems, the stabilizing effects of biodiversity can be mediated by its positive effect on either population stability or asynchrony (Figure 1c). Nevertheless, we found that the mean effect size of the asynchrony–ecosystem stability relationships was significantly positive for both terrestrial and aquatic studies (Figure 3b), suggesting that asynchrony contributes to ecosystem stability in both types of studies. On the other hand, our meta-analysis showed that the mean effect size of the diversity–asynchrony relationships was positive for terrestrial studies but did not differ from zero for aquatic studies (Figure 3a), suggesting that asynchrony increased with species diversity only in terrestrial systems; this result, however, was based on an extremely small sample size ($N = 2$) for aquatic studies. More studies are thus urgently needed to better understand the stabilizing role of asynchrony in relation to diversity in aquatic habitats.

Our finding, that increasing species diversity generally increased asynchrony (Figure 3a), and in turn, ecosystem stability (Figure 3b), supports increased asynchrony as an important mechanism stabilizing more diverse communities (McNaughton, 1977; Yachi & Loreau, 1999). This finding is at odds with previous reports that asynchrony tend to be rare in natural communities (Houlahan et al., 2007; Vasseur et al., 2014) but is consistent with the accumulating evidence of asynchrony being more prevalent in nature (Gonzalez & Loreau, 2009; Valencia et al., 2020) and more frequently detected in recent diversity–stability studies (e.g., Hector et al., 2010; Ma et al., 2017; Roscher et al., 2011). The discrepancy between studies may be, at least partly, attributed to their different approaches of quantifying asynchrony. For example, although Houlahan et al., (2007) used positive covariance in abundance among species as evidence for the lack of asynchrony, later work showed that asynchrony may not be adequately quantified using covariance metrics (Loreau & de Mazancourt, 2008) but could be better characterized by more specific metrics (e.g., the one suggested by Loreau & de Mazancourt, 2008 and used in all the asynchrony studies in our meta-analysis). The importance of asynchrony metrics is probably best illustrated by Valencia et al., (2020), who showed that species diversity–asynchrony relationships were mostly positive when using the asynchrony metric of Loreau and de Mazancourt (2008), but mostly negative when using the metric of Gross et al., (2014), across 79 natural and seminatural plant communities. Given that many studies of asynchrony have adopted the metric of Loreau and de Mazancourt (2008), there is a need to evaluate its performance against alternative asynchrony metrics (e.g., by analysing simulated data with known degrees of asynchrony).

The importance of asynchrony for stabilizing diverse communities underscores the need for the identification of their underlying mechanisms. Among a host of factors potentially contributing to asynchrony (Gonzalez & Loreau, 2009), differential species responses to environmental change and interspecific competition have received the most attention. Synthesizing several existing grassland biodiversity experiments, Gross et al., (2014) found that species responses to environmental fluctuations did not contribute to ecosystem-level stability, whereas interspecific competition increased the asynchrony of population dynamics among species, suggesting that observed asynchrony in these experiments were primarily driven by species interactions. By contrast, emerging patterns from natural communities suggest that species responses to environmental variation were often the most important driver of asynchrony (Mutshinda et al., 2009; Thibaut et al., 2012; Tredennick et al., 2017). It is currently unknown whether the difference between experimentally and naturally assembled communities or difference in the analytical tools used between the studies has contributed to this discrepancy. Future diversity-stability studies should move beyond just quantifying asynchrony to explore their underlying mechanisms, in order to gain a more mechanistic understanding of diversity–ecosystem stability relationships.

Among our most important findings is that the effect of species diversity on ecosystem stability remained positive after accounting for the potentially confounding effects of other environmental variables. Experiments that directly manipulated biodiversity have proven consequential in elucidating diversity–stability relationships and mechanisms (e.g., Hector et al., 2010; Tilman et al., 2006). However, it has been suggested that these experiments may not directly inform us about the role of species diversity in natural communities, where a host of other factors influence species diversity, and community and ecosystem dynamics (Huston, 1997; Wardle, 2016). Nevertheless, mechanisms identified in biodiversity experiments are known to operate in natural communities, and results from biodiversity experiments have facilitated our understanding of the functional significance of biodiversity in natural communities (Eisenhauer et al., 2016; Jochum et al., 2020). Our analyses indicate that the stabilizing role of species diversity does not diminish after considering the effects of abiotic environmental covariates, suggesting that for ecosystem stability, findings of controlled experiments may also be applied to natural communities. One plausible explanation for this result is that asynchrony may increase with diversity similarly across both naturally and experimentally assembled communities under various environmental conditions (Figure 3a). A note of caution here is that this aspect of our meta-analysis was based on relatively small sample sizes and thus needs to be confirmed by future studies. Also note that that our analysis was only able to consider one environmental covariate per study, and future work should consider multiple covariates simultaneously when such data become increasingly available.

Our study identified a consistently positive relationship between species diversity and ecosystem temporal stability, as well as asynchrony as an important mechanism contributing to positive diversity–ecosystem stability relationships. These results thus lend strong support to McNaughton's (1977) hypothesis. These results also echo those of meta-analytic studies reporting positive relationships between biodiversity and the magnitude of ecosystem functioning (e.g., Cardinale et al., 2012; Duffy et al., 2017), providing additional ecological rationales for preserving Earth's biodiversity to safeguard the sustainable provisioning of ecosystem products and services. Importantly, our study identified contrasting effects of species diversity on population temporal stability between terrestrial and aquatic systems, pointing to the different ways species diversity stabilizes ecosystem properties between the two habitats (Figure 1a and c). Future studies should aim to improve our understanding of mechanisms driving diversity–stability relationships in aquatic ecosystems, which have been underexplored relative to terrestrial ecosystems.

## CODE AVAILABILITY

All data analyses were conducted in R. The R code is available upon request.

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## CONFLICT OF INTERESTS

The authors declare no competing interests.

## AUTHOR CONTRIBUTIONS

Lin Jiang and Michel Loreau conceived the study. Qianna Xu collected the data. Qianna Xu, Xian Yang, Ying Yan and Shaopeng Wang analysed the data. Qianna Xu and Lin Jiang wrote the first draft of the manuscript. All authors contributed substantially to revisions.

## PEER REVIEW

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## DATA AVAILABILITY STATEMENT

All data that support the findings of this study have been deposited to the Dryad Digital Repository (https://doi.org/10.5061/dryad.pk0p2ngnc).

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## SUPPORTING INFORMATION

Additional supporting information may be found online in the Supporting Information section.

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