

# **ECOLOGICAL DETERMINANTS OF ECOSYSTEM STABILITY**

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The Academic Faculty

By

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# ECOLOGICAL DETERMINANTS OF ECOSYSTEM STABILITY

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*To the unexpected.*

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## SUMMARY

Understanding mechanisms underpinning the stability of ecological systems is crucial for maintaining the sustainability of the goods and services provided by Earth's ecosystems, and it has been an important goal of community ecology. However, to date the roles of various ecological factors in regulating ecological stability remain poorly understood. In this dissertation, I present three studies examining how several important ecological factors, including species diversity, nutrient enrichment, and interspecific competition, influence ecological stability. One quantitative meta-analysis (Chapter 1) synthesized the findings of existing empirical studies of the relationships between species diversity and temporal stability of ecosystem functions and properties. One field experiment (Chapter 2) examined the effects of nutrient enrichment on multiple dimensions of compositional and functional stability of a temperate semi-arid grassland. A third study (Chapter 3) used bacterivorous ciliated protozoan species as model organisms to experimentally explore the roles of interspecific competition, and species niche and fitness differences, in regulating ecosystem temporal stability through their influences on species asynchrony (i.e., asynchrony in population dynamics among species) and population-level temporal stability.

In Chapter 1, I ask whether there is a general relationship between species diversity and ecosystem temporal stability and whether influences from abiotic factors would confound the species diversity effects on ecosystem stability. To address this question, I conducted comprehensive meta-analyses to synthesize the findings of existing empirical studies of the relationships between species richness and temporal stability of ecosystem properties. I show that a general, consistently positive relationship exists between species richness and ecosystem temporal stability, a robust finding that holds even after accounting for the confounding effects

of environmental covariates. This study also identified species asynchrony as an important mechanism underlying the observed positive diversity-ecosystem stability relationships.

In Chapter 2, I examine the effects of nutrient enrichment on multiple dimensions of grassland compositional and functional stability, using data from an experiment conducted in a temperate steppe of Inner Mongolia, China. I show that nitrogen enrichment reduced grassland functional and compositional temporal stability, resistance, and recovery, but increased grassland functional and compositional resilience. Importantly, nitrogen enrichment influenced different functional stability dimensions by altering their corresponding compositional stability dimensions, whereas reduced species diversity under nitrogen enrichment contributed little to the observed changes in grassland stability. These findings highlight the need to consider community compositional stability for a more mechanistic understanding of ecosystem dynamics under ongoing global environmental change.

In the final chapter, I report a laboratory protist microcosm experiment exploring the effects of interspecific competition on species asynchrony and population temporal stability and link these two important determinants of ecosystem temporal stability to mechanisms of species coexistence (i.e., considering species niche and relative fitness differences). I show that the presence of interspecific competition promoted species asynchrony under various environmental conditions. I also found that species niche differences increased species asynchrony, whereas species fitness differences decreased population temporal stability, resulting in changes in the temporal stability of total community abundances. This study provides, to our knowledge, the first experimental evidence of the linkage between mechanisms regulating species coexistence and the determinants of ecosystem temporal stability.

## CHAPTER 1

# CONSISTENTLY POSITIVE EFFECT OF SPECIES DIVERSITY ON ECOSYSTEM, BUT NOT POPULATION, TEMPORAL STABILITY

### 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, 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.

## 1.1 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 (MacArthur 1955; Elton 1958; 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 1990s, 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 (Tilman *et al.* 2006; Hector *et al.* 2010). 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; Yachi & Loreau 1999; Loreau & De Mazancourt 2013). 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.

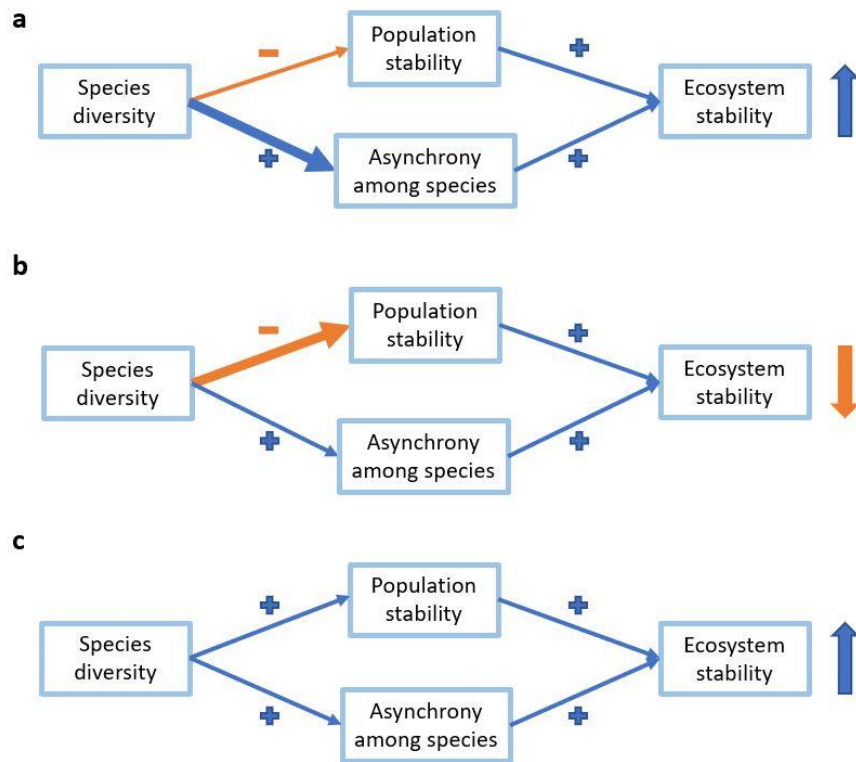
Our meta-analyses emphasize the framework that population stability of species embedded in an ecological community, and asynchronous population dynamics among these co-occurring species, combine to determine the temporal stability of aggregated ecosystem properties (Fig. 1.1). Partitioning the stability 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 (Fig. 1.1). In situations where average population stability declines with diversity, which has been frequently reported in grassland biodiversity experiments (e.g., Tilman *et al.* 2006; Hector *et al.* 2010; Roscher *et al.* 2011), increasing asynchrony must overcome lower population stability to confer great ecosystem-level stability in more diverse communities (Fig. 1.1a). This scenario corresponds to the theoretical prediction that species diversity may stabilize ecosystem properties while having a destabilizing effect on population dynamics (May 1974; Ives *et al.* 1999; Lehman & Tilman 2000). 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 (Fig. 1.1b). Under situations where average population stability increases with diversity, which has been frequently reported in aquatic biodiversity studies (e.g., Romanuk *et al.* 2006; Downing *et al.* 2014), asynchrony may combine with increased population stability to promote the stability of more diverse ecosystems (Fig. 1.1c). 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 (Houlahan *et al.* 2007; Gonzalez & Loreau 2009; Mutshinda *et al.* 2009; Vasseur *et al.* 2014; Valencia *et al.* 2020), 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 (Gross *et al.* 2014; Craven *et al.* 2018; Houlahan *et al.* 2018; van der Plas 2019; Valencia *et al.* 2020). In a previous meta-analysis, Jiang & Pu (2009) found that species diversity tended to stabilize both population and ecosystem dynamics in multi-trophic (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 multi-trophic/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

reevaluated 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 multi-trophic/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 (Walther *et al.* 2002; Reay *et al.* 2008; Fischer & Knutti 2015), 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.



**Figure 1.1** 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.

## 1.2 Materials and methods

### *Literature search and dataset 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 A: Fig. A1). 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., Jiang & Pu 2009; Campbell *et al.* 2011; Gross *et al.* 2014; van der Plas 2019) to further expand our database. Finally, we obtained the open-access data from the multi-site 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 dataset 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 A: Table A1; Appendix B). These studies are globally distributed (Appendix A: Fig. A2). 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 A: Table A2). 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. multi-trophic). 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 A: Table A3), all quantified as community-wide species asynchrony (Loreau & de Mazancourt 2008) of biomass (26 entries) or abundance (three entries), and the relationship between asynchrony and ecosystem temporal stability (51 entries). Community-wide species asynchrony was calculated as:  $1 - \sigma^2 / (\sum_{i=1}^S \sigma_i)^2$ , where  $\sigma^2$  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 (un-manipulated) vs. 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

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

where r is the correlation coefficient between species diversity and temporal variability. Note that a negative effect size in Equation (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 analyzed using random-effects models (Gurevitch & Hedges 1999; Gurevitch *et al.* 2001) that incorporate effect size variations among studies. We considered effect sizes as significant if their 95% confidence intervals (CIs) did not intercept zero (Borenstein *et al.* 2011). 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; Cochran 1954). 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 log<sub>10</sub>-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).

### 1.3 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 (Fig. 1.2a), 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  $Q_B = 0.424$ ,  $P = 0.515$ ; Fig. 1.2a), aquatic and terrestrial studies ( $Q_B = 0.080$ ,  $P = 0.777$ ; Fig. 1.2a), or single- and multi-trophic studies ( $Q_B = 0.091$ ,  $P = 0.763$ ; Fig. 1.2a). 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 A: Fig. A3), the range of species diversity gradient ( $P = 0.911$ ; Appendix A: Fig. A4a), the minimum level of

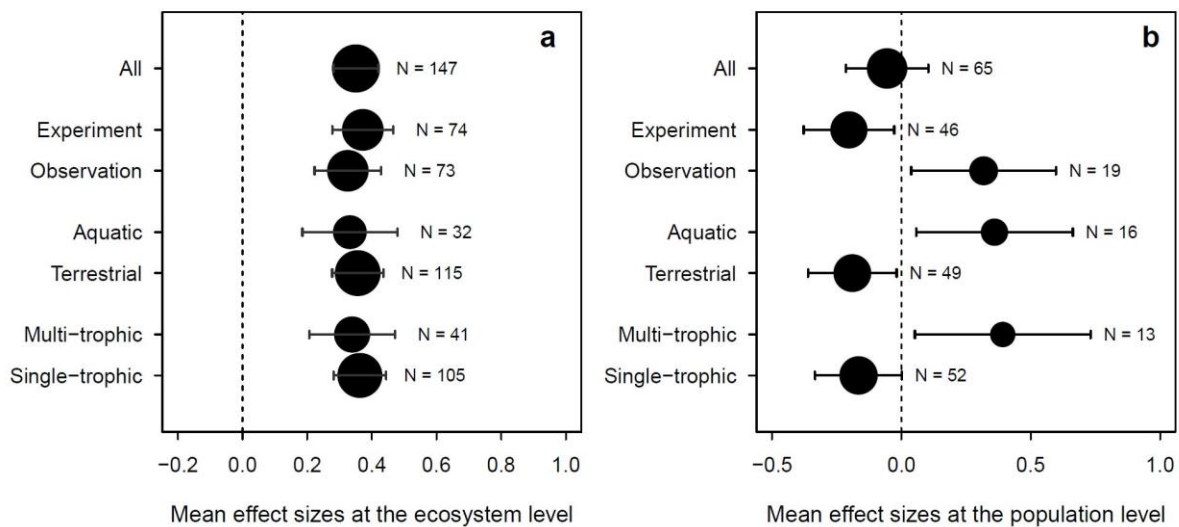
species diversity ( $P = 0.309$ ; Appendix A: Fig. A4b), and experimental duration ( $P = 0.928$ ; Appendix A: Fig. A4c). The cumulative forest plot revealed that the species diversity-ecosystem stability relationship became more positive over time (Fig. A5). The effect sizes of functional/phylogenetic diversity and ecosystem stability relationships were similarly positive (Appendix A: Fig. A6).

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 (Fig. 1.2b). 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 (Fig. 1.2b), indicating that population temporal stability increased with species diversity in observational/aquatic/multi-trophic 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 multi-trophic 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 A: Fig. A7).

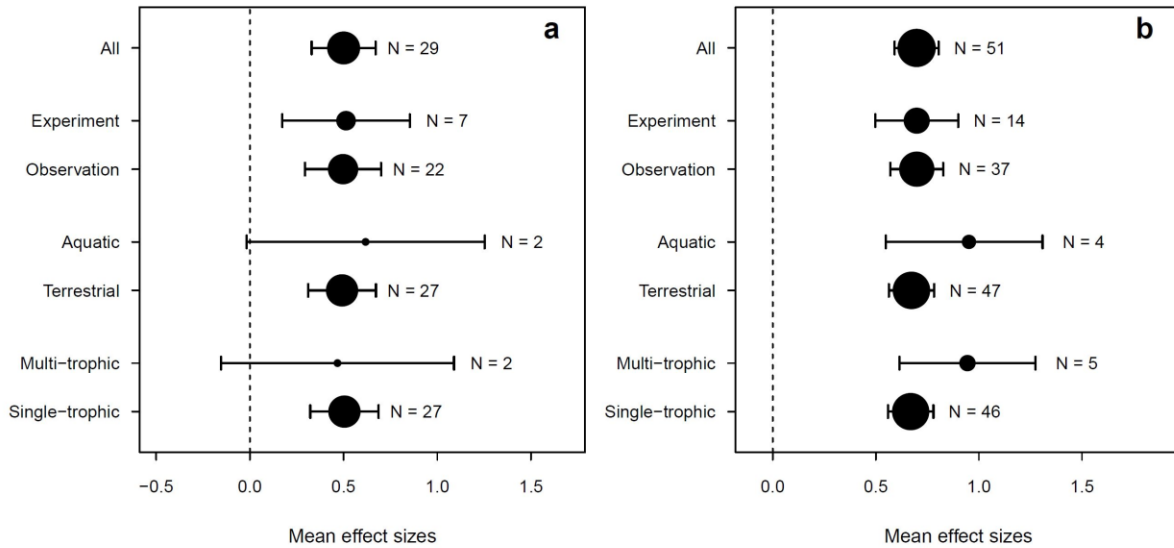
#### *The species diversity-asynchrony and asynchrony-stability relationships*

We found a significant positive relationship between species diversity and community-wide species asynchrony, except for aquatic and multi-trophic systems for which the number of studies was small ( $N = 2$  in both groups) and effect sizes did not differ from zero (Fig. 1.3a). We

also found a significant positive relationship between species asynchrony and ecosystem temporal stability, a pattern that held for all categories of studies (Fig. 1.3b).



**Figure 1.2** The relationships between species diversity and temporal stability. (a) Mean effect sizes ( $\pm$  95% CIs) of the relationships between species diversity and ecosystem-level temporal stability. (b) Mean effect sizes ( $\pm$  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 vs. observational, terrestrial vs aquatic, and single-trophic vs. multi-trophic 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.



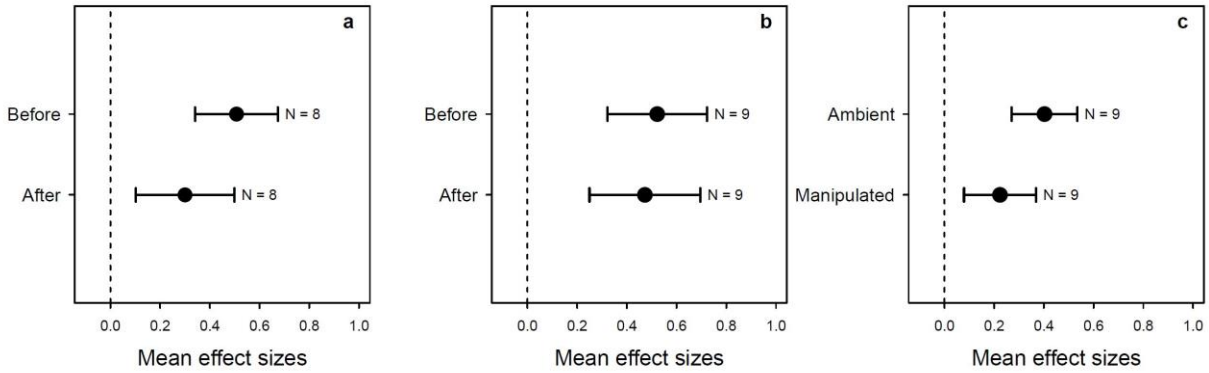
**Figure 1.3** The relationships between species diversity, community-wide species asynchrony, and ecosystem temporal stability. (a) Mean effect sizes ( $\pm$  95% CIs) of the relationships between species diversity and asynchrony. (b) Mean effect sizes ( $\pm$  95% CIs) of the relationships between 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 vs. observational, terrestrial vs. aquatic, and single-trophic vs. multi-trophic 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.

### *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 (Fig. 1.4a, 4b). 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 Fig. 1.4a;  $P = 0.778$  for Fig. 1.4b). A similar pattern was found when comparing studies conducted under manipulated vs. ambient environmental conditions (Fig. 1.4c;  $P = 0.132$ ).

### *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 A: Fig. A8a) 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 A: Fig. A8b;  $z = 1.775$ ,  $P = 0.076$ ; Fail-Safe number = 737).



**Figure 1.4** The diversity-stability relationships before and after accounting for environmental covariates. (a) Mean effect sizes ( $\pm$  95% 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 ( $\pm$  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 was statistically accounted for. (c) Mean effect sizes ( $\pm$  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.

## 1.4 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/multi-trophic 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 (Jiang & Pu 2009; Campbell *et al.* 2011; Gross *et al.* 2014; Houlahan *et al.* 2018), 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, while Jiang & Pu (2009) reported positive diversity-ecosystem stability relationships in multi-, but not single-trophic communities, our results showed that trophic complexity did not alter diversity-ecosystem stability relationships, which were consistently positive in both multi- and single-trophic communities. This discrepancy presumably arose from the greater statistical power ( $\rho = 1.00$  for single-trophic studies) of our

meta-analysis, in which the number of single-trophic studies ( $N = 105$ ) more than tripled that in Jiang & Pu (2009;  $N = 27$ ;  $\rho = 0.378$  for single-trophic studies), demonstrating the importance of adequate sample sizes (i.e., the number of data entries in the dataset) for identifying general ecological patterns via meta-analysis.

In addition to species diversity, other dimensions of biodiversity, such as functional (e.g., Roscher *et al.* 2011; Carrara *et al.* 2015; Craven *et al.* 2018) and phylogenetic (e.g., Cadotte *et al.* 2012; Pu *et al.* 2014; Craven *et al.* 2018; Mazzochini *et al.* 2019) 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 A: Fig. A6). 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/multi-trophic 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 ( $\rho = 0.616$ , compared to  $\rho = 0.459$  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 multi-trophic 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 (McCann *et al.* 1998; Jiang *et al.* 2009; 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 to 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 (Fig. 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 (Fig. 1c). In other words, whereas in terrestrial ecosystems the stabilizing effects of biodiversity must be mediated by its positive effect on asynchrony (Fig. 1a), in aquatic ecosystems the stabilizing effects of biodiversity can be mediated by its positive effect on either population stability or asynchrony (Fig. 1c). Nevertheless, we found that the mean effect size of the asynchrony-ecosystem stability relationships was significantly positive for both terrestrial and aquatic studies (Fig. 1.3b), 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 (Fig. 1.3a), 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 (Fig. 1.3a), and in turn, ecosystem stability (Fig. 1.3b), 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; Mutshinda *et al.* 2009), but is consistent with the accumulating evidence of asynchrony being more prevalent in nature (Gonzalez & Loreau 2009) and more frequently detected in recent diversity-stability studies (Hector *et al.* 2010; Roscher *et al.* 2011; Ma *et al.* 2017). The discrepancy between studies may be, at least partly, attributed to their different approaches of quantifying asynchrony. For example, while 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 & 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 & de Mazancourt

(2008), there is a need to evaluate its performance against alternative asynchrony metrics (e.g., by analyzing 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, have 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. Tilman *et al.* 2006; Hector *et al.* 2010). 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 (Fig. 1.3a). 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 (Fig. 1.1a, 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.

## 1.5 References

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## CHAPTER 2.

# NITROGEN ENRICHMENT ALTERS MULTIPLE DIMENSIONS OF GRASSLAND FUNCTIONAL STABILITY VIA CHANGING COMPOSITIONAL STABILITY

### **Abstract**

Anthropogenic nutrient enrichment is known to alter the composition and functioning of plant communities. However, how nutrient enrichment influences multiple dimensions of community- and ecosystem-level stability remains poorly understood. Using data from a nitrogen (N) and phosphorus (P) addition experiment in a temperate semi-arid grassland that experienced a natural drought, we show that N enrichment, not P enrichment, decreased grassland functional and compositional temporal stability, resistance, and recovery, but increased functional and compositional resilience. Compositional stability and species asynchrony, rather than species diversity, were identified as key determinants of all dimensions of grassland functional stability, except for recovery. Whereas grassland functional recovery was decoupled from compositional recovery, N enrichment altered other dimensions of functional stability primarily through changing their corresponding compositional stability dimensions. Our findings highlight the need to examine ecological stability at the community level for a more mechanistic understanding of ecosystem dynamics in the face of environmental change.

## 2.1 Introduction

Anthropogenic nitrogen (N) and phosphorus (P) enrichment, due to increased fossil fuel use and agricultural fertilizer applications, are among the most significant global environmental changes affecting the world's ecosystems (Vitousek *et al.* 1997; Smil 2000; Galloway *et al.* 2004; Galloway *et al.* 2008; Yuan *et al.* 2018). Nitrogen is an essential component of proteins, nucleic acids, and chlorophyll, and thus critical for many cellular and physiological processes (Chapin 1980; Field & Mooney 1986). Phosphorus constitutes a major ingredient of cellular membranes and nucleic acids (DNA and RNA; Schachtman *et al.* 1998). Grasslands, which cover approximately 40% of the Earth's ice-free land area (White *et al.* 2000), are often limited by the availability of reactive N and P (Walker & Syers 1976; Vitousek & Howarth 1991; Elser *et al.* 2007; Harpole *et al.* 2011; Fay *et al.* 2015). Increased N and P input into grasslands, either individually or in combination, has often resulted in increased primary productivity (Elser *et al.* 2007; Harpole *et al.* 2011; Fay *et al.* 2015; Li *et al.* 2016; Hou *et al.* 2020). There is also mounting evidence that N enrichment often reduces grassland plant diversity (Bobbink *et al.* 1998; Stevens *et al.* 2004; Payne *et al.* 2017; Midolo *et al.* 2019), although the effects of P enrichment on grassland diversity are mixed (Soons *et al.* 2017; DeMalach 2018). N and P enrichment are also known to alter other compositional (e.g., Yang *et al.* 2011a; Zhao *et al.* 2019) and functional (Song *et al.* 2019) properties of grasslands. However, how N and P enrichment influences various aspects of grassland stability remains poorly understood.

Ecological stability encompasses multiple dimensions, such as temporal stability, resistance, resilience, and recovery, each of which captures the dynamics of ecological systems and their responses to environmental changes in different ways (Fig. 1; Pimm 1984; Ives & Carpenter 2007; Donohue *et al.* 2013, 2016). Efforts to understand the dimensionality of

ecological stability have revealed various relationships between different stability components (Donohue *et al.* 2013; Donohue *et al.* 2016; Hillebrand *et al.* 2018; Radchuk *et al.* 2019; Polazzo & Rico 2021), indicating that one stability component may not necessarily substitute for another. Thus, adopting the multidimensional framework in stability research is becoming increasingly important for gaining a comprehensive understanding of ecological stability (Donohue *et al.* 2013; Pennekamp *et al.* 2018; Kéfi *et al.* 2019; Yang *et al.* 2019), and for fully characterizing ecosystem dynamics in response to global environmental changes. However, most studies of ecological stability have focused on a single dimension of stability (Donohue *et al.* 2016), risking a potentially biased understanding of the overall stability of ecological systems.

Recent stability research has primarily focused on the stability of ecosystem processes and functions (i.e., functional stability; Xu *et al.* 2021), coinciding with ecologists' interest in understanding the consequences of biodiversity loss for ecosystem functioning over the last three decades (Loreau *et al.* 2022). Previous studies have reported positive effects of species diversity on the temporal stability (Tilman *et al.* 2006; Hector *et al.* 2010), resistance (Isbell *et al.* 2015; Baert *et al.* 2016), resilience (Van Ruijven & Berendse 2010), and recovery (Kreyling *et al.* 2017) of ecosystem functions. These positive biodiversity-functional stability relationships may be attributed to two primary mechanisms: increased asynchronous population dynamics among species (i.e., the insurance effect; Ives *et al.* 1999; Yachi & Loreau 1999; Loreau & de Mazancourt 2008, 2013), and the increased presence of dominant, stable species in more diverse communities (i.e., the selection effect; Loreau & Hector 2001). On the other hand, as predicted by the mass ratio hypothesis (Grime 1998), ecosystem-level stability may be largely driven by the stability of dominant species, rather than species diversity, if one or a few species contribute predominantly to ecosystem functioning (Doak *et al.* 1998; Steiner *et al.* 2005; Hillebrand *et al.*

2008). Nutrient enrichment is known to affect species richness (Suding *et al.* 2005; DeMalach 2018), asynchronous dynamics among species (hereafter species asynchrony; Hautier *et al.* 2014; Zhang *et al.* 2016), and the stability of dominant species (Liu *et al.* 2019), with consequences for ecosystem temporal stability (Hautier *et al.* 2014; Zhang *et al.* 2016). By comparison, few studies have examined nutrient enrichment effects on ecosystem resistance to disturbance (Xu *et al.* 2014; Hofer *et al.* 2017), resilience after disturbance (Kinugasa *et al.* 2012; Xu *et al.* 2014), or recovery to the pre-disturbance state (Xu *et al.* 2014). Overall, the effects of nutrient enrichment on multiple dimensions of functional stability have rarely been explored, leaving a significant gap in our knowledge.

Compared to functional stability, community compositional stability, which considers changes in community membership and species relative abundance (Micheli *et al.* 1999; Sankaran & McNaughton 1999), has received considerably less attention. Several earlier studies have examined compositional stability in relation to species diversity and documented various relationships between the two (Frank & McNaughton 1991; Sankaran & McNaughton 1999; Foster *et al.* 2002; Shurin *et al.* 2007; Wang *et al.* 2010). These results suggest varied importance of species diversity for regulating community compositional stability. More recent investigations have explored the relationship between functional and compositional stability, echoing calls for the need to investigate both types of stability concurrently (Micheli *et al.* 1999; Lamy *et al.* 2021). These investigations have also produced mixed results. On the one hand, some studies have reported that compositional and functional stability are positively associated (Baert *et al.* 2016; Guelzow *et al.* 2017; Hillebrand *et al.* 2018). On the other hand, functional stability has been found to be decoupled from compositional stability. This could happen, for instance, when dominant species largely determine ecosystem functioning despite appreciable changes in

community composition (e.g., Hoover *et al.* 2014), or when species asynchrony maintains the stability of aggregated ecosystem properties (Yachi & Loreau 1999; Xu *et al.* 2021). However, how nutrient enrichment influences multiple dimensions of compositional stability and functional-compositional stability relationships remains a largely open question.

By taking advantage of a resource addition experiment in a temperate semiarid grassland that experienced a severe, natural drought, we investigated how N and P enrichment affected multiple dimensions of ecological stability, including resistance, resilience, recovery, and temporal stability, at both ecosystem and community levels. The temperate semi-arid grassland, located in Inner Mongolia, China, is a part of the Eurasian grassland biome. It has been subjected to intensifying environmental changes, including increased N and P input (Niu *et al.* 2010; Yang *et al.* 2011a), and more frequent and intense droughts (Angerer *et al.* 2008; Yu *et al.* 2014). In 2007, our study site experienced the worst drought in nearly 60 years, offering a unique opportunity to explore how nutrient enrichment influences grassland stability properties. Our study aimed at addressing three main questions. First, how does N and P enrichment influence multiple dimensions of grassland functional and compositional stability? Second, what are the relative contributions of species richness, species asynchrony, and the stability of dominant species in stabilizing ecosystem function and community composition? Third, what are the relationships between functional and compositional stability? Table 2.1 summarizes our hypotheses corresponding to these questions.

**Table 2.1 Our hypotheses corresponding to the three research questions.**

<b>Hypotheses</b>	<b>Relevant literature</b>
<p>H1: Nutrient enrichment would decrease functional and compositional temporal stability, resistance, and recovery, but may increase resilience (i.e., increased rate of return to the pre-disturbance state, due to nutrient-induced increases in growth rate). We expect that lower resistance under nutrient enrichment contributes to lower recovery and temporal stability but allows more room for higher resilience.</p>	<p>Hautier <i>et al.</i> 2014                      Isbell <i>et al.</i> 2015                      Xu <i>et al.</i> 2014</p>
<p>H2: Nutrient enrichment reduces species richness, species asynchrony and the stability of dominant species, with ensuing consequences for grassland functional and compositional stability.</p>	<p>Hautier <i>et al.</i> 2014                      Liu <i>et al.</i> 2019                      Zhang <i>et al.</i> 2016</p>
<p>H3: Across stability dimensions, functional and compositional stability would exhibit positive relationships as lesser changes in community composition favor lesser changes in ecosystem functions.</p>	<p>Hillebrand <i>et al.</i> 2018</p>

## 2.2 Material and Methods

### *Study site*

Our study was conducted at the Duolun Restoration Ecology Research Station (42°02' N, 116°17' E, 1324 m. a. s. l.) of the Institute of Botany, Chinese Academy of Sciences, located in Inner Mongolia, China. The study site has a semi-arid, continental monsoon climate with a relatively short growing season (from May to September). The mean annual precipitation is 378 mm; the mean annual temperature is 2.1°C. The year 2007 was the driest on record in our study area since 1953 (Fig. C1), with a growing season precipitation of 185.0 mm, compared to the long-term growing season average of 328.3 mm. The vegetation is dominated by perennial plant species, such as *Agropyron cristatum*, *Artimesia frigida*, *Medicago ruthenica*, and *Stipa krylovii*. Large herbivores have been excluded from our study site by fencing since 2001.

### *Experimental design and sampling*

Our experiment was established in 2005, using a randomized complete block design. Four 92m x 60m blocks were established with a 5-meter-wide buffer zone between adjacent blocks. Each block was divided into four 44m x 28m plots, with each plot randomly assigned to one of the four nutrient addition treatments: control (i.e., ambient condition with no nutrient addition), N enrichment (10g N/m<sup>2</sup> per year in the form of ammonium nitrate), P enrichment (5g P/m<sup>2</sup> per year in the form of triple superphosphate), and the combined enrichment of N and P (10g N/m<sup>2</sup> + 5g P/m<sup>2</sup> per year). Pelletized fertilizer was evenly distributed by hand into designated plots in July each year. The background rate of N deposition in the study area is approximately 1.47 g N/m<sup>2</sup> per year (Zhang *et al.* 2017); the amount of N applied in our experiment is comparable to the rate of atmospheric N deposition in the North China Plain (about 8.33g N/m<sup>2</sup> per year; He *et al.* 2007). The amount of P fertilizer applied is comparable to

those in several other grassland experiments that manipulated P availability (e.g., Harpole & Tilman 2007).

Plant communities in the experimental plots were surveyed in August, when our study grassland attained its peak biomass, annually from 2006 to 2008. We estimated plant cover, rather than biomass, as a proxy of primary production. The non-destructive plant cover survey avoids disturbances associated with biomass estimation; our prior work also indicates strong positive relationships between plant species cover and biomass at our experimental site (Fig. S2; Xia *et al.* 2009). Plant cover was measured by placing a 1m x 1m frame with 100 10cm x 10cm grids above a 1m x 1m permanent quadrat. We identified all species in each grid and estimated the percent cover of each species based on their occurrence within the 100 grids. Percent coverage was summed across species to obtain total community cover. Species richness was quantified as the number of species recorded within each quadrat; evenness was quantified using the Simpson index:  $E = 1 - \sum_{i=1}^S P_i^2$ , where  $P_i$  is the relative abundance of species  $i$ . We classified all species into dominant (relative abundance > 5%), subordinate (relative abundance between 1% to 5%), and rare (relative abundance < 1%) species.

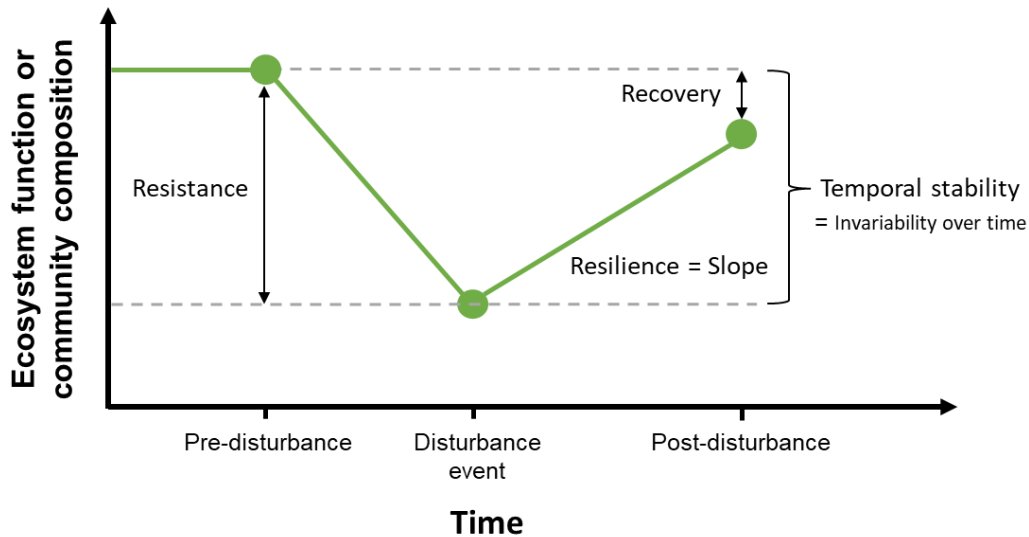
### *Stability calculations*

We quantified four stability dimensions (temporal stability, resistance, resilience, and recovery) for both total plant cover and community composition as measures of functional and compositional stability, respectively. We define resistance as the grassland's ability to withstand disturbance (Pimm 1984; Ives & Carpenter 2007), resilience as the rate of return to the pre-disturbance state after disturbance (i.e., engineering resilience; Holling 1973; Pimm 1984; Pimm *et al.* 2019), recovery as the extent to which ecosystem function or community composition, following disturbance, returns to its pre-disturbance state (Hillebrand *et al.* 2018), and temporal

stability as the degree of constancy of community or ecosystem properties over time (Pimm 1984, Tilman *et al.* 2006). We illustrated how these stability dimensions are measured in Fig. 2.1 and provided details on their calculation in Table 2.2. All the stability metrics were also calculated for each of species abundance groups. Species asynchrony was quantified as the community-wide asynchrony index, following Loreau & de Mazancourt (2008). Species asynchrony was calculated separately for each dimension of stability, using the data from the years relevant to the stability component (i.e., data from 2006 and 2007 for resistance, data from 2007 and 2008 for resilience, data from 2006 and 2008 for recovery, and data from 2006, 2007, and 2008 for temporal stability).

### *Statistical analysis*

Linear mixed-effects models were used to assess the effects of N enrichment, P enrichment, and year on plant cover and richness, in which N enrichment, P enrichment, and year were treated as fixed factors, and block was treated as a random factor. Likewise, permutational multivariate analysis of variance (PERMANOVA) was used to assess treatment effects on community composition, with among-plot Bray-Curtis dissimilarity as the dependent variable. We also used linear mixed-effects models to assess the effects of N and P enrichment on different dimensions of stability at the ecosystem level (functional stability) and the community level (compositional stability), species asynchrony, and the stability of dominant species. We also assessed the treatment effects on subordinate and rare species stability (see Fig. C3) but focused on dominant species stability in subsequent analyses given their greater contributions to community and ecosystem stability (see Results).



**Figure 2.1** A conceptual diagram of the four dimensions of ecological stability examined in this study. Resistance is defined as the ability to withstand disturbance and quantified as the difference in ecosystem function or community composition between the disturbance year and pre-disturbance year. Resilience is defined as the rate of return of ecosystem function or community composition to the pre-disturbance state and quantified as the slope of change following disturbance. Recovery is defined as the extent to which ecosystem function or community composition, following disturbance, returns to its pre-disturbance state, and quantified as the difference between the post-disturbance year and the pre-disturbance year. Temporal stability is defined as the degree of constancy of ecosystem function or community composition over time. Table 2 provides more details on the calculations of these stability dimensions.

**Table 2.2** The four stability dimensions investigated in this study, as well as how each stability dimension was quantified and its interpretation at the ecosystem (i.e., functional stability) and community (i.e., compositional stability) levels. Note: F = ecosystem function of interest.

Stability dimension	FUNCTION		COMPOSITION	
	Method of quantification	Interpretation	Method of quantification	Interpretation
<i>a</i> : Temporal stability	The inverse of coefficient of variation (1/CV) of total plant cover in each experimental plot over time (2006-2008).	Larger values indicate greater temporal stability over time.	One minus the mean Euclidean distance from each plot to its three-year (2006-2008) plot centroid, with distance calculated based on cross-year Bray-Curtis dissimilarity among communities of the same plot.	Larger values indicate greater temporal stability over time.
<i>b</i> : Resistance	Log response ratio (i.e., log transformed proportional changes) of total plant cover between drought (2007) and pre-drought (2006) years.  $b = \ln(F_{07}/F_{06})$	More negative values indicate lower resistance  0 = max resistance	Bray-Curtis similarity between pre-drought and drought communities.	Range: 0 - 1  Larger values correspond to greater resistance.

<i>c</i> : Resilience	<p>Slope of change in total plant cover between post-drought (2008) and drought (2007) years (equivalent as the difference between 2008 and 2007)</p> $c = \ln(F_{08}/F_{07})$	<p>More positive values indicate greater resilience.</p> <p>0 = no resilience</p>	<p>Bray-Curtis dissimilarity between drought and post-drought communities.</p>	<p>Range: 0 - 1</p> <p>Larger values correspond to greater resilience.</p>
<i>d</i> : Recovery	<p>Log response ratio between post-drought (2008) and pre-drought (2006) years.</p> $d = \ln(F_{08}/F_{06})$	<p>More negative values indicate lower recovery</p> <p>0 = max recovery</p>	<p>Bray-Curtis similarity between pre-drought and post-drought communities.</p>	<p>Range: 0 - 1</p> <p>Larger values correspond to greater recovery.</p>

Simple linear regressions were used to assess how species asynchrony, species richness, and the stability of dominant species relate to each dimension of grassland functional and compositional stability. Linear regressions were also used to assess the relationships between functional and compositional temporal stability, resistance, resilience, and recovery. We further performed piecewise structural equation modeling (SEMs) to examine the pathways through which nutrient enrichment affected grassland functional and compositional stability. A separate SEM was constructed for each dimension of stability. We first constructed *a priori* models that included all plausible pathways (Fig. C4) and then obtained the final SEMs by eliminating non-significant pathways. For species richness, we considered either initial richness (species richness in 2006 for resistance, recovery, and temporal stability, and species richness in 2007 for resilience) or species richness averaged across the three years. As the SEMs based on initial and average species richness were similar, we focus on results based on average species richness here (see Fig. C5 for SEMs based on initial species richness). We also considered evenness but found that it was a non-significant factor in the SEMs (see Fig. C6). Model adequacy was evaluated using Shipley's test of directed separation on Fisher's *C* statistic (Shipley 2013) and Akaike information criteria corrected for sample size (AICc).

All statistical analyses were conducted in R version 4.1.2 (R Core Team 2021). The 'nlme' package was used for conducting linear mixed-effects models, the 'vegan' package for calculating Bray-Curtis dissimilarity and conducting PERMANOVA, and the 'piecewiseSEM' package for constructing SEMs (Lefcheck 2016).

## 2.3 Results

### *Effects of nutrient enrichment on functional and compositional stability*

N enrichment increased total plant cover and dominant species cover (linear mixed-effects model:  $P < 0.001$  and  $P = 0.012$ , respectively; Fig. C7a, b, Table C1), but decreased species richness ( $P = 0.017$ , Fig. C7c, Table C1), whereas P enrichment had little effect ( $P = 0.159$ ,  $P = 0.810$ , and  $P = 0.991$  for total plant cover, dominant species cover, and species richness, respectively; Fig. C7, Table C1). However, the effects of N enrichment on total plant cover and dominant species cover were stronger under P enrichment, resulting in a significant N  $\times$  P term in the linear mixed-effects models ( $P = 0.012$  and  $P = 0.011$ , respectively; Fig. C7a, b, Table C1). Likewise, PERMANOVA revealed a significant N  $\times$  P effect on community composition (Table C2).

N enrichment significantly reduced functional temporal stability (linear mixed-effects model:  $P < 0.001$ ; Fig. 2.2a, Table C3), functional resistance ( $P < 0.001$ ; Fig. 2.2c, Table C3), and functional recovery ( $P = 0.018$ ; Fig. 2.2g, Table C3), but increased functional resilience ( $P < 0.001$ ; Fig. 2.2e, Table C3). The effects of N enrichment on different dimensions of compositional stability largely mirrored those on functional stability (Fig. 2.2b, d, f, h, Table C3). By contrast, P enrichment had no discernable effect on functional or compositional stability ( $P > 0.05$ ; Fig. 2.2, Table C3). Similar trends were found for dominant species (Table C4, Fig. C8). No significant N  $\times$  P term was detected for any stability metrics (Tables C3, C4).

### *Pathways through which nutrient enrichment affected stability*

SEM confirmed that both functional and compositional temporal stability, resistance, and recovery decreased with N enrichment, while functional and compositional resilience increased with N enrichment (Fig. 2.3). P enrichment had similar, albeit considerably weaker, effects on

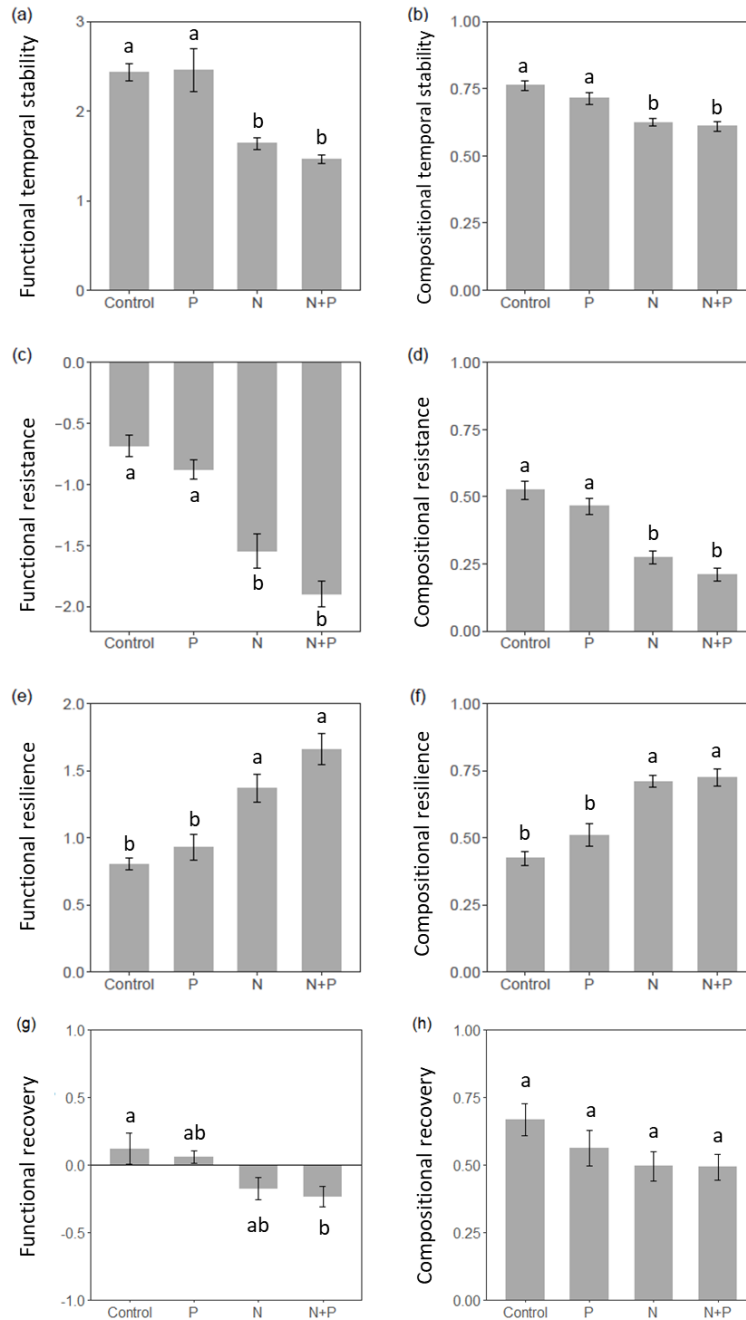
temporal stability and resistance, and did not affect resilience or recovery (Fig. 2.3). SEM also confirmed that N enrichment reduced species richness; however, species richness did not affect temporal stability, resilience, or recovery, except for a small effect on resistance (Fig. 2.3). We also found that species asynchrony, which was unaffected by nutrient enrichment (Fig. C9), contributed positively to functional temporal stability and resistance, but negatively to functional resilience; species asynchrony had no discernable effect on functional recovery (Fig. 2.3). Importantly, with the exception of recovery, the effects of N enrichment on functional stability were largely modulated by its effects on corresponding compositional stability (Fig. 2.3).

*Relationships between compositional and functional stability, and between stability dimensions*

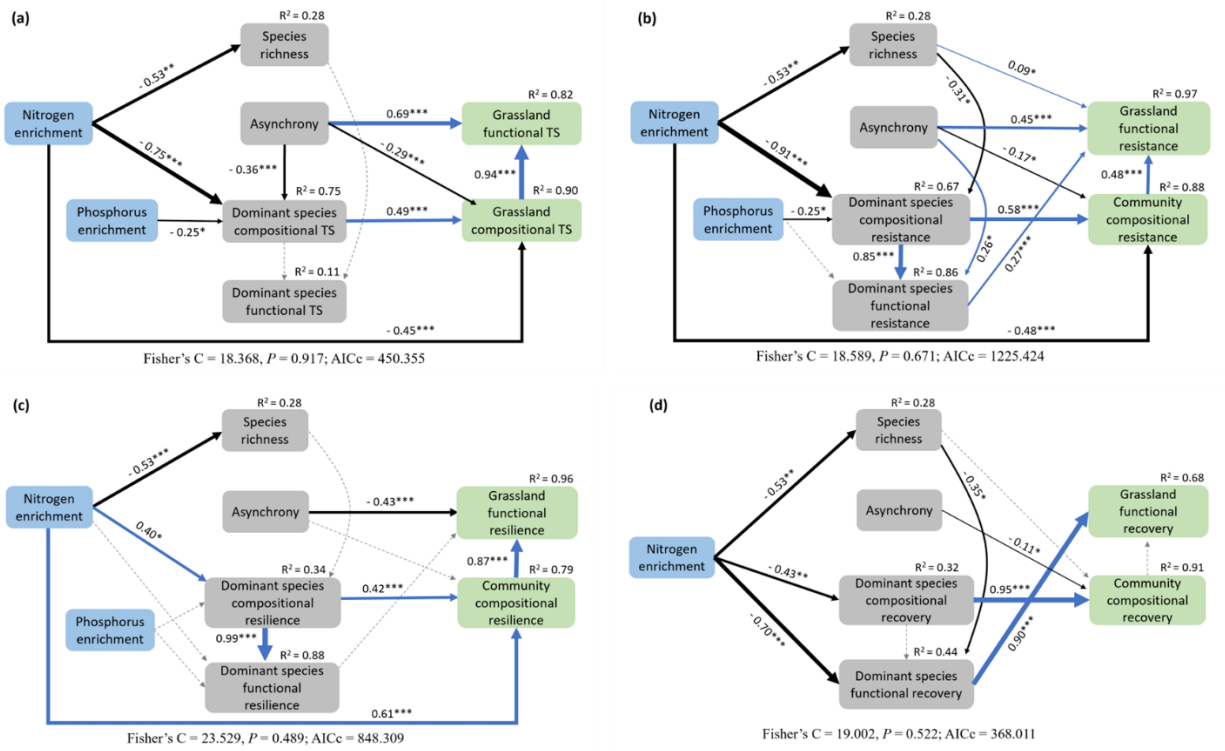
Consistent with SEM results, linear regressions showed that across all treatments, strong positive relationships existed between compositional and functional temporal stability, resistance, and resilience, but not recovery (Fig. 2.4). Different stability dimensions also tended to show strong relationships with each other (Fig. C10). For example, resistance was positively associated with temporal stability and recovery, but negatively associated with resilience, at both ecosystem (Fig. C10a) and community (Fig. C10b) levels.

## 2.4 Discussion

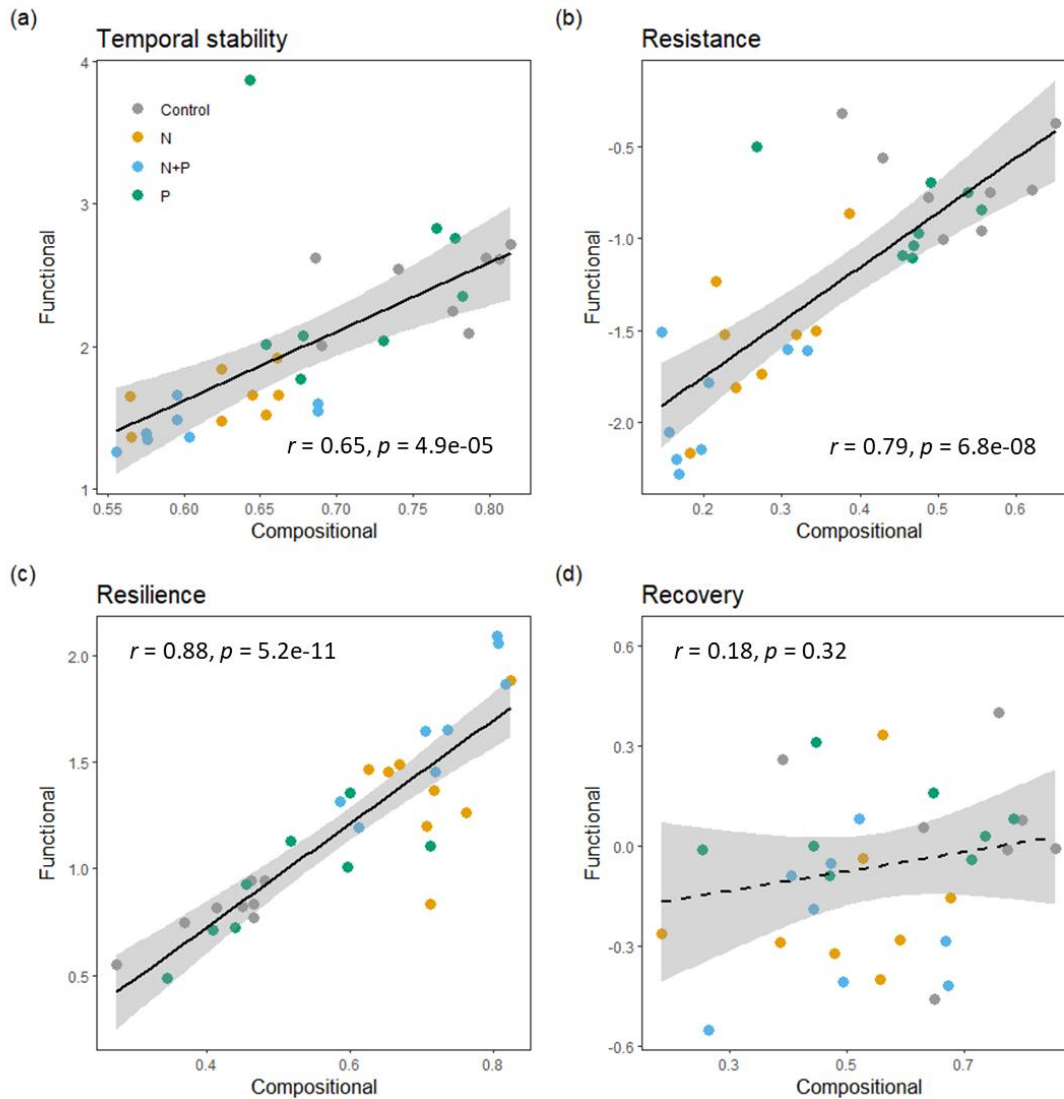
Ecologists have long recognized the significance of disturbances in shaping ecological communities and ecosystems (Sousa 1984; White & Pickett 1985). However, a general understanding of the mechanisms underlying community and ecosystem stability remains elusive, which is, at least in part, due to the multidimensional nature of ecological stability. Our study explored the effects of N and P enrichment on the multiple dimensions of functional and compositional stability of a temperate grassland that had experienced a severe drought and yielded three notable findings. First, N enrichment negatively affected grassland functional and compositional resistance, recovery, and temporal stability, but positively affected resilience. The effects of P enrichment were either considerably weaker or non-significant compared to those of N. Second, different dimensions of grassland functional stability were largely independent of species richness, but were influenced by species asynchrony, and to a greater extent, by the corresponding grassland compositional stability (Fig. 2.3). Third, the effects of N enrichment on grassland functional stability, except for recovery, were largely modulated by its effects on compositional stability (Fig. 2.3). Correspondingly, we found a positive relationship between functional and compositional resistance, resilience, and temporal stability (Figs. 2.3 & 2.4). These results provide novel insights into grassland stability in the face of ongoing global environmental change.



**Figure 2.2** Effects of nitrogen and phosphorus enrichment on multiple stability dimensions of grassland functional (a, c, e, g) and compositional (b, d, f, h) stability. Control: no nutrient enrichment; P: phosphorous enrichment; N: nitrogen enrichment; N+P: nitrogen and phosphorous enrichment. Bars indicate means ( $\pm 1$  s.e.). Treatments sharing the same letter are not statistically different from each other in a *post hoc* Tukey's HSD test at the level of  $P = 0.05$ .



**Figure 2.3** The final structural equation models showing the direct and indirect effects of nutrient enrichment on grassland functional and compositional (a) temporal stability (TS), (b) resistance, (c) resilience, and (d) recovery. Blue and black arrows indicate positive and negative pathways, respectively ( $*P < .05$ ,  $**P < .01$ ,  $***P < .001$ ). Numbers along the arrows indicate standardized path coefficients. Arrow width is proportional to the strength of the relationship. The proportion of variance explained ( $R^2$ ) appears alongside response variables in the models.



**Figure 2.4 Bivariate relationships between grassland functional and compositional stability for the four stability dimensions: (a) temporal stability, (b) resistance, (c) resilience, and (d) recovery. Each dot represents an individual plot from the experiment. Significant relationships are denoted as solid regression lines. The shaded areas represent 95% confidence intervals.**

### *Effects of nutrient enrichment on grassland functional and compositional stability*

Consistent with previous studies conducted at our study site (Xu *et al.* 2012a, 2012b), we found that N enrichment resulted in increased total plant cover. Although we observed a lack of grassland cover response to P enrichment alone, P enrichment significantly increased plant cover in combination with N enrichment (Fig. C7a). This finding indicates serial co-limitation (Harpole *et al.* 2011), implying that N is the more limiting resource in our study grassland than P. This result supports the idea that N and P co-limitation is common throughout the world's ecosystems (Elser *et al.* 2007; Bracken *et al.* 2015; Fay *et al.* 2015; Li *et al.* 2016).

In support of our first hypothesis (Table 2.1), we found that N enrichment alone and in combination with P significantly altered different dimensions of functional stability. Specifically, N and N+P enrichment reduced functional temporal stability, resistance, and recovery, but increased resilience (Fig. 2.2). By comparison, P enrichment alone had a much weaker or non-significant effect on the four dimensions of functional stability (Figs. 2.2 & 2.3). Our findings are consistent with several empirical studies reporting that N enrichment can reduce grassland functional temporal stability (e.g., Yang *et al.* 2012; Hautier *et al.* 2014; Zhang *et al.* 2016; but see Grman *et al.* 2010) and resistance (Xu *et al.* 2014; Bharath *et al.* 2020). However, our finding that N enrichment increased functional resilience but decreased functional recovery contrasts with that of Xu *et al.* (2014), who reported no effect of N addition on grassland functional resilience and recovery. This discrepancy may have been caused by the differences in N application regime between the two studies. First, while our experiment used ammonium nitrate as the N fertilizer, Xu *et al.* (2014) used urea, where nitrogen availability for plants could have been reduced by ammonium volatilization (Soares *et al.* 2012). Second, while N fertilizer was applied once in July in our experiment, the same total amount of N fertilizer was divided to two

equal amounts and applied in early May and late June in Xu *et al.* (2014). Prior work has shown that less frequent application of the same amount of N fertilizers had stronger impact on grassland communities (Zhang *et al.* 2014).

Our study provides, to our knowledge, the first empirical evidence of nutrient enrichment influencing multiple dimensions of community compositional stability. The effects of nutrient enrichment on compositional stability largely mirror those on functional stability. Specifically, we found that N enrichment negatively affected grassland compositional temporal stability, resistance, and recovery, but positively affected compositional resilience (Figs. 2.2 & 2.3), both directly and indirectly via influencing dominant species compositional stability (Fig. 2.3). By comparison, P enrichment had a much lesser negative effect on compositional temporal stability and resistance through reducing dominant species compositional stability and did not affect compositional resilience or recovery (Figs. 2.2 & 2.3). Furthermore, in line with the mass ratio hypothesis (Grime 1998), we found that the dominant species compositional stability, not species richness, was the most important determinant of grassland compositional stability for all four stability dimensions (Fig. 2.3). These patterns emerged as the three most dominant species in our experiment increased in abundance following N and N+P enrichment in 2006, lost proportionally more biomass in the N and N+P enrichment plots when experiencing drought in 2017, and recovered their biomass more quickly in these plots in 2008 (Fig. C11). These changes in the abundance of dominant species under N enrichment thus translated into reduced compositional resistance and temporal stability, but increased compositional resilience. Our study extended the mass ratio hypothesis, which has been previously applied to functional stability at the ecosystem level (Lepš 2004; Polley *et al.* 2007; Grman *et al.* 2010; Sasaki & Lauenroth 2011; Yang *et al.* 2011b), to compositional stability at the community level.

### *Species diversity and asynchrony as potential drivers of stability*

N enrichment can reduce grassland functional temporal stability via diversity-mediated effects on the temporal variation of primary production (Yang *et al.* 2012; Hautier *et al.* 2015, 2020). Our study showed that species richness decreased with N enrichment but not P enrichment (Figs. 2.3 & C7a), which is consistent with the frequently reported negative effects of N enrichment on plant diversity (Stevens *et al.* 2004; Suding *et al.* 2005; Midolo *et al.* 2019; Tognetti *et al.* 2021), while also providing empirical evidence for a lack of P effect on plant diversity (Soons *et al.* 2017; DeMalach 2018). In partial contrast to our second hypothesis (Table 2.1), SEMs revealed that the negative effect of N enrichment on functional temporal stability and recovery, and the positive effect of N enrichment on resilience were not modulated by species richness, whereas the negative effect of N enrichment on functional resistance through species richness was quite small (Fig. 2.3). The lack of diversity effect on multiple stability dimensions in our study could be partly attributed to the modest gradient (9-18 species) of species richness observed in our experiment, compared to studies that experimentally established large diversity gradients (e.g., 1-16 species in Tilman *et al.* 2006 and Roscher *et al.* 2011; 1-32 species in Hector *et al.* 2010). On the other hand, the nonsignificant diversity effect may not negate the contribution of other factors, such as species asynchrony, to ecosystem stability.

Species asynchrony has been recognized as an important mechanism promoting temporal stability of ecosystem functions (Loreau & de Mazancourt 2008; Xu *et al.* 2021), but its role for other stability dimensions has been much less appreciated. In our experiment, species asynchrony, which was unaffected by nutrient enrichment or species richness (Figs. 2.3 & C9), was a significant predictor of all but one dimensions of grassland functional stability (Fig. 2.3). For example, we found a positive relationship between species asynchrony and functional

temporal stability, supporting species asynchrony as an important stabilizing mechanism in plant communities (e.g., Hector *et al.* 2010; Roscher *et al.* 2011; Ma *et al.* 2017). We also found that species asynchrony increased functional resistance to drought, but decreased functional resilience after drought. Drought reduced the abundance of dominant species in our experiment, allowing a few less abundant but more drought-tolerant species (e.g., *Potentilla bifurca*, *Allium ramosum*, *Phlomis umbrosa*; Yi *et al.* 2019), to increase in abundance and compensate for the reduced abundance of dominant species. The asynchronous responses of different species to drought thus contributed to high functional resistance and stable ecosystem dynamics over time. Note that increasing species asynchrony is expected to translate into decreased compositional stability, as observed for three of four stability dimensions (temporal stability, resistance, and recovery; Fig. 2.3). However, for temporal stability and resistance, the direct positive effect of species asynchrony on functional stability overwhelmed its indirect, negative effect through compositional stability (Fig. 2.3). On the other hand, high species asynchrony for resilience indicates large difference in the degree of growth among species in the year following drought. This means that the growth of dominant species may have been slowed down by the increased abundances of the previously less abundant species, resulting in the slow resilience of community biomass. Overall, our results highlight the role of species asynchrony as an important determinant of multiple dimensions of functional stability.

#### *Relationships between compositional and functional stability, and between stability dimensions*

Among our most important findings is that the effects of nutrient enrichment on functional stability were largely mediated by changes in compositional stability, where functional stability was positively related to the corresponding compositional stability for all but one of stability dimensions (Figs. 2.3 & 2.4). These findings, which lend support to our third

hypothesis (Table 2.1), suggest that preserving and restoring the pre-drought community composition is important for maintaining functional stability of our study grassland. These findings echo these of several experimental studies conducted in aquatic systems (Baert *et al.* 2016; Guelzow *et al.* 2017; Hillebrand *et al.* 2018; Polazzo & Rico 2021) as well as a recent meta-analysis (Hillebrand & Kunze 2020) reporting that the maintenance of pre-disturbance community composition favors ecosystem functional stability. Our study differs, however, from previous work by examining the consequences of nutrient enrichment for multiple dimensions of both functional and compositional stability of a natural grassland. It should be noted that functional stability may not be necessarily associated with compositional stability (Hillebrand & Kunze 2020), which could occur when functional redundancy among species helps maintain ecosystem functioning despite changes in community composition (Yachi & Loreau 1999; Allison & Martiny 2008). For example, Hoover *et al.* (2014) subjected a tallgrass prairie to simulated drought and found that full recovery of plant community biomass was achieved despite drought-induced shifts in community composition, as the increased biomass of one dominant grass species compensated for the loss in the biomass of a dominant forb species. This is also the case for recovery in our experiment, where functional and compositional recovery were decoupled as total plant cover have fully recovered or were close to pre-drought values, but community composition recovery was incomplete (Fig. 2.2).

In our study, the generally strong relationships between stability dimensions suggest a lower stability dimensionality than the number of actual stability components considered (Donohue *et al.* 2013), offering hope for reduced effort to obtain a comprehensive understanding of the stability of a particular ecological system. For example, resistance exhibited significant relationships with all other stability dimensions at both community and ecosystem levels (Fig.

C10), pointing to the intriguing possibility of using resistance to project community and ecosystem post-disturbance dynamics. Indeed, it has been reported that grassland resistance to climate events strongly influences their functional temporal stability (Isbell *et al.* 2015). However, this hope is complicated by the fact that stability dimensionality can vary considerably across environmental context (Donohue *et al.* 2013; Polazzo & Rico 2021). Overall, our understanding of relationships between different stability dimensions and their context dependency is still in its infancy and deserves further attention from ecologists.

### *Caveats*

One caveat of note is that several studies of drought effects on ecological stability have compared stability under control and drought conditions, where drought was experimentally manipulated by implementing rain shelters in the field to reduce precipitation (Fay *et al.* 2000). Our study, on the other hand, took advantage of a severe natural drought to investigate the effects of nutrient enrichment on multiple dimensions of stability, by comparing grassland community composition and cover across the pre-drought, mid-drought, and post-drought years. While drought manipulation experiments allow for explicit tests of the role of drought characteristics such as intensity and duration, our study, together with a number of other studies (Tilman & Downing 1994; Van Ruijven & Berendse 2010; Mariotte *et al.* 2013; Xu *et al.* 2014; Isbell *et al.* 2015), provide assessment of how natural drought events influence the study ecosystems. Another caveat is that our experiment was conducted at small spatial scales. An interesting question to ask next is whether our findings can be generalized to larger spatial scales where spatial variability among local communities may contribute to regional stability (Wang & Loreau 2016; Zhang *et al.* 2019; Hautier *et al.* 2020). Also note that our examination of stability was based on data from three years (2006-2008). Data beyond 2008 were not considered because

2009 was another drought year; including 2009 data may potentially complicate the analysis of resilience and recovery. Nevertheless, the negative nitrogen enrichment effect on functional temporal stability, observed in our study, is consistent with the finding of a seven-year (2005-2011) study conducted at the same experimental site (Yang *et al.* 2012).

### *Conclusion*

Our study is the first, to our knowledge, to link nutrient enrichment effects on the multiple dimensions of functional stability to its effects on the respective dimensions of compositional stability. By so doing, we show that nitrogen enrichment altered grassland functional stability primarily via its effect on the corresponding compositional stability, for three important stability dimensions (resistance, resilience, and temporal stability). While highlighting the importance of nutrient enrichment in influencing grassland ecosystem dynamics, our study points to the need to incorporate compositional stability into future stability research to obtain a more mechanistic understanding of ecosystem dynamics under ongoing global environment change.

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# **CHAPTER 3**

## **EXPERIMENTAL DEMONSTRATION OF THE ROLE OF INTERSPECIFIC COMPETITION IN REGULATING ECOSYSTEM TEMPORAL STABILITY**

### **Abstract**

Although evidence for the stabilizing effects of species diversity on ecosystem functions and properties has been accumulating, the roles of some basic ecological processes, such as interspecific competition, for ecosystem temporal stability remain poorly understood. Modern coexistence theory has recognized the importance of species niche and relative fitness differences for determining competitive outcomes, but their linkage to ecosystem temporal stability has yet to be explored. Using laboratory microcosms containing assemblages of freshwater bacterivorous protists as a model system, we show that interspecific competition promoted species asynchrony, but did not alter population temporal stability. Moreover, we found that species niche differences increased species asynchrony, whereas species fitness differences decreased population stability, resulting in changes in temporal stability of total community abundance. These results provide rare experimental evidence that mechanisms regulating species coexistence influence ecosystem stability, facilitating a more mechanistic understanding of the role of competition for ecosystem stability.

### 3.1 Introduction

Ecologists have long been interested in understanding ecological factors and processes that influence temporal stability of ecosystem functions and properties (MacArthur 1955; Elton 1958; Odum 1969; May 1974; King & Pimm 1983). Over the past three decades, a considerable number of studies have provided compelling evidence that more diverse communities tend to be temporally more stable in their ecosystem functions and properties (Tilman *et al.* 2006; Hector *et al.* 2010; Xu *et al.* 2021). Recent diversity-stability research has also identified population stability at the species level (Thibaut & Connolly 2013) and asynchronous population dynamics across species (i.e., species asynchrony; Ives *et al.* 1999; Yachi & Loreau 1999; Loreau & De Mazancourt 2013) as two important determinants of ecosystem temporal stability. Species diversity can, therefore, promote ecosystem temporal stability by increasing species asynchrony and/or population stability (Loreau & De Mazancourt 2013; Thibaut & Connolly 2013; Xu *et al.* 2021). Nevertheless, compared with the substantial progress in understanding diversity-stability relationships and the underlying ecological mechanisms (Hautier & Van der Plas 2022; Jiang & Xu 2022; Loreau 2022), we know relatively very little about the roles of other fundamental ecological processes, such as interspecific competition (hereafter competition), for ecological stability. Competition has been recognized as one of the major biotic forces structuring ecological communities (Elton 1946; Tilman 1982; Connell 1983; Schoener 1983; Gurevitch *et al.* 1992). Much of our knowledge on biodiversity and ecosystem functioning, including diversity-stability relationships, is based on studies of competitive communities (Tilman *et al.* 2014). However, we have rather limited understanding of how competition contributes to population and ecosystem temporal stability, especially from the empirical perspective. This represents a significant knowledge gap that hampers our ability to predict the stability of

ecosystems experiencing more frequent and intense environmental disturbances in the face of ongoing global climate changes.

Theory suggests that adding competition or increasing its strength in an ecological community should generally destabilize population dynamics (Hughes & Roughgarden 1998; Ives *et al.* 1999; Loreau & De Mazancourt 2013). This perceived negative effect of competition on population temporal stability arises presumably from higher population variability of individual species when subjected to the variation in the populations of its competing species. Moreover, population stability is predicted to be further reduced by asymmetries in species' competitive abilities (Hughes & Roughgarden 1998; Loreau & De Mazancourt 2013). However, empirical tests of these predictions have been lacking. On the other hand, theory also predicts that competition would desynchronize population dynamics of coexisting species and promote species asynchrony (Loreau & De Mazancourt 2013). Under competition, increased species asynchrony may fully or partially counteract decreased population temporal stability (Loreau & De Mazancourt 2013), resulting in nonsignificant or negative effects of competition on ecosystem temporal stability (Ives *et al.* 1999; Loreau & De Mazancourt 2013). However, the few empirical studies have provided conflicting evidence for the contribution of competition to species asynchrony (Thibaut *et al.* 2012; Gross *et al.* 2014; Tredennick *et al.* 2017; Lepš *et al.* 2019). For example, Gross *et al.* (2014) synthesized data from 27 biodiversity experiments and found that interspecific competition tended to increase the asynchrony of population dynamics among species, although the effects were stronger in grasslands than in algal communities. Similar results were reported in a 13-year temperate grassland experiment, where the biomass of grasses and forbs was positively associated in separate when one functional group was removed but negatively related in mixture plots, indicating that competition caused asynchrony between

the two functional groups (Lepš *et al.* 2019). In contrast, by fitting empirical data to community dynamics models, Tredennick *et al.* (2017) and Thibaut *et al.* (2012) showed that species asynchrony was primarily driven by species differential responses to environmental fluctuations, but not competition, in semi-arid grasslands and coral reef herbivorous fish assemblages, respectively.

Modern species coexistence theory suggests that the competitive outcome between species is determined by stabilizing mechanisms that increase species niche differences and equalizing mechanisms that reduce species relative fitness differences (Chesson 2000; Adler *et al.* 2007). Species niche differences, which increase intraspecific competition relative to interspecific competition, tend to reduce competition and promote coexistence (Adler *et al.* 2007). By contrast, relative fitness differences, which are essentially differences in species competitive ability, enhance asymmetric competition between species (Adler *et al.* 2007). Linking species niche and relative fitness differences to ecosystem temporal stability would help foster a more mechanistic understanding of the role of competition in regulating ecological stability. A few recent studies have linked niche complementary and sampling effects, which contribute to positive biodiversity-ecosystem functioning relationships, to ecosystem temporal stability (Isbell *et al.* 2009; Wang *et al.* 2021; Yan *et al.* 2021; Wu *et al.* 2022). Both theoretical (Carroll *et al.* 2011; Loreau *et al.* 2012; Turnbull *et al.* 2013) and empirical (Godoy *et al.* 2020) studies have shown that species niche differences contribute to selection effects, whereas species relative fitness differences contribute to complementarity effects. However, there is a lack of empirical evidence for a direct correspondence between complementary and selection effects and niche and relative fitness differences, making it difficult to draw conclusions about the relationships between species coexistence mechanisms and ecosystem stability. On the one hand,

greater niche differences between species could decrease species asynchrony but increases population stability by weakening the strength of competition (Ives *et al.* 1999; Loreau & De Mazancourt 2013). On the other hand, greater niche differences might indicate greater trait dissimilarities among species, which may potentially translate into increased species asynchrony as a result of more dissimilar responses to environmental disturbances. Moreover, we expect that greater relative fitness differences, which imply greater asymmetry in the strength of competitive interactions, could potentially reduce population stability and species asynchrony, resulting in lower ecosystem stability.

In this study, we used communities of bacterivorous ciliated protists established in laboratory microcosms as model systems to examine the role of competition for temporal stability. The short generation times (< 10 hours) of our study organisms permitted us to collect data on multi-generational population and community dynamics in a relatively short period of time (Benton *et al.* 2007), facilitating more rigorous investigations of temporal stability (e.g., Jiang *et al.* 2009; Pu *et al.* 2014; Pennekamp *et al.* 2018). Specifically, we aimed to answer two questions: (1) How does competition affect ecosystem temporal stability and its two determinants, population temporal stability of individual species and the asynchrony of their population dynamics? (2) How are species niche and relative fitness differences associated with population temporal stability and species asynchrony, and, in turn, ecosystem temporal stability?

## 3.2 Materials and methods

### *Experimental organisms and microcosms*

Our experiment used three freshwater bacterivorous ciliate protozoan species, including *Colpidium striatum* (CS), *Paramecium tetraurelia* (PT), and *Tetrahymena pyriformis* (TP). These species were chosen because of their morphological distinctness and differences in competitive ability (Violle *et al.* 2010). Each protozoan species had been separately cultured in the laboratory on a mixture of bacterial preys (*Bacillus cereus*, *Bacillus subtilis*, *Enterobacter aerogenes*, and *Serratia marcescens*) prior to this experiment.

The microcosms were loosely capped 250-mL Pyrex glass bottles each filled with 100 mL of bacterized protozoan pellet medium (PPM). The PPM was prepared by dissolving 0.55 g of protozoan pellets (Carolina Biological Supply Company, Burlington, NC, USA) in one liter of deionized water, and was autoclave-sterilized before inoculating with the mixture of four bacterial species. In addition, we added two sterilized wheat seeds to each microcosm to provide a slow release of carbon (Altermatt *et al.* 2015). The bacterized PPM was incubated at 22°C for 48 hours before being distributed into individual microcosms. To replenish nutrients, 10% of the content in each microcosm was replaced with fresh, autoclave-sterilized PPM weekly during the experiment. All microcosms were maintained in incubators with lights turned off throughout the experiment to prevent algal contamination.

### *Experimental design and setup*

Our experiment used a three-way factorial design with two temperature treatments (22°C vs. 26°C), two environment treatments (constant and fluctuating), and seven assemblages of protist species. We established three one-species cultures (CS, PT, TP), three two-species

cultures (CS+PT, TP+CS, TP+PT), and one three-species culture (TP+CS+PT), taking advantage of the inherent differences in species competitive ability, as well as niche and relative fitness differences. We further manipulated species niche and relative fitness differences by altering ambient temperature (22°C vs. 26°C). To explore whether environmental disturbances influence the role of competition for temporal stability, we simulated mortality-causing disturbances using sonication, following previous microcosm studies (Fox 2002; Steiner 2005; Jiang & Patel 2008). We assigned each microcosm to either a constant environment or a fluctuating environment once all protist populations had reached steady states, when communities in the fluctuating environment were subjected to weekly sonication disturbances (50% amplitude for 30 seconds) using an ultrasonic cell disruptor (Sonic Dismembrator 150E, Fisher Scientific, Hampton, NH, USA). Each treatment combination was replicated three times, resulting in a total of 84 microcosms.

At the initiation of the experiment, each microcosm received 100 individuals of each protist species from laboratory stock cultures that were grown to their respective carrying capacities at 22°C. The assembled protist communities were maintained in incubators at designated temperatures in the dark for 20 days, at which time the first sonication disturbance took place. We also inoculated 100 individuals of each species into its designated microcosm weekly to simulate colonization from nearby. To estimate the population density of each protist species (in the unit of individuals per ml), we sampled each experimental microcosm every two days throughout the experiment, resulting in a time series of 21 time points over a period of 40 days. We pipetted 0.4 mL of homogenized content of each microcosm, distributed it into multiple drops on a petri dish, and counted the number of individuals of each species under a stereoscopic microscope. Samples containing large populations were diluted before counting.

### *Quantifying niche and relative fitness differences*

We quantified species pairwise niche and relative fitness differences through mutual invasion experiments, following previous work (Carroll *et al.* 2011; Narwani *et al.* 2013; Li *et al.* 2019). For each species pair, we introduced 100 individuals of one species into competitor-free microcosms, and into microcosms where its competitor had established a steady-state population, with each treatment replicated three times. For each microcosm, we then sampled the population density of each species daily and estimated its intrinsic growth rates in the absence ( $\mu_{\text{alone}}$ ) and presence ( $\mu_{\text{invading}}$ ) of a competitor. The intrinsic growth rate of each species was calculated as the slope of the linear regression of natural logarithm of population density versus time. Intrinsic growth rate was then used to calculate species' sensitivity ( $S$ ) to competition, defined as the proportional reduction in growth rate due to interspecific competition (Carroll *et al.* 2011):

$S = (\mu_{\text{alone}} - \mu_{\text{invading}}) / \mu_{\text{alone}}$ . Following Carroll *et al.* (2011) and Narwani *et al.* (2013),

niche difference (ND) was calculated as one minus the geometric mean of species' sensitivities:

$ND = 1 - \sqrt{S_1 S_2}$ , and the RFD was calculated as the geometric standard deviation of

sensitivities:  $RFD = \sqrt{S_1 / S_2}$ . Species niche and relative fitness differences were estimated under BOTH ambient temperatures (22°C and 26°C).

### *Statistical analysis*

For each microcosm, we calculated ecosystem temporal stability as the inverse of the coefficient of variation (SD/mean) of total species abundance over time (Tilman 1999). For each species, its species-specific population temporal stability was calculated as the inverse of the coefficient of variation of population abundance over time. No significant temporal trend in species abundance was detected at the population level or ecosystem level during the

experimental period; thus, no detrending was conducted. Species asynchrony was quantified as the Gross' weighted asynchrony index ( $-\eta_w$ , Blüthgen *et al.* 2016). This index ranges from -1 (perfect synchrony) to 1 (perfect asynchrony) and is centered at 0 when species fluctuate independently. Species asynchrony, population temporal stability, and ecosystem temporal stability were quantified over days 18 – 40, corresponding to the time immediately before the first disturbance and the last day of the experiment, respectively.

Data on species-specific population temporal stability and species asynchrony in mixtures (i.e., communities containing more than one species) were compared to those collected from single-species communities to investigate how the presence of competition influences these two determinants of ecosystem temporal stability under different ambient temperatures and environmental conditions. We then used linear mixed-effects models to assess the effects of increased ambient temperature, environmental fluctuation, species niche differences, and species relative fitness differences on population-level temporal stability and species asynchrony measured in communities containing more than one species. Temperature, environmental fluctuation, species niche and relative fitness differences were treated as fixed factors, and species compositions within communities was treated as a random factor. Simple linear regressions were used to assess how species asynchrony and population temporal stability relate to ecosystem temporal stability. We further performed piecewise structural equation modeling (SEM) to examine the pathways of how temperature, environmental fluctuation, and species niche and relative fitness differences, through influencing population temporal stability and species asynchrony, affected ecosystem temporal stability. We first constructed an *a priori* model that included all plausible pathways (Fig. S1) and then obtained the final SEM by eliminating nonsignificant pathways. Model adequacy was evaluated using Shipley's test of

directed separation on Fisher's  $C$  statistic (Shipley 2013) and Akaike information criteria corrected for small sample size ( $AICc$ ).

All statistical analyses were conducted in R version 4.1.2 (R Core Team 2021), with the 'nlme' package for linear mixed-effects models, and the 'piecewiseSEM' package for constructing the SEM (Lefcheck 2016).

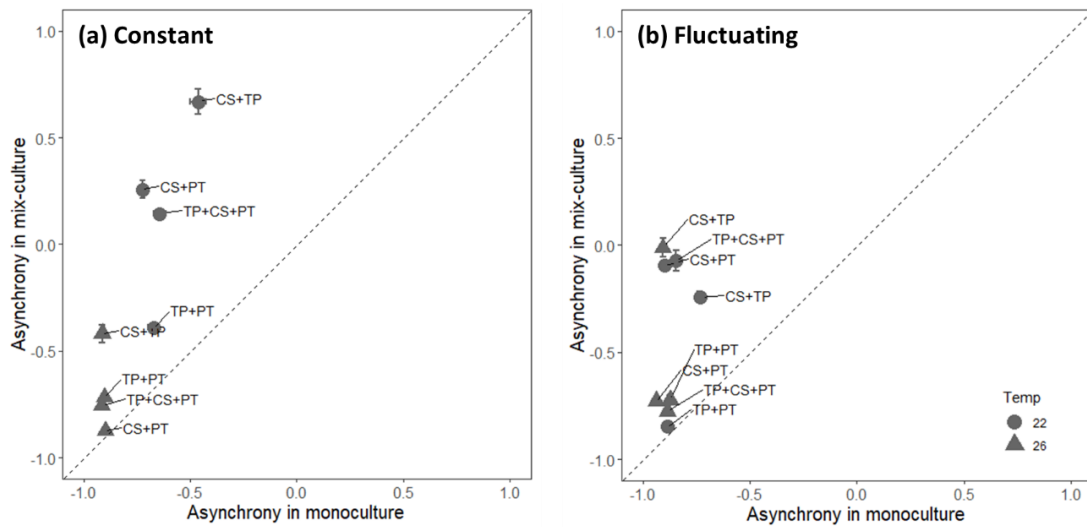
### 3.3 Results

Overall, higher ambient temperature decreased species asynchrony (Fig. 3.1; linear mixed-effects model:  $p < 0.001$ ; Table D1), but the effect was less consistent in communities that experienced periodic environmental disturbances (Fig. 3.1b; linear mixed-effects model: temperature x environmental fluctuation interaction  $p < 0.001$ ; Table D1). Environmental fluctuation tended to decrease species asynchrony (Fig. 3.1; linear mixed-effects model:  $p < 0.001$ ; Table D1). Both increased temperature and environmental fluctuation decreased population temporal stability averaged across species within a community (Fig. 3.2; linear mixed-effects model:  $p < 0.001$  for temperature, environmental fluctuation, and their interaction; Table D1).

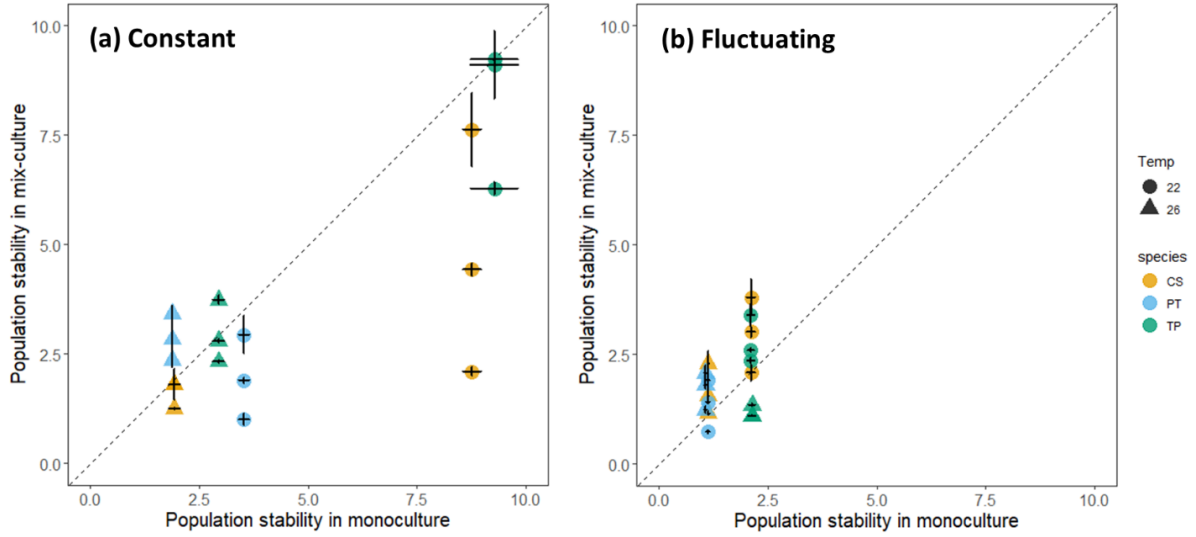
For most species pairs, species asynchrony was higher in multi-species mixtures than asynchrony among the same species grown separately in their respective monocultures under both consistent and fluctuating environmental conditions (Fig. 3.1), indicating that competition increased species asynchrony. By contrast, species-specific population temporal stability scattered around the line of equality (slope = 1) in the constant environment, although lower species-specific population temporal stability in mixtures occurred more often at 22°C (Fig.

3.2a). Under environmental disturbance, individual species exhibited higher population temporal stability in mixtures than when they were grown in monocultures (Fig. 3.2b).

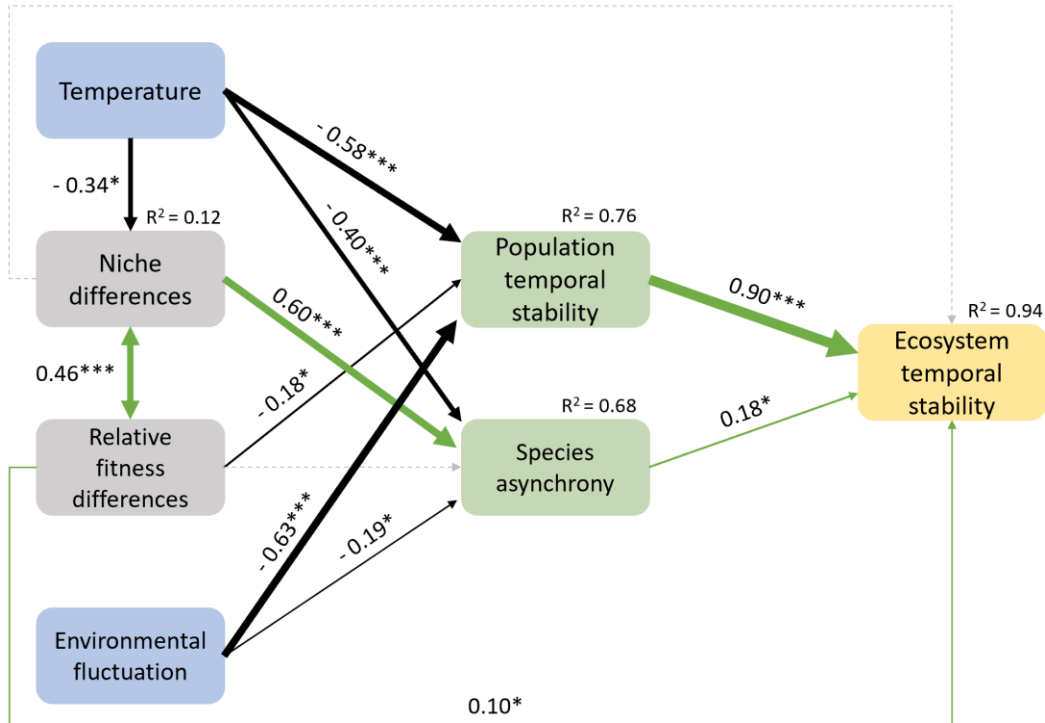
SEM confirmed the negative effects of increased temperature and environmental fluctuation on species asynchrony and population temporal stability (Fig. 3.3). Higher ambient temperature reduced species niche differences (Figs. 3.3 & D2a) but did not affect species relative fitness differences (Figs. 3.3 & D2b). SEM also revealed that species niche differences, but not relative fitness differences, promoted species asynchrony (Figs. 3.3), and in turn, contributed to ecosystem temporal stability. On the other hand, species relative fitness differences reduced population stability (Fig. 3.3; Table D1), resulting in decline in ecosystem temporal stability.



**Figure 3.1 Asynchrony among species in the multi-species mixtures versus asynchrony among the same species grown alone in monocultures under (a) constant and (b) fluctuating environmental conditions.**



**Figure 3.2 Species-specific population temporal stability in the multi-species mixtures versus population temporal stability of the same species grown alone in monoculture under (a) constant and (b) fluctuating environmental conditions.**



AICc = 99.015, Fisher's  $C = 15.696$ ,  $P = 0.109$

**Figure 3.3 Structural equation model (SEM) depicting the effects of temperature, environmental fluctuation, species niche and relative fitness differences on population-level temporal stability and species asynchrony, and in turn, ecosystem temporal stability. Single-headed arrows indicate unidirectional relationships among variables, whereas the double-headed arrow indicates a correlated error, with positive and negative pathways marked in green and black, respectively ( $*P < .05$ ,  $**P < .01$ ,  $***P < .001$ ). Numbers along the arrows indicate standardized path coefficients. Arrow width is proportional to the strength of the relationship. The proportion of variance explained ( $R^2$ ) appears alongside response variables in the models.**

### 3.4 Discussion

Despite the well-recognized importance of competition in structuring ecological communities, its role in regulating ecological stability remains poorly understood. Using bacterivorous protozoan communities as model systems, we experimentally explored how competition, under different ambient temperature and environmental fluctuation regimes, influences ecosystem temporal stability. Our study is the first, to our knowledge, to link species coexistence mechanisms to ecosystem temporal stability and its determinants. Our experiment yielded three notable findings. First, increased temperature and environmental fluctuation negatively affected species asynchrony and population temporal stability, thus reducing ecosystem temporal stability. Second, the presence of competition promoted asynchronous species dynamics but did not affect population temporal stability. Last, we found that species niche differences increased asynchrony while relative fitness differences decreased population temporal stability, translating into changes in ecosystem temporal stability.

#### *Effects of environmental factors on species asynchrony and population stability*

Differential species responses to environmental fluctuations have been identified as an important mechanism contributing to stability of ecosystem functions and properties (Loreau & De Mazancourt 2013). Environmental disturbance events are known to be a key determinant of the dynamics of populations and communities in nature (Houlahan *et al.* 2007; Mutshinda *et al.* 2009; Vellend 2016). Theoretical studies predicted that environmental fluctuation could increase species asynchrony, which would counteract its negative effects on population temporal stability, resulting in more stable aggregated ecosystem functions and properties (Ives *et al.* 1999; Loreau & De Mazancourt 2013; Firkowski *et al.* 2022). The results showed that changes in

environmental conditions, including increased ambient temperature and the presence of environmental disturbance, negatively impacted both species-specific population temporal stability (Fig. 3.2) and species asynchrony (Fig. 3.1). Our finding of reduced population temporal stability in fluctuating environment was consistent with previous work that reported lower population temporal stability in the presence of environmental disturbances in the form of nutrient pulses, light availability, and acidification (Steiner *et al.* 2011; Brown *et al.* 2016; Firkowski *et al.* 2022). However, these previous studies reported either positive (Brown *et al.* 2016) or nonsignificant effects of environmental disturbance on species asynchrony, which is at odds with our finding that increased ambient temperature and environmental fluctuation decreased species asynchrony. This discrepancy may be explained by the low species response diversity, that is, the diversity of species responses to environmental changes (Elmqvist *et al.* 2003), in our study. In our experiment, species abundance of all three protists were negatively affected by sonication disturbance (Fig. D3), which led to population dynamics that fluctuated in the same direction, resulting in lower species asynchrony. Future studies should directly explore the importance of response diversity of an ecological community for species asynchrony and ecosystem stability.

#### *Effects of competition on species asynchrony and population stability*

In line with model predictions that competition could increase species asynchrony (Tilman 1996; Ives *et al.* 1999; Loreau & De Mazancourt 2013), our results showed that species asynchrony was consistently higher when species were grown together in multi-species mixtures than when they were grown separately in their respective monocultures (Fig. 3.1), indicating that the presence of competition increased the magnitude of species asynchrony. These results are in agreement with Gross *et al.* (2014) and Leps *et al.* (2019) who reported positive competition

effects on asynchrony between plant species and functional groups, respectively, in grassland experiments. However, our findings are at odds with a few studies that showed differential species responses to environmental changes, not competition, were the primary driver of asynchrony in natural communities (Mutshinda *et al.* 2009; Thibaut *et al.* 2012; Tredennick *et al.* 2017). One possible explanation for the discrepancy among studies is that different ecological systems are characterized by various levels of competition strength. Further direct assessment is needed to elucidate how varying competition strength can affect species asynchrony.

Temporal fluctuations in populations are important for the stability of aggregate community and ecosystem properties (Loreau & de Mazancourt 2008, 2013). Theory suggests that competition should destabilize individual populations (Hughes & Roughgarden 1998; Ives *et al.* 1999; Loreau & De Mazancourt 2013). We found that population temporal stability of individual protist species grown in mixed cultures was neither consistently higher nor lower than that in monocultures across all treatment combinations (Fig. 3.2). Yet, it is important to note that populations grown under constant environment at 22°C were more stable in monocultures compared to when grown in mixed cultures. This result suggests that competition negatively affected population temporal stability, however, the effect could be modified by environmental stochasticity, echoing calls for the need to study the significance of environmental disturbance for ecological stability. There are still few empirical assessments of how competition affects population temporal stability at the species level (Firkowski *et al.* 2022). Our finding that competition decreased population temporal stability in the absence of environmental changes agrees with that of Leps *et al.* (2019), who reported destabilizing effects of competition on biomass of plant functional groups. Overall, our results highlight the role of competition as an important driver of species asynchrony and population temporal stability.

*Relationships between niche and relative fitness differences and determinants of ecosystem stability*

Modern species coexistence theory emphasizes the importance of both species niche differences and relative fitness differences for determining competitive outcomes (Chesson 2000). Higher species niche differences could potentially lower species asynchrony because niche differences cause species to limit themselves more than their competitors, which in turn weakens competition between species (Ives *et al.* 1999; Loreau & De Mazancourt 2013). However, our SEM revealed that higher species niche differences had a strong positive effect on asynchrony, contributing to stabilizing species abundances at the ecosystem level. This positive relationship suggests that processes promoting species niche difference may also desynchronize population fluctuations, and, in turn, stabilize ecosystem functions and properties. Previous theoretical studies suggest that complementarity effects, an important mechanism underlying the positive biodiversity-ecosystem functioning relationships, could imply a larger range of species-specific responses to environmental fluctuations (higher temporal niche differences), thus higher species asynchrony (Gonzalez & Loreau 2009; Wang *et al.* 2021). Although complementarity effects cannot be readily translated into niche differences, a recent study that coupled mathematical modeling with a biodiversity-functioning experiment demonstrated a positive relationship between complementarity effects and species niche differences (Godoy *et al.* 2020). Higher niche differences thus could be indicative of more variable environmental responses among species, contributing to higher species asynchrony. The protist species used in our experiment exhibited different rates of population growth at different ambient temperatures (Fig. D4), as well as varying degrees of responses to disturbance (Fig. D3), which could result in asynchronous dynamics among coexisting species (Loreau & de Mazancourt 2008; Thibaut &

Connolly 2013). Another important finding revealed by our SEM was that species relative fitness differences decreased population temporal stability (Fig. 3), although this negative relationship was much weaker than the relationship between species niche differences and asynchrony. Greater relative fitness differences, reflecting larger differences in species competitive ability, may be indicative of more asymmetric competition between species (Adler *et al.* 2007). Our results therefore support the theoretical prediction that asymmetry in the strength of competition is strongly destabilizing at both the population and ecosystem levels (Hughes & Roughgarden 1998; Loreau & De Mazancourt 2013). Moreover, species niche and relative fitness differences could be correlated with distinctive species functional traits (Mayfield & Levine 2010; Kraft *et al.* 2015). In fact, trait differences have already been used as proxies for niche differences between species (Silvertown 2004; McGill *et al.* 2006; Adler *et al.* 2013). Yet, there is lack of a framework for effectively translating species' functional traits or evolutionary relatedness into niche and relative fitness differences, which might be able to provide a more explicit understanding of the factors and processes that influence the stability of ecological communities.

### *Caveats*

Two caveats are worth noting. First, our study, like many other laboratory experiments, used a small number of species to assemble ecological communities. We limited our analysis to two- and three-species communities to avoid introducing other confounding factors, which would make it difficult to distinguish the contributions of species ecological differences (i.e., niche and relative fitness differences) to stabilizing ecosystem functions. An important challenge for future research is addressing how niche and relative fitness differences relate to stabilizing mechanisms of ecosystem properties in more diverse communities. Second, we estimated species

niche and relative fitness difference based on species' sensitivity to competition as reflected by changes in growth rates, following previous studies (Carroll *et al.* 2011; Narwani *et al.* 2013). However, the quantification of niche and relative fitness differences in complex natural communities is more difficult to achieve with our current methods (Saavedra *et al.* 2017). Nevertheless, the use of laboratory assembled protist communities allows us to take a first step towards applying species coexistence theory for prediction ecological stability.

### *Conclusion*

Our study provides new empirical evidence that competition can have positive effects on species asynchrony but did not affect population temporal stability, contributing to stabilizing ecosystem functions and properties. We also report the first, to our knowledge, assessment of the links between species niche and relative fitness differences and the determinants of ecosystem temporal stability. Most importantly, by linking mechanisms of species coexistence with ecological stability, our study reveals that species niche difference promotes ecosystem stability via increasing species asynchrony, whereas species relative fitness difference destabilizes ecosystem properties at the community level via decreasing population temporal stability. These findings illustrate the significance of incorporating modern coexistence theory for a more mechanistic understanding of the maintenance of ecological stability.

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## APPENDIX A.

### SUPPLEMENT TO CHAPTER 1

**Table A1. The list of studies, including their correlation coefficients ( $r$ ) between species diversity and temporal variability (measured as coefficient of variation, CV), included in our meta-analyses of the relationships between species diversity and temporal stability. Temporal variability was measured at ecosystem and population levels. Study type: experimental (E) vs. observational (O). Trophic complexity: single- vs. multi-trophic. N: sample size in each study.**

Author	Year	Study Type	System	Trophic complexity	Taxa	Ecosystem function	Response level	$r$ (Diversity – CV)	N
Bezemer	2007	E	terrestrial	single	Grasses	biomass	ecosystem	0.33	15
Caldeira	2005	E	terrestrial	single	Grasses	biomass	ecosystem	-0.373	52
DeClerck	2006	O	terrestrial	single	Trees	biomass	ecosystem	0.265	40
Dodd	1994	O	terrestrial	single	Grasses	biomass	ecosystem	-0.06	45
Ebeling	2008	E	terrestrial	multiple	Pollinator	pollinator visits	ecosystem	-0.405	62
Hector	2010	E	terrestrial	single	Grasses	ANPP	ecosystem	0.267	60
Hector	2010	E	terrestrial	single	Grasses	ANPP	ecosystem	-0.311	56
Hector	2010	E	terrestrial	single	Grasses	ANPP	ecosystem	-0.299	64
Hector	2010	E	terrestrial	single	Grasses	ANPP	ecosystem	-0.648	52
Hector	2010	E	terrestrial	single	Grasses	ANPP	ecosystem	-0.064	70
Hector	2010	E	terrestrial	single	Grasses	ANPP	ecosystem	-0.053	58
Hector	2010	E	terrestrial	single	Grasses	ANPP	ecosystem	-0.112	52
Hector	2010	E	terrestrial	single	Grasses	ANPP	ecosystem	-0.127	66
Ji	2009	E	terrestrial	single	Grasses, forbs	biomass	ecosystem	-0.574	22
Jiang	2009	E	aquatic	multiple	Protists	biovolume	ecosystem	-0.5017	22
Jiang	2009	E	aquatic	single	Protists	biovolume	ecosystem	0.2726	26
van Klink	2019	O	terrestrial	single	Ground beetles	abundance	ecosystem	-0.2916	19
Leps	2017	O	terrestrial	single	Meadow	biomass	ecosystem	-0.8161	12
Li	2014	O	terrestrial	single	Plants	abundance	ecosystem	-0.8307	12
McGrady-Steed	2000	E	aquatic	multiple	Protists	abundance	ecosystem	-0.1265	50
McGrady-Steed	2000	E	aquatic	multiple	Protists	abundance	ecosystem	-0.255	50
McGrady-Steed	2000	E	aquatic	multiple	Protists	abundance	ecosystem	-0.527	50
McGrady-Steed	2000	E	aquatic	multiple	Protists	abundance	ecosystem	-0.6036	20
McNaughton	1985	O	terrestrial	single	grasses	biomass	ecosystem	-0.2259	25
McNaughton	1985	O	terrestrial	multiple	herbivores	biomass	ecosystem	-0.2957	25

Mouillot	2005	O	aquatic	multiple	Fish parasite	biomass	ecosystem	-0.8426	15
Petchey	2002	E	aquatic	single	Protists	biomass	ecosystem	0.47	15
Petchey	2002	E	aquatic	single	Protists	biomass	ecosystem	0	29
Petchey	2002	E	aquatic	single	Protists	biomass	ecosystem	0.22	28
Pfisterer	2004	E	terrestrial	single	grasses	biomass	ecosystem	-0.254	60
Polley	2007	O	terrestrial	single	grasses	biomass	ecosystem	0.3873	24
Polley	2007	O	terrestrial	single	grasses	biomass	ecosystem	0.246	24
Rakowski	2016	E	aquatic	single	Algae	biomass	ecosystem	-0.2865	49
Rakowski	2016	E	aquatic	multiple	Algae, cladocerans	biomass	ecosystem	-0.3844	41
Rakowski	2016	E	aquatic	multiple	Algae, cladocerans	biomass	ecosystem	0.7298	48
Rodriguez	2000	O	terrestrial	multiple	Parasite	parasitism rate	ecosystem	0.146	30
Romanuk	2002	O	aquatic	multiple	invertebrates	abundance	ecosystem	-0.428	49
Romanuk	2006	E	aquatic	multiple	invertebrates	abundance	ecosystem	-0.5967	15
Romanuk	2006	E	aquatic	multiple	invertebrates	abundance	ecosystem	0.0447	15
Romanuk	2006	E	aquatic	multiple	invertebrates	abundance	ecosystem	-0.4219	15
Romanuk	2009	E	aquatic	multiple	invertebrates	abundance	ecosystem	-0.574	24
Romanuk	2009	E	aquatic	multiple	invertebrates	abundance	ecosystem	-0.398	28
Romanuk	2009	E	aquatic	multiple	invertebrates	abundance	ecosystem	-0.235	30
Sanderson	2010	E	terrestrial	single	Grasses, legumes	biomass	ecosystem	-0.14	50
Sanderson	2010	E	terrestrial	multiple	Grasses, legumes	biomass	ecosystem	-0.06	93
Sanderson	2010	E	terrestrial	single	Grasses, legumes	biomass	ecosystem	-0.36	32
Stachowicz	2008	E	aquatic	multiple	Seaweed	biomass	ecosystem	-0.4609	44
Steiner	2005	O	aquatic	multiple	zooplankton	biomass	ecosystem	-0.6277	18
Steiner	2005	E	aquatic	multiple	bacteria, algae, protozoa, rotifer	biomass	ecosystem	-0.1152	47
Steiner	2005	E	aquatic	multiple	bacteria, algae, protozoa, rotifer	biomass	ecosystem	-0.5299	48
Tilman	1996	O	terrestrial	single	grasses	biomass	ecosystem	-0.39	54
Tilman	1996	O	terrestrial	single	grasses	biomass	ecosystem	-0.32	54
Tilman	1996	O	terrestrial	single	grasses	biomass	ecosystem	-0.09	54
Tilman	1996	O	terrestrial	single	grasses	biomass	ecosystem	-0.53	45
Tracy	2004	O	terrestrial	single	Grasses, legumes	biomass	ecosystem	0.3058	48
Tracy	2004	O	terrestrial	single	Grasses, legumes	biomass	ecosystem	0.3233	48
Tylianakis	2006	O	terrestrial	multiple	Bees, parasites	parasitism rate	ecosystem	-0.8746	48
Valone	2003	O	terrestrial	single	Annual plants	abundance	ecosystem	-0.22	24
Valone	2003	O	terrestrial	single	Annual plants	abundance	ecosystem	-0.17	24
Valone	2003	O	terrestrial	single	Annual plants	abundance	ecosystem	-0.32	96
Valone	2003	O	terrestrial	single	Annual plants	abundance	ecosystem	-0.3	96
Vogt	2006	E	aquatic	multiple	Meiofauna	abundance	ecosystem	-0.5675	24

Wang	2020	O	terrestrial	single	Grasses	biomass	ecosystem	-0.08	23
Wilby	2004	O	terrestrial	multiple	Shrubs	abundance	ecosystem	-0.0911	8
Wilby	2004	O	terrestrial	multiple	Shrubs	abundance	ecosystem	-0.6278	8
Wilby	2004	O	terrestrial	single	Shrubs	abundance	ecosystem	-0.2402	8
Wilby	2004	O	terrestrial	multiple	Shrubs	abundance	ecosystem	-0.3258	8
Wilby	2004	O	terrestrial	multiple	Shrubs	abundance	ecosystem	-0.1272	8
Wilby	2004	O	terrestrial	multiple	Shrubs	abundance	ecosystem	0.2969	8
Wilby	2004	O	terrestrial	single	Shrubs	abundance	ecosystem	0.7264	8
Wilby	2004	O	terrestrial	multiple	Shrubs	abundance	ecosystem	-0.4077	8
Yang	2012	O	terrestrial	single	Grasses	biomass	ecosystem	-0.6164	32
Zhang	2006	E	aquatic	single	algae	biomass	ecosystem	-0.7162	19
Zhang	2006	E	aquatic	single	algae	biomass	ecosystem	-0.209	19
Borer	2012	E	terrestrial	multiple	Grasses	biomass	ecosystem	-0.3207	64
Borer	2012	E	terrestrial	multiple	Anthropods	biomass	ecosystem	-0.5297	64
Chalcraft	2013	O	terrestrial	single	Grasses	ANPP	ecosystem	-0.5867	15
Chen	2016	O	terrestrial	single	Grasses	ANPP	ecosystem	-0.4126	36
Dijkstra	2018	E	terrestrial	single	Grasses	biomass	ecosystem	-0.1347	25
Dorado	2014	O	terrestrial	single	Flower	biomass	ecosystem	-0.7241	14
Dorado	2014	O	terrestrial	single	Flower	biomass	ecosystem	-0.7271	14
Franssen	2011	O	aquatic	multiple	fish	biomass	ecosystem	-0.393	35
Jia	2020	O	terrestrial	single	Grasses	ANPP	ecosystem	-0.4318	24
Koerner	2016	O	terrestrial	single	grasses	ANPP	ecosystem	-0.1632	48
Kuiters	2013	O	terrestrial	single	plants	abundance	ecosystem	-0.4704	61
Lamy	2020	O	aquatic	single	benthic algae, invertebrates	biomass	ecosystem	-0.8073	30
Lamy	2020	O	aquatic	single	benthic algae, invertebrates	biomass	ecosystem	-0.6433	31
Liang	2020	O	terrestrial	single	nematode	abundance	ecosystem	-0.4045	144
Ma	2020	O	terrestrial	single	grass and forbs	ANPP	ecosystem	-0.6009	30
Post	2013	E	terrestrial	multiple	plants	biomass	ecosystem	-0.6781	43
Ren	2018	O	terrestrial	multiple	grass and forbs	ANPP	ecosystem	0.6745	14
Ren	2018	O	terrestrial	multiple	grass and forbs	ANPP	ecosystem	0.2913	14
Sasaki	2011	O	terrestrial	single/multiple	Grasses, forbs, shrubs	abundance	ecosystem	0.4539	24
Schnabel	2019	E	terrestrial	single	trees	biomass	ecosystem	-0.4551	24
Song	2019	O	terrestrial	single	Grasses, forbs	biomass	ecosystem	-0.4984	18
Tilman	2006	E	terrestrial	single	plants	biomass	ecosystem	-0.28	162
Valdivia	2009	O	aquatic	multiple	algae	biomass	ecosystem	0.446	39
Valone	2018	O	terrestrial	single	shrubs	abundance	ecosystem	0.2721	20
van Ruijven	2007	E	terrestrial	single	grasses	biomass	ecosystem	-0.4723	94
van Moorsel	2020	E	terrestrial	single	perennial grasses	biomass	ecosystem	-0.6503	46
Veen	2018	E	terrestrial	single	plants	biomass	ecosystem	0.3897	50
Verma	2020	O	terrestrial	single	herbaceous plants	biomass	ecosystem	-0.459	12

Wagg	2018	O	terrestrial	single	fungus	abundance	ecosystem	-0.5311	24
Wagg	2018	O	terrestrial	single	bacterial	abundance	ecosystem	-0.0194	24
Wu	2019	O	terrestrial	single	grass and forbs	ANPP	ecosystem	-0.0076	14
Wu	2020	O	terrestrial	single	grass and forbs	ANPP	ecosystem	-0.2852	24
Xu	2015	O	terrestrial	single	grasses	biomass	ecosystem	-0.219	28
Yang	2017	O	terrestrial	single	Perennial plants	biomass	ecosystem	0.2673	16
Yu	2020	O	terrestrial	single	Woody plants	biomass	ecosystem	-0.9613	6
Yu	2020	O	terrestrial	single	Woody plants	biomass	ecosystem	0.5357	7
Yu	2020	O	terrestrial	single	Woody plants	biomass	ecosystem	-0.7951	8
Yu	2020	O	terrestrial	single	Woody plants	biomass	ecosystem	-0.9747	7
Zhang	2016	O	terrestrial	single	Perennial plants	ANPP	ecosystem	-0.3991	181
Zhang	2018	O	terrestrial	single	Perennial plants	ANPP	ecosystem	-0.7385	10
Zhang	2018	O	terrestrial	single	Perennial plants	ANPP	ecosystem	-0.6376	10
Dolezal	2020	O	terrestrial	single	trees	biomass	ecosystem	-0.3899	207
Guelzow	2014	E	aquatic	single	phytoplankton	biomass	ecosystem	-0.3500	105
Hallett	2014	I	terrestrial	single	plants	abundance	ecosystem	-0.5315	8
Liu	2019	O	terrestrial	single	Grasses, legumes, forbs	biomass	ecosystem	-0.0185	36
Qin	2019	O	terrestrial	multiple	Grasses, forbs	biomass	ecosystem	-0.5857	26
Qin	2019	O	terrestrial	multiple	Grasses, forbs	biomass	ecosystem	-0.3024	19
Qin	2019	O	terrestrial	multiple	Grasses, forbs	biomass	ecosystem	-0.1840	23
Zhou	2020	O	terrestrial	single	grasses	biomass	ecosystem	-0.3796	12
Agrodiversity Experiment	2021	E	terrestrial	single	Grasses, legumes	biomass	ecosystem	-0.3990	30
Agrodiversity Experiment	2021	E	terrestrial	single	Grasses, legumes	biomass	ecosystem	-0.4970	30
Agrodiversity Experiment	2021	E	terrestrial	single	Grasses, legumes	biomass	ecosystem	-0.45021	30
Agrodiversity Experiment	2021	E	terrestrial	single	Grasses, legumes	biomass	ecosystem	-0.4723	30
Agrodiversity Experiment	2021	E	terrestrial	single	Grasses, legumes	biomass	ecosystem	-0.4843	29
Agrodiversity Experiment	2021	E	terrestrial	single	Grasses, legumes	biomass	ecosystem	-0.6316	30
Agrodiversity Experiment	2021	E	terrestrial	single	Grasses, legumes	biomass	ecosystem	-0.8520	30
Agrodiversity Experiment	2021	E	terrestrial	single	Grasses, legumes	biomass	ecosystem	-0.3142	30
Agrodiversity Experiment	2021	E	terrestrial	single	Grasses, legumes	biomass	ecosystem	-0.7797	30
Agrodiversity Experiment	2021	E	terrestrial	single	Grasses, legumes	biomass	ecosystem	-0.7754	30
Agrodiversity Experiment	2021	E	terrestrial	single	Grasses, legumes	biomass	ecosystem	-0.0661	30
Agrodiversity Experiment	2021	E	terrestrial	single	Grasses, legumes	biomass	ecosystem	-0.4054	30
Agrodiversity Experiment	2021	E	terrestrial	single	Grasses, legumes	biomass	ecosystem	-0.3201	30
Agrodiversity Experiment	2021	E	terrestrial	single	Grasses, legumes	biomass	ecosystem	-0.6767	30

Agrodiversity Experiment	2021	E	terrestrial	single	Grasses, legumes	biomass	ecosystem	-0.3680	30
Agrodiversity Experiment	2021	E	terrestrial	single	Grasses, legumes	biomass	ecosystem	-0.6659	30
Agrodiversity Experiment	2021	E	terrestrial	single	Grasses, legumes	biomass	ecosystem	0.34795	30
Agrodiversity Experiment	2021	E	terrestrial	single	Grasses, legumes	biomass	ecosystem	-0.7493	30
Agrodiversity Experiment	2021	E	terrestrial	single	Grasses, legumes	biomass	ecosystem	-0.7211	30
Agrodiversity Experiment	2021	E	terrestrial	single	Grasses, legumes	biomass	ecosystem	-0.2154	30
Agrodiversity Experiment	2021	E	terrestrial	single	Grasses, legumes	biomass	ecosystem	-0.6219	30
Agrodiversity Experiment	2021	E	terrestrial	single	Grasses, legumes	biomass	ecosystem	-0.5231	30
Agrodiversity Experiment	2021	E	terrestrial	single	Grasses, legumes	biomass	ecosystem	-0.4423	30
Agrodiversity Experiment	2021	E	terrestrial	single	Grasses, legumes	biomass	ecosystem	-0.6167	30
Chalcraft	2013	O	terrestrial	single	grasses, shrubs	biomass	population	0.4418	15
Dovciak	2010	O	terrestrial	single	forest herb	cover	population	-0.3538	191
Hector	2010	E	terrestrial	single	grass, legume, forbs	biomass	population	0.499	244
Hector	2010	E	terrestrial	single	grass, legume, forbs	biomass	population	0.350	142
Hector	2010	E	terrestrial	single	grass, legume, forbs	biomass	population	0.264	281
Hector	2010	E	terrestrial	single	grass, legume, forbs	biomass	population	0.231	275
Hector	2010	E	terrestrial	single	grass, legume, forbs	biomass	population	0.138	215
Hector	2010	E	terrestrial	single	grass, legume, forbs	biomass	population	0.293	161
Hector	2010	E	terrestrial	single	grass, legume, forbs	biomass	population	0.241	188
Hector	2010	E	terrestrial	single	grass, legume, forbs	biomass	population	0.305	264
Jiang	2009	E	aquatic	single	protozoa	biomass	population	0.7847	26
Jiang	2009	E	aquatic	multiple	protozoa	biomass	population	-0.3299	22
Kolasa	2003	O	aquatic	multiple	aquatic invertebrates	abundance	population	-0.4235	49
Kuiters	2013	O	terrestrial	single	grasses	abundance	population	-0.4556	60
Li	2014	O	terrestrial	single	plant	abundance	population	-0.9165	11
Petchey	2000	E	aquatic	multiple	flagellate, ciliates	biomass	population	-0.0206	26
Romanuk	2006	E	aquatic	multiple	zooplankton, benthic invertebrates	abundance	population	-0.8626	15
Romanuk	2006	E	aquatic	multiple	zooplankton, benthic invertebrates	abundance	population	-0.502	15
Romanuk	2006	E	aquatic	multiple	zooplankton, benthic invertebrates	abundance	population	-0.1549	15
Romanuk	2009	E	aquatic	multiple	zooplankton, benthic invertebrates	abundance	population	-0.633	24
Romanuk	2009	E	aquatic	multiple	zooplankton, benthic invertebrates	abundance	population	-0.424	28

Romanuk	2009	E	aquatic	multiple	zooplankton, benthic invertebrates	abundance	population	-0.182	30
Song	2019	O	terrestrial	single	grasses	biomass	population	-0.6807	18
Steiner	2005	E	aquatic	multiple	algae, protozoa, rotifers	biomass	population	-0.1936	48
Steiner	2005	E	aquatic	multiple	algae, protozoa, rotifers	biomass	population	-0.1101	48
Tilman	2006	E	terrestrial	single	grasses	biomass	population	0.5591	161
Valdivia	2009	O	aquatic	multiple	algae, macro-benthic invertebrates	cover	population	0.1508	40
Valone	2003	O	terrestrial	single	annual plants	abundance	population	-0.3341	47
Valone	2003	O	terrestrial	single	annual plants	abundance	population	-0.2618	53
Vogt	2006	E	aquatic	multiple	aquatic invertebrates	abundance	population	-0.6986	24
Wagg	2018	O	terrestrial	single	soil bacteria	abundance	population	-0.5707	12
Wagg	2018	O	terrestrial	single	soil bacteria	abundance	population	-0.6371	12
Wagg	2018	O	terrestrial	single	soil fungi	abundance	population	0.7881	12
Wagg	2018	O	terrestrial	single	soil fungi	abundance	population	0.7236	12
Yang	2012	O	terrestrial	single	perennial herbs	cover	population	-0.7141	32
Yang	2012	O	terrestrial	single	perennial herbs	cover	population	-0.5	32
van Klink	2019	O	terrestrial	single	beetles	abundance	population	0.2801	19
Lamy	2020	O	aquatic	single	algae, sessile invertebrates	biomass	population	-0.7963	31
Lamy	2020	O	aquatic	single	algae, sessile invertebrates	biomass	population	-0.5496	31
van Moorsel	2020	E	terrestrial	single	grasses	biomass	population	0.7004	90
Wang	2020	O	terrestrial	single	plants	biomass	population	0.130	23
Agrodiversity Experiment	2021	E	terrestrial	single	Grasses, legumes	biomass	population	0.8678	30
Agrodiversity Experiment	2021	E	terrestrial	single	Grasses, legumes	biomass	population	-0.2300	30
Agrodiversity Experiment	2021	E	terrestrial	single	Grasses, legumes	biomass	population	0.3972	30
Agrodiversity Experiment	2021	E	terrestrial	single	Grasses, legumes	biomass	population	-0.2244	30
Agrodiversity Experiment	2021	E	terrestrial	single	Grasses, legumes	biomass	population	-0.3683	29
Agrodiversity Experiment	2021	E	terrestrial	single	Grasses, legumes	biomass	population	-0.4446	30
Agrodiversity Experiment	2021	E	terrestrial	single	Grasses, legumes	biomass	population	0.4729	30
Agrodiversity Experiment	2021	E	terrestrial	single	Grasses, legumes	biomass	population	0.6001	30
Agrodiversity Experiment	2021	E	terrestrial	single	Grasses, legumes	biomass	population	-0.7029	30
Agrodiversity Experiment	2021	E	terrestrial	single	Grasses, legumes	biomass	population	-0.4993	30
Agrodiversity Experiment	2021	E	terrestrial	single	Grasses, legumes	biomass	population	0.6601	30
Agrodiversity Experiment	2021	E	terrestrial	single	Grasses, legumes	biomass	population	0.6790	30
Agrodiversity Experiment	2021	E	terrestrial	single	Grasses, legumes	biomass	population	0.7871	30

Agrodiversity Experiment	2021	E	terrestrial	single	Grasses, legumes	biomass	population	0.3851	30
Agrodiversity Experiment	2021	E	terrestrial	single	Grasses, legumes	biomass	population	0.7542	30
Agrodiversity Experiment	2021	E	terrestrial	single	Grasses, legumes	biomass	population	0.3719	30
Agrodiversity Experiment	2021	E	terrestrial	single	Grasses, legumes	biomass	population	0.4427	30
Agrodiversity Experiment	2021	E	terrestrial	single	Grasses, legumes	biomass	population	0.1738	30
Agrodiversity Experiment	2021	E	terrestrial	single	Grasses, legumes	biomass	population	-0.2912	30
Agrodiversity Experiment	2021	E	terrestrial	single	Grasses, legumes	biomass	population	0.7583	30
Agrodiversity Experiment	2021	E	terrestrial	single	Grasses, legumes	biomass	population	0.6338	30
Agrodiversity Experiment	2021	E	terrestrial	single	Grasses, legumes	biomass	population	0.8770	30
Agrodiversity Experiment	2021	E	terrestrial	single	Grasses, legumes	biomass	population	0.7108	30
Agrodiversity Experiment	2021	E	terrestrial	single	Grasses, legumes	biomass	population	-0.2178	30

**Table A2. The list of studies, including their correlation coefficients ( $r$ ) of functional/phylogenetic diversity-ecosystem temporal stability relationships, included in our meta-analyses of functional/phylogenetic diversity and ecosystem temporal stability relationships. Study type: experimental (E) vs. observational (O). Trophic complexity: single- vs. multi-trophic. N: sample size in each study.**

Author	Year	Study Type	System	Trophic complexity	Taxa	Ecosystem function	Diversity measure	$r$	N
Biondini	2007	O	Terrestrial	single	grass, forbs	biomass	Functional	0.281	119
Dolezal <i>et al.</i>	2020	O	Terrestrial	single	trees	biomass	Functional	0.4504	207
Huang <i>et al.</i>	2020	O	Terrestrial	single	grass	abundance	Functional	0.2664	48
Romanuk <i>et al.</i>	2010	E	Aquatic	multiple	meiofauna	abundance	Functional	0.305	34
Sasaki and Lauenroth	2011	O	Terrestrial	single	grass, forbs, shrubs	abundance	Functional	-0.01	24
Veen <i>et al.</i>	2018	E	Terrestrial	single	plant	biomass	Functional	0.1735	60
Cadotte <i>et al.</i>	2012	E	Terrestrial	single	grasses, legumes, forbs	biomass	Phylogenetic	0.4359	164
Pu <i>et al.</i>	2014	E	Aquatic	single	protists	biomass	Phylogenetic	0.6993	12
Pu <i>et al.</i>	2014	E	Aquatic	single	protists	biomass	Phylogenetic	0	15
Yu <i>et al.</i>	2020	O	Terrestrial	single	trees, shrubs	biomass	Phylogenetic	0.9346	6
Yu <i>et al.</i>	2020	O	Terrestrial	single	trees, shrubs	biomass	Phylogenetic	0.4147	7
Yu <i>et al.</i>	2020	O	Terrestrial	single	trees, shrubs	biomass	Phylogenetic	0.9459	7
Yu <i>et al.</i>	2020	O	Terrestrial	single	trees, shrubs	biomass	Phylogenetic	0.9801	7
Dolezal <i>et al.</i>	2020	O	Terrestrial	single	trees	biomass	Phylogenetic	0.5067	206

**Table A3. The list of studies, including their correlation coefficients ( $r$ ) of species diversity-asynchrony relationships and asynchrony-ecosystem stability relationships, included in our meta-analyses of species diversity-asynchrony relationships and asynchrony-ecosystem stability relationships. Study type: experimental (E) vs. observational (O). Trophic complexity: single- vs. multi-trophic. N: sample size in each study.**

Author	Year	Study Type	System	Trophic complexity	Taxa	Ecosystem function	Relationship reported	r	N
Borer	2012	E	Terrestrial	multiple	arthropod	biovolume	Diversity-asynchrony	0.34	64
Chen	2016	O	Terrestrial	single	plant	biomass	Diversity-asynchrony	0.4698	36
Gilbert	2020	O	Terrestrial	single	plant	biomass	Diversity-asynchrony	0.2412	150
Jucker	2014	E	Terrestrial	single	trees	biomass	Diversity-asynchrony	0.6856	209
Lamy	2020	O	Aquatic	single	benthic algae	biomass	Diversity-asynchrony	0.554	32
Lamy	2020	O	Aquatic	single	sessile invertebrates	biomass	Diversity-asynchrony	0.5447	32
Lep	2018	O	Terrestrial	single	plant	biomass	Diversity-asynchrony	0.89	12
Li	2014	O	Terrestrial	single	plant	abundance	Diversity-asynchrony	0.5388	12
Ma	2017	O	Terrestrial	single	plant	biomass	Diversity-asynchrony	0.3873	30
Roscher	2011	E	Terrestrial	single	plant	biomass	Diversity-asynchrony	0.6626	58
Schnabel	2019	E	Terrestrial	single	trees	biomass	Diversity-asynchrony	0.5001	12
Song	2020	O	Terrestrial	multiple	plant	biomass	Diversity-asynchrony	0.5292	36
van Moorsel	2020	E	Terrestrial	single	perennial grass	biomass	Diversity-asynchrony	0.8742	46
Wagg	2018	E	Terrestrial	single	fungi	abundance	Diversity-asynchrony	-0.0311	24
Wagg	2018	E	Terrestrial	single	bacteria	abundance	Diversity-asynchrony	-0.4266	24
Wu	2020	O	Terrestrial	single	grass and forbs	biomass	Diversity-asynchrony	-0.0843	24
Wu	2019	O	Terrestrial	single	plant	biomass	Diversity-asynchrony	0.2025	15
Xu	2015	O	Terrestrial	single	plant	biomass	Diversity-asynchrony	0.1183	28
Yu	2020	O	Terrestrial	single	trees	biomass	Diversity-asynchrony	0.6894	7
Yu	2020	O	Terrestrial	single	trees	biomass	Diversity-asynchrony	0.573	8
Yu	2020	O	Terrestrial	single	trees	biomass	Diversity-asynchrony	0.3846	8
Yu	2020	O	Terrestrial	single	trees	biomass	Diversity-asynchrony	0.9816	7
Zhang	2017	O	Terrestrial	single	plant	biomass	Diversity-asynchrony	0.1064	360
Zhang	2018	O	Terrestrial	single	plant	biomass	Diversity-asynchrony	0.7141	50

Zhang	2017	O	Terrestrial	single	plant	biomass	Diversity- asynchrony	0.7595	10
Liu	2019	O	Terrestrial	single	grasses, legumes, forbs	biomass	Diversity- asynchrony	0.3063	36
Wang	2020	O	Terrestrial	single	plants	biomass	Diversity- asynchrony	0.0332	23
Ouyang	2020	O	Terrestrial	single	trees	biomass	Diversity- asynchrony	0.595	242
Dolezal	2020	O	Terrestrial	single	trees	biomass	Diversity- asynchrony	-0.01	207
Chen	2016	O	Terrestrial	single	grass	biomass	Asynchrony- stability	0.7483	36
Chi	2019	O	Terrestrial	single	plant	biomass	Asynchrony- stability	0.6083	60
Douda	2018	E	Terrestrial	single	plant	biomass	Asynchrony- stability	0.6325	24
Dijkstra	2018	E	Terrestrial	single	plant	biomass	Asynchrony- stability	0.6708	25
Gilbert	2020	O	Terrestrial	single	plant	biomass	Asynchrony- stability	0.2217	180
Haughey	2018	E	Terrestrial	single	plant	biomass	Asynchrony- stability	-0.1061	24
Haughey	2018	E	Terrestrial	single	plant	biomass	Asynchrony- stability	-0.1417	23
Haughey	2018	E	Terrestrial	single	plant	biomass	Asynchrony- stability	0.6158	24
Haughey	2018	E	Terrestrial	single	plant	biomass	Asynchrony- stability	0.6977	23
Isbell	2009	E	Terrestrial	single	plant	biomass	Asynchrony- stability	0.6708	36
Jia	2020	O	Terrestrial	single	plant	biomass	Asynchrony- stability	0.3425	24
Jucker	2014	E	Terrestrial	single	trees	biomass	Asynchrony- stability	0.6403	209
Klink	2019	O	Terrestrial	single	beetle	biomass	Asynchrony- stability	0.7805	19
Lamy	2020	O	Aquatic	single	benthic algae	biomass	Asynchrony- stability	0.6942	31
Lamy	2020	O	Aquatic	single	sessile invertebrates	biomass	Asynchrony- stability	0.6609	29
Li	2017	E	Aquatic	multiple	protist	abundance	Asynchrony- stability	0.609	40
Li	2017	E	Aquatic	multiple	algae	abundance	Asynchrony- stability	0.8917	40
Li	2014	O	Terrestrial	single	plant	abundance	Asynchrony- stability	0.6003	12
Ma	2020	O	Terrestrial	single	plant	biomass	Asynchrony- stability	0.7746	30
Ma	2017	E	Terrestrial	single	perennial plants	biomass	Asynchrony- stability	0.728	30
Niu	2018	O	Terrestrial	single	grass	biomass	Asynchrony- stability	0.5648	30
Polley	2013	E	Terrestrial	single	plant	biomass	Asynchrony- stability	0.3606	28
Roscher	2011	E	Terrestrial	single	plant	biomass	Asynchrony- stability	0.5815	67
Schnabel	2019	E	Terrestrial	single	trees	biomass	Asynchrony- stability	0.8367	12
Song	2019	O	Terrestrial	single	plant	biomass	Asynchrony- stability	0.8775	18
Wang	2020	O	Terrestrial	single	plants	biomass	Asynchrony- stability	0.5191	23

Wu	2020	O	Terrestrial	single	grass and forbs	biomass	Asynchrony-stability	0.62	24
Wu	2019	O	Terrestrial	single	plant	biomass	Asynchrony-stability	0.4583	25
Xu	2015	O	Terrestrial	single	grass	biomass	Asynchrony-stability	0.7981	28
Yang	2020	O	Terrestrial	single	grass and forbs	biomass	Asynchrony-stability	0.5385	20
Yang	2020	O	Terrestrial	single	grass and forbs	biomass	Asynchrony-stability	0.6708	20
Yang	2011	O	Terrestrial	single	grass	biomass	Asynchrony-stability	0.1	16
Yang	2012	O	Terrestrial	single	plant	biomass	Asynchrony-stability	0.5568	64
Yang	2017	O	Terrestrial	single	plant	biomass	Asynchrony-stability	0.5208	12
Yu	2020	O	Terrestrial	single	trees	biomass	Asynchrony-stability	0.8072	6
Yu	2020	O	Terrestrial	single	trees	biomass	Asynchrony-stability	0.8725	7
Yu	2020	O	Terrestrial	single	trees	biomass	Asynchrony-stability	0.6432	8
Yu	2020	O	Terrestrial	single	trees	biomass	Asynchrony-stability	0.9598	7
Yuan	2019	O	Terrestrial	single	trees	biomass	Asynchrony-stability	0.1315	120
Yuan	2019	O	Terrestrial	single	trees	biomass	Asynchrony-stability	0.133	120
Zhang	2018	O	Terrestrial	single	grass	biomass	Asynchrony-stability	0.8246	50
Zhang	2017	O	Terrestrial	single	plant	biomass	Asynchrony-stability	0.8581	10
Zhang	2017	O	Terrestrial	single	plant	biomass	Asynchrony-stability	0.7416	360
Zhang	2016	O	Terrestrial	single	plant	biomass	Asynchrony-stability	0.5	180
Liu	2019	O	Terrestrial	single	grasses, legumes, forbs	biomass	Asynchrony-stability	0.5191	36
Ouyang	2020	O	Terrestrial	single	trees	biomass	Asynchrony-stability	0.3286	242
Qin	2019	O	Terrestrial	multiple	grasses, forbs	biomass	Asynchrony-stability	0.7701	25
Qin	2019	O	Terrestrial	multiple	grasses, forbs	biomass	Asynchrony-stability	0.8843	19
Qin	2019	O	Terrestrial	multiple	grasses, forbs	biomass	Asynchrony-stability	0.1414	22
Dolezal	2020	O	Terrestrial	single	trees	biomass	Asynchrony-stability	0.2707	207
Zhou	2020	O	Terrestrial	single	grasses	biomass	Asynchrony-stability	0.5618	12

## APPENDIX B.

### A LIST OF STUDIES INCLUDED IN META-ANALYSES OF DIVERSITY- STABILITY RELATIONSHIPS IN CHAPTER 1

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## APPENDIX C.

### SUPPLEMENT TO CHAPTER 2

**Table C1. Results (*F*-value) of linear mixed-effects models testing the effect of nitrogen enrichment (N), phosphorous enrichment (P) and their interactions (N x P) on species richness, total plant cover, and dominant species cover. Significant P values are shown in bold.**

	Species richness		Total plant cover		Dominant species cover	
	<i>F</i>	<i>P</i>	<i>F</i>	<i>P</i>	<i>F</i>	<i>P</i>
N	4.63	<b>0.017</b>	21.60	<b>&lt;0.001</b>	7.43	<b>0.012</b>
P	0.01	0.991	2.11	0.159	0.06	0.810
N: P	0.52	0.597	7.41	<b>0.012</b>	7.54	<b>0.011</b>

**Table C2. Results of permutational multivariate analysis of variance (PERMANOVA) on the effects of N enrichment, P enrichment, and their interactions on community composition. The analyses were performed using 999 permutations. Significant P values are shown in bold.**

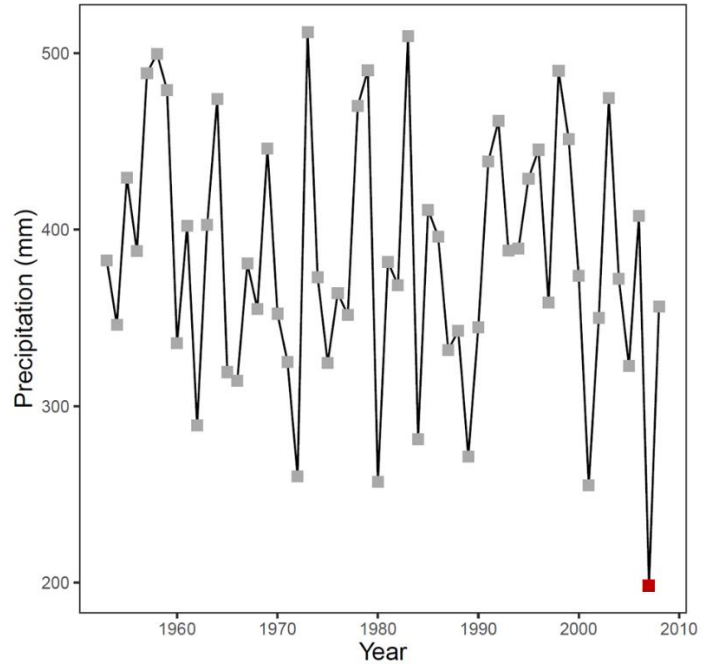
	Community composition	
	<i>F</i>	<i>P</i>
N	6.35	<b>0.001</b>
P	2.89	<b>0.006</b>
Year	12.52	<b>0.001</b>
N: P	4.31	<b>0.001</b>
N: Year	2.88	<b>0.001</b>
P: Year	0.92	0.525
N: P: Year	1.03	0.406

**Table C3. Results (*F*-value) of linear mixed-effects models testing the effect of nitrogen enrichment (N), phosphorous enrichment (P) and their interactions (N x P) on multiple dimensions of grassland functional and compositional stability. Significant P values are shown in bold.**

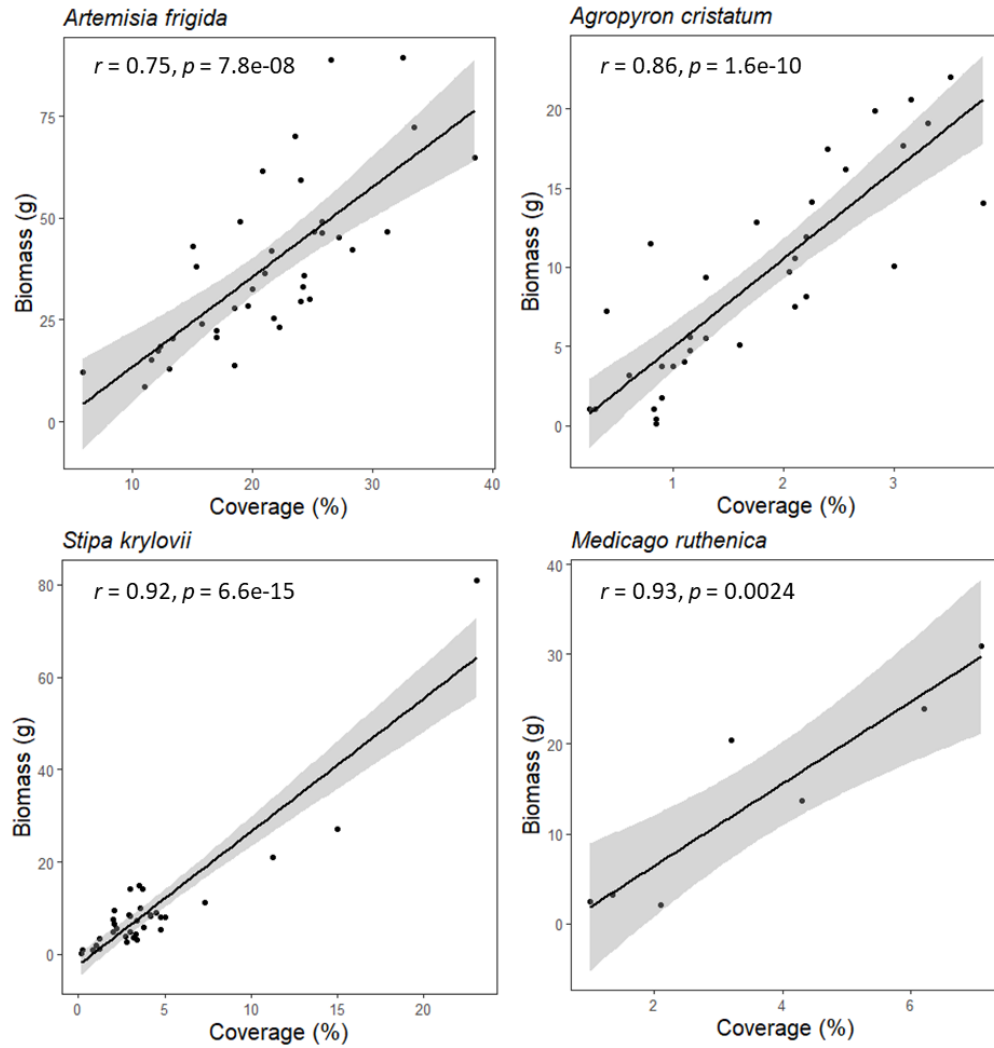
		Temporal stability		Resistance		Resilience		Recovery	
		<i>F</i>	<i>P</i>	<i>F</i>	<i>P</i>	<i>F</i>	<i>P</i>	<i>F</i>	<i>P</i>
Functional stability	N	18.14	<b>&lt;0.001</b>	39.26	<b>&lt;0.001</b>	17.58	<b>&lt;0.001</b>	6.31	<b>0.018</b>
	P	0.03	0.867	1.92	0.178	0.89	0.353	0.29	0.597
	N * P	0.64	0.430	0.70	0.412	0.74	0.398	0.00	0.992
Compositional stability	N	33.51	<b>&lt;0.001</b>	42.80	<b>&lt;0.001</b>	42.02	<b>&lt;0.001</b>	5.25	<b>0.031</b>
	P	4.24	0.050	2.42	0.132	3.84	0.060	1.95	0.175
	N * P	1.00	0.327	0.00	0.947	1.32	0.260	0.92	0.346

**Table C4. Results (*F*-value) of linear mixed-effects models testing the effect of nitrogen enrichment (N), phosphorous enrichment (P) and their interactions (N x P) on multiple dimensions of dominant species functional and compositional stability. Significant P values are shown in bold.**

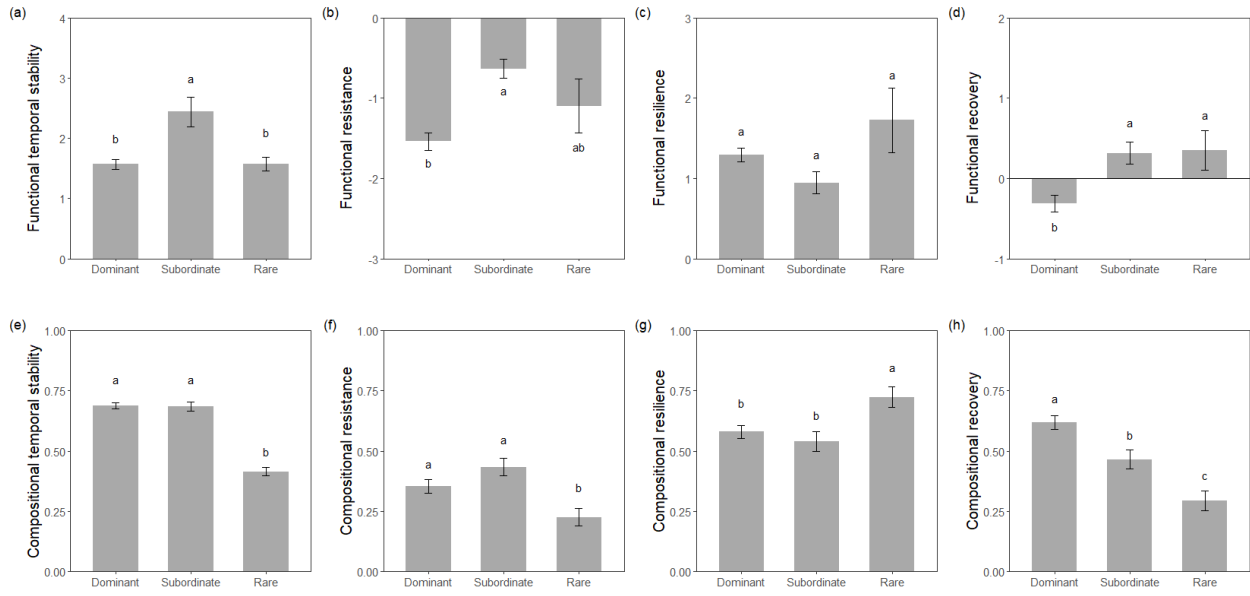
		Temporal stability		Resistance		Resilience		Recovery	
		<i>F</i>	<i>P</i>	<i>F</i>	<i>P</i>	<i>F</i>	<i>P</i>	<i>F</i>	<i>P</i>
Functional stability	N	16.48	<b>&lt;0.001</b>	18.12	<b>&lt;0.001</b>	3.26	0.082	7.18	<b>0.012</b>
	P	0.78	0.385	1.03	0.321	0.76	0.391	0.05	0.824
	N * P	0.17	0.685	0.01	0.915	0.03	0.869	0.00	0.97
Compositional stability	N	26.86	<b>&lt;0.001</b>	21.92	<b>&lt;0.001</b>	6.15	<b>0.019</b>	8.57	<b>0.007</b>
	P	6.11	<b>0.021</b>	2.80	0.107	1.58	0.219	2.84	0.105
	N * P	0.82	0.374	0.05	0.827	0.03	0.870	1.57	0.221



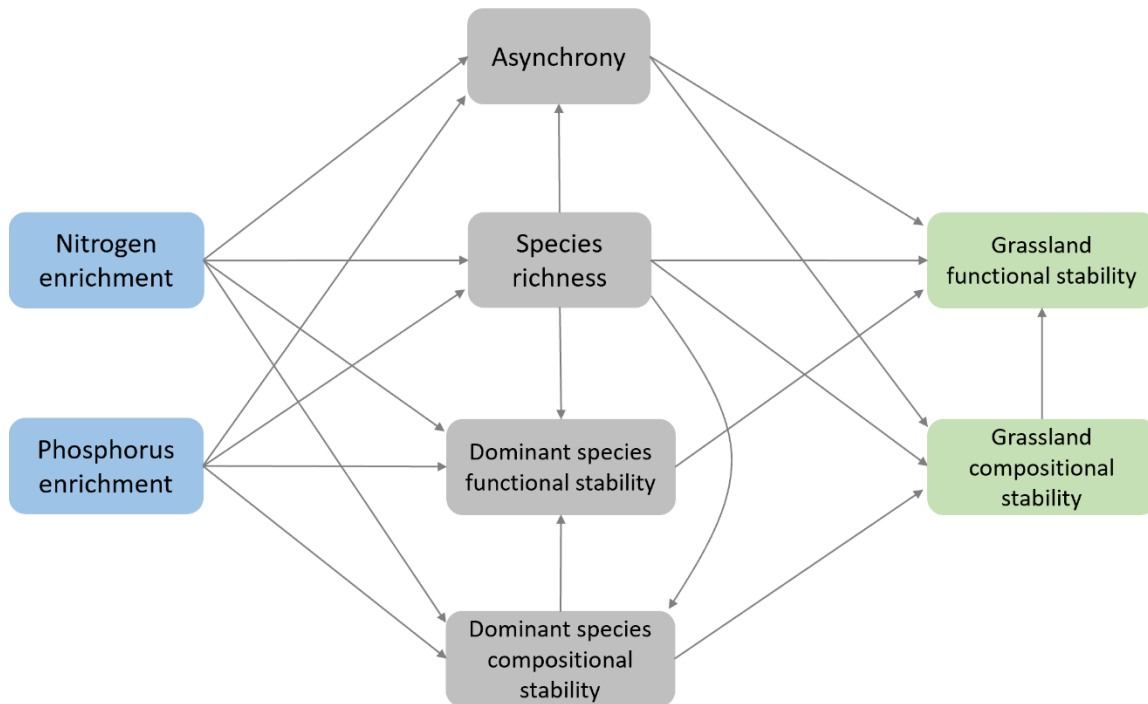
**Figure C1. Annual precipitation (mm) in the study area from 1953 to 2008. The drought year (2007) is denoted as a red square.**



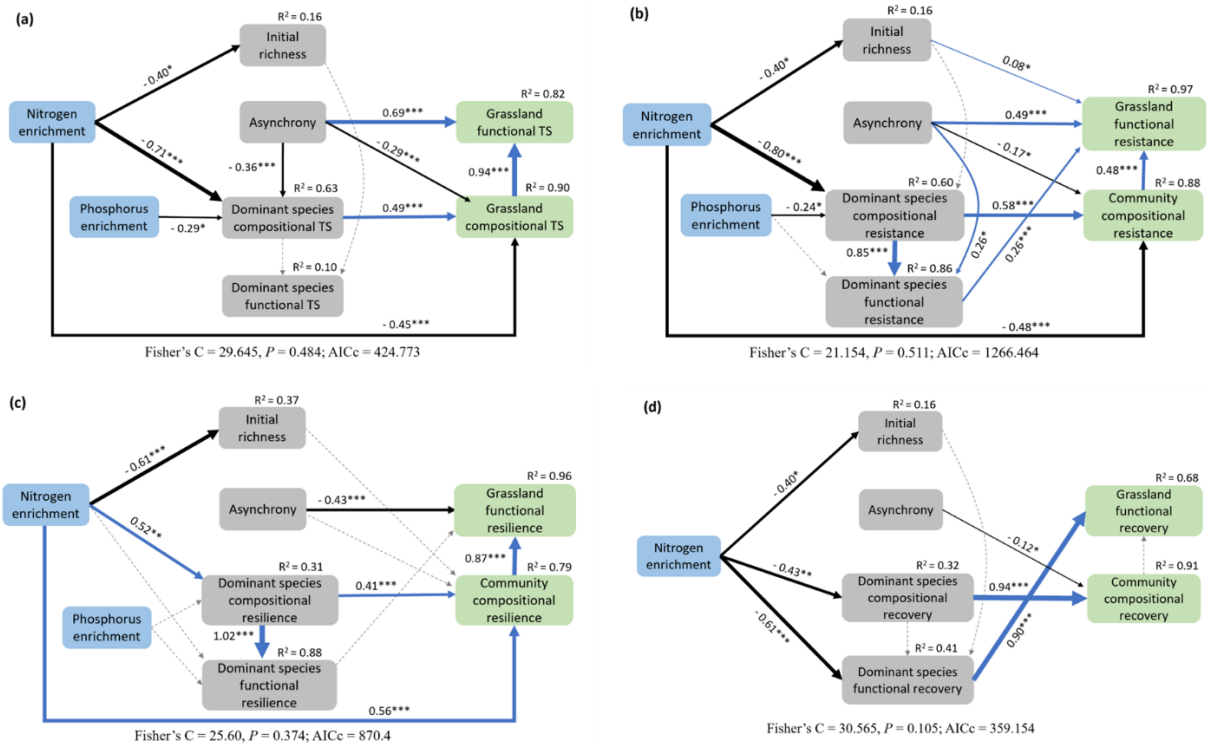
**Figure C2. The relationships between species coverage and biomass for the four most abundant species at our study site. The four dominant species, on average, accounted for 60.76% of the total plant cover.**



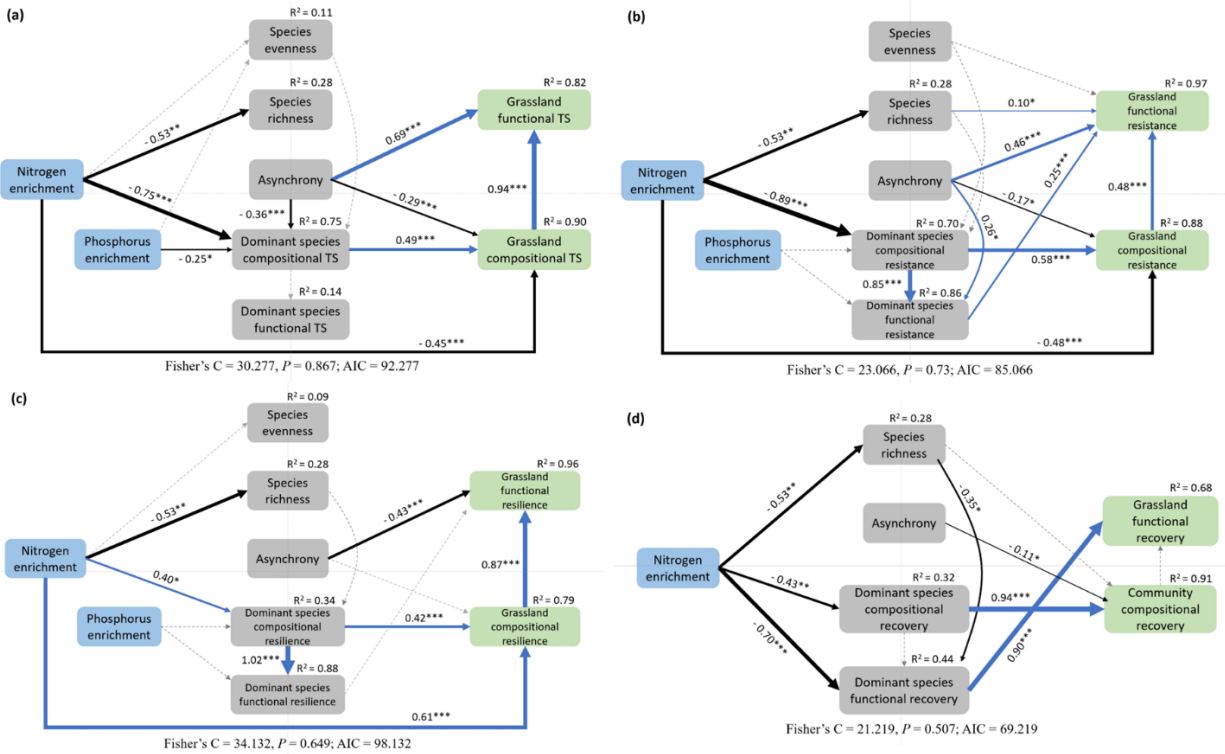
**Figure C3. Functional (a-e) and compositional (f-h) stability of dominant (species with relative abundance > 5%), subordinate (species with relative abundance between 1% to 5%), and rare species (species with relative abundance < 1%) across different nutrient enrichment treatments. The three groups consisted of 4, 12, and 20 species that accounted for 60.76%, 32.53%, and 6.71% of total plant cover, respectively.**



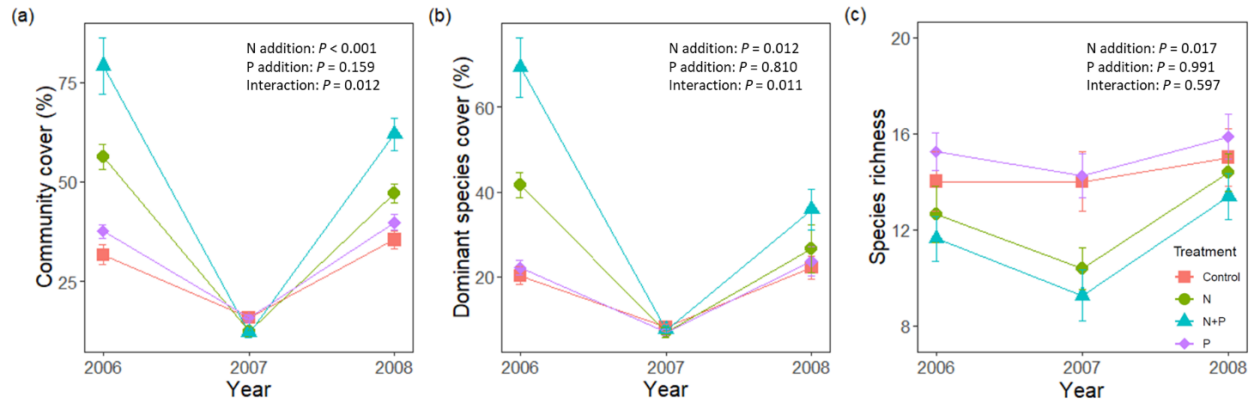
**Figure C4.** The *a priori* model considering all plausible pathways through which nitrogen and phosphorous enrichment influences grassland functional and compositional stability.



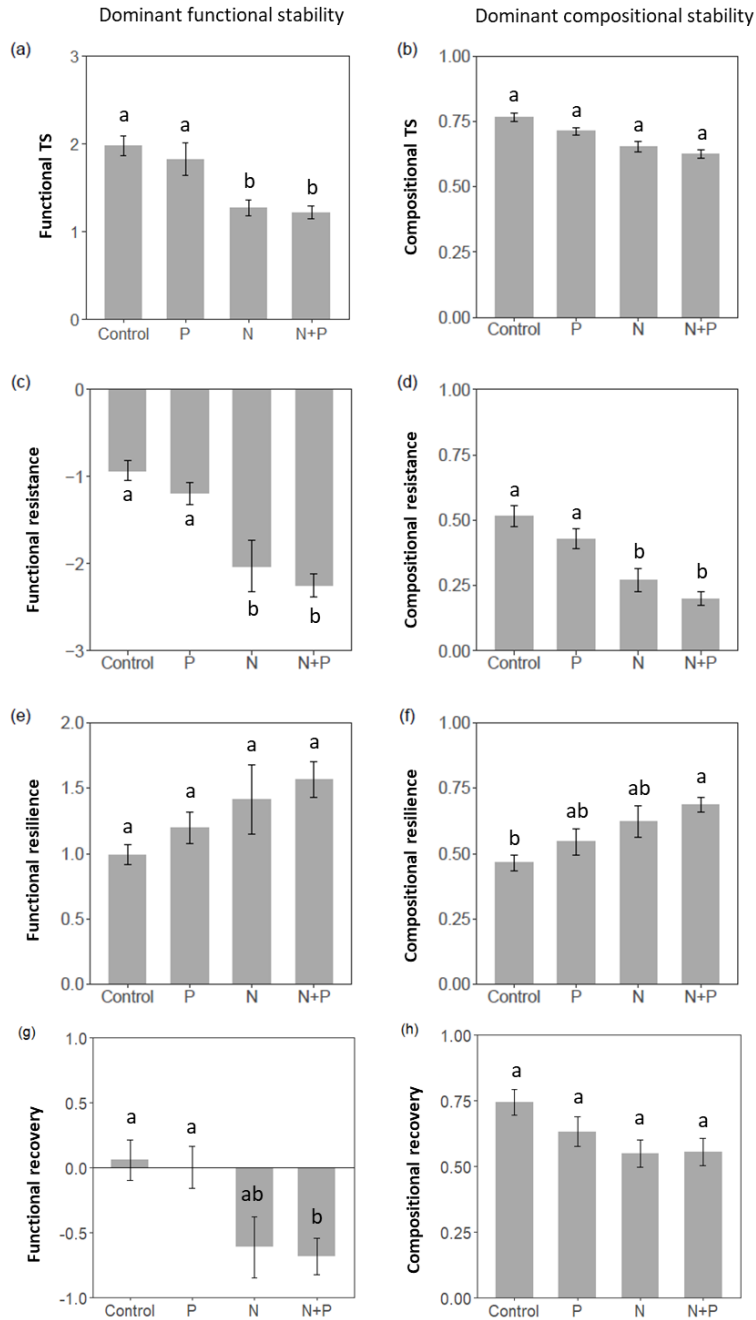
**Figure C5. The final structural equation models showing the effects of nutrient enrichment on grassland functional and compositional (a) temporal stability (TS), (b) resistance, (c) resilience, and (d) recovery both directly and indirectly through affecting initial species richness, asynchrony, and dominant species stability. Blue and black arrows indicate positive and negative pathways, respectively (\* $P < .05$ , \*\* $P < .01$ , \*\*\* $P < .001$ ). Numbers along the arrows indicate standardized path coefficients. Arrow width is proportional to the strength of the relationship. The proportion of variance explained ( $R^2$ ) appears alongside response variables in the models.**



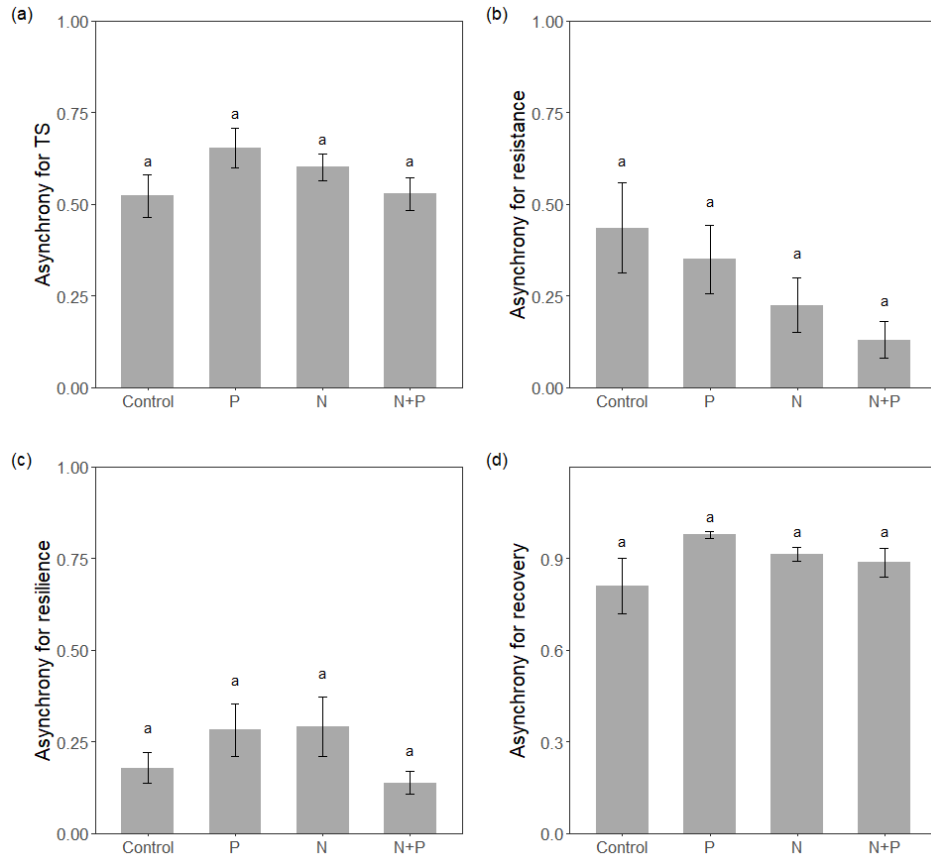
**Figure C6.** The final structural equation models showing the effects of nutrient enrichment on grassland functional and compositional (a) temporal stability (TS), (b) resistance, (c) resilience, and (d) recovery both directly and indirectly through affecting species evenness, richness, asynchrony, and dominant species stability. Blue and black arrows indicate positive and negative pathways, respectively (\* $P < .05$ , \*\* $P < .01$ , \*\*\* $P < .001$ ). Numbers along the arrows indicate standardized path coefficients. Arrow width is proportional to the strength of the relationship. The proportion of variance explained ( $R^2$ ) appears alongside response variables in the models.



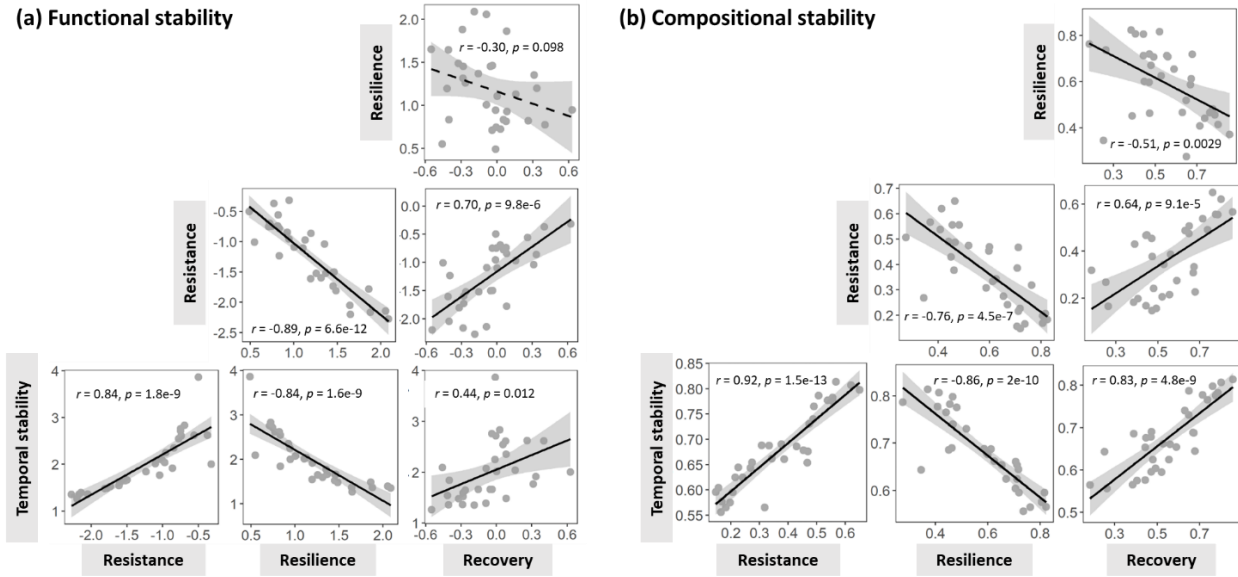
**Figure C7. Plant cover and species richness in different nutrient enrichment treatments. Shown are (a) total community cover (linear mixed-effects model; N enrichment:  $P < 0.001$ ; P enrichment:  $P = 0.159$ ; interaction:  $P = 0.012$ ); (b) dominant species cover (linear mixed-effects model; N enrichment:  $P = 0.012$ ; P enrichment:  $P = 0.810$ ; interaction:  $P = 0.011$ ) and (c) species richness (linear mixed-effects model; N enrichment:  $P = 0.017$ ; P enrichment:  $P = 0.991$ ; interaction:  $P = 0.597$ ). Vertical bars indicate means ( $\pm 1$  s.e.).**



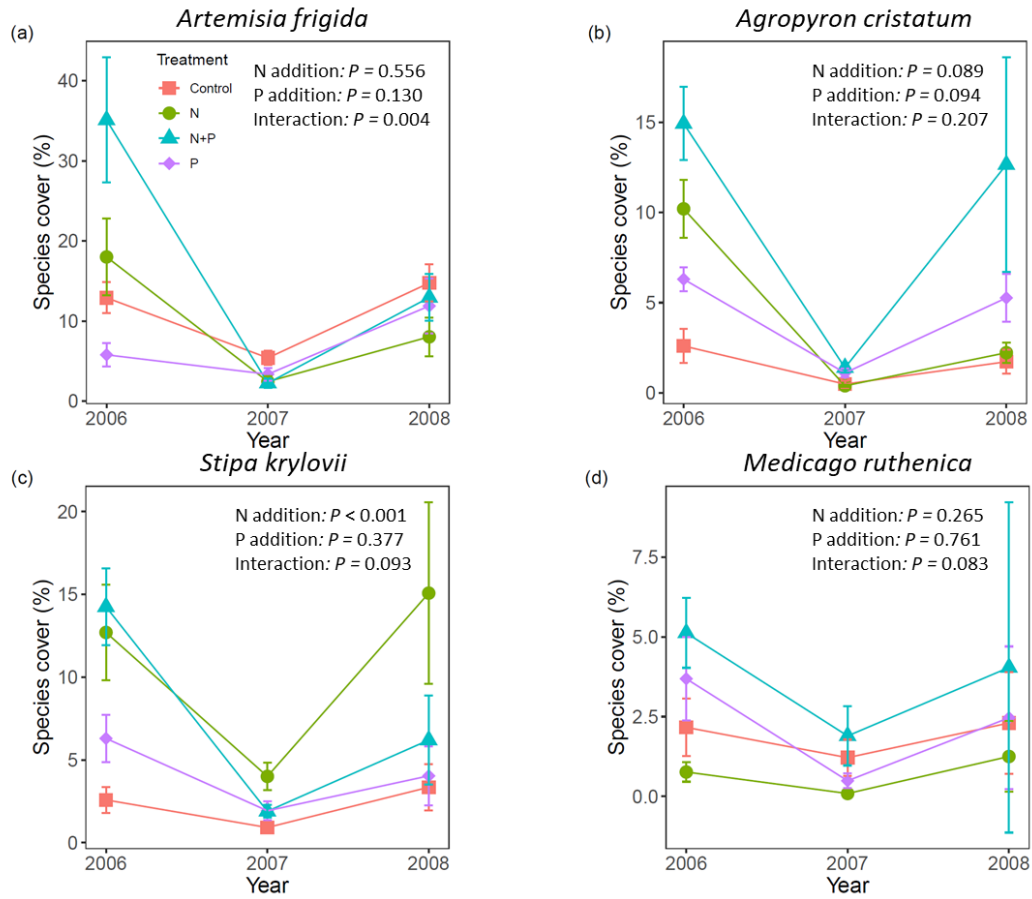
**Figure C8. Effects of nitrogen and phosphorus enrichment on multiple dimensions of dominant species stability. TS: temporal stability. Control: no nutrient enrichment; P: phosphorous enrichment; N: nitrogen enrichment; N+P: nitrogen and phosphorous enrichment. Bars indicate means ( $\pm 1$  s.e.). Treatments sharing the same letter are not statistically different in a *post hoc* Tukey's HSD test at the level of  $P = 0.05$ .**



**Figure C9. Effects of nitrogen and phosphorous enrichment on species asynchrony calculated for (a) temporal stability (TS), (b) resistance, (c) resilience, and (d) recovery. Control: no nutrient enrichment; P: phosphorous enrichment; N: nitrogen enrichment; N+P: nitrogen and phosphorous enrichment. Bars indicate means ( $\pm 1$  s.e.). Treatments sharing the same letter are not statistically different in a *post hoc* Tukey's HSD test at the level of  $P = 0.05$ .**



**Figure C10. Bivariate relationships between different dimensions of (a) functional stability and (b) compositional stability. Each dot represents an individual plot from the experiment. Black solid lines indicate significant relationships. The shaded areas represent 95% confidence intervals.**



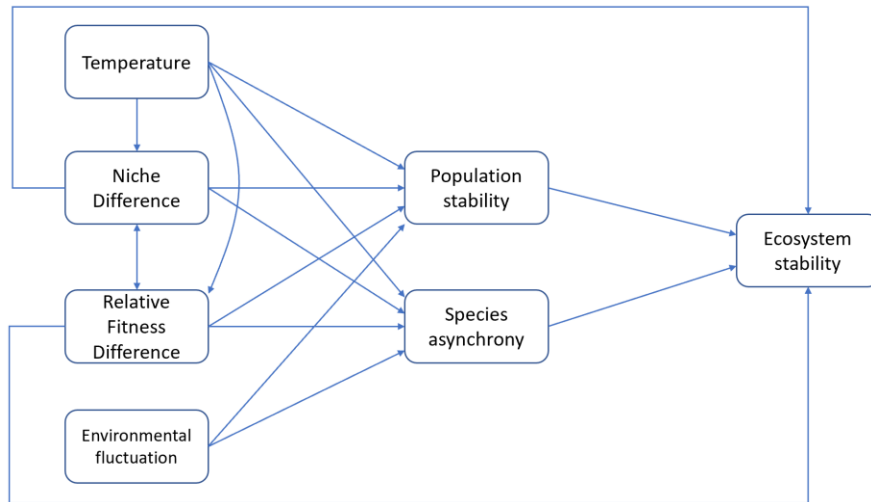
**Figure C11. Plant cover of the four dominant species in different nutrient enrichment treatments for the three years of the experiment. Shown are (a) *Artemisia frigida*; (b) *Agropyron cristatum*; (c) *Stipa krylovii*; and (d) *Medicago ruthenica*. Vertical bars indicate means ( $\pm 1$  s.e.).**

## APPENDIX D.

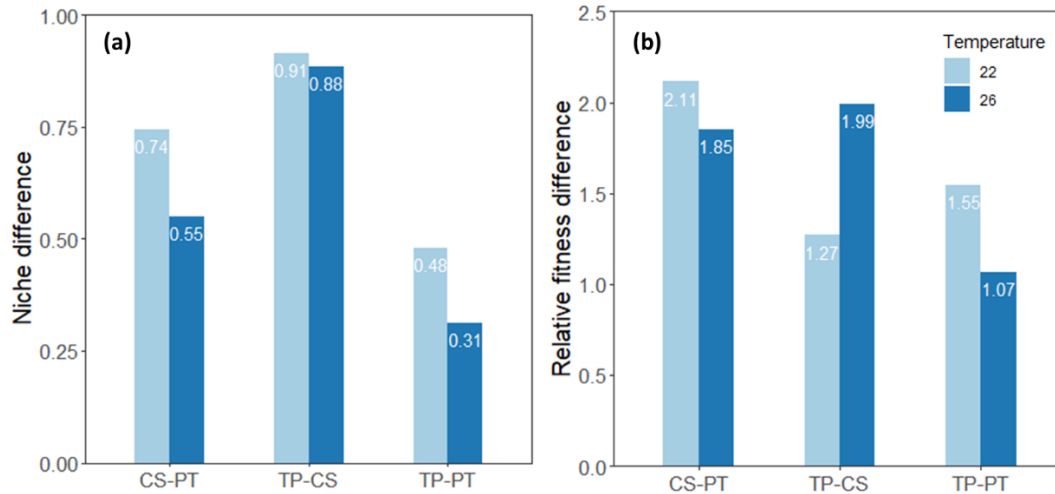
### SUPPLEMENT TO CHAPTER 3

**Table D1. Results (*F*-value) of linear mixed-effects models testing the effect of species niche difference (ND) and relative fitness difference (RFD), temperature (Temp), environmental fluctuation (Env), and the interaction between temperature and environmental fluctuation on population stability and species asynchrony.**

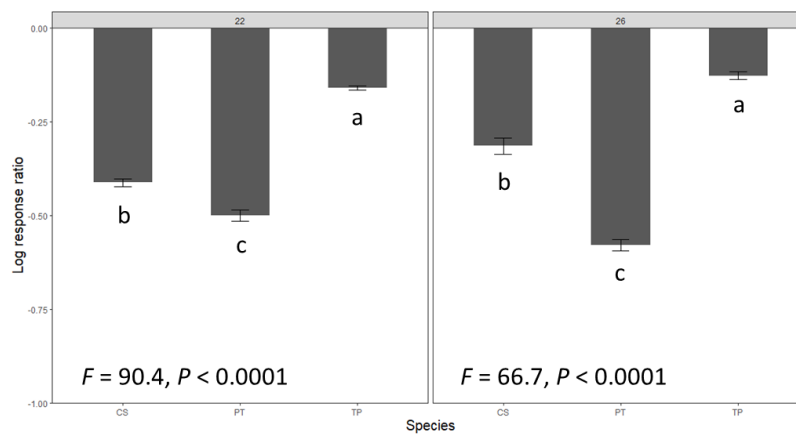
	Population temporal stability		Species asynchrony	
	<i>F</i>	<i>P</i>	<i>F</i>	<i>P</i>
<b>ND</b>	0.425	0.626	50.482	<0.001
<b>RFD</b>	4.501	0.068	1.901	0.175
<b>Temp</b>	96.867	<0.001	48.932	<0.001
<b>Env</b>	135.387	<0.001	27.305	<0.001
<b>Temp x Env</b>	28.182	<0.001	22.109	<0.001



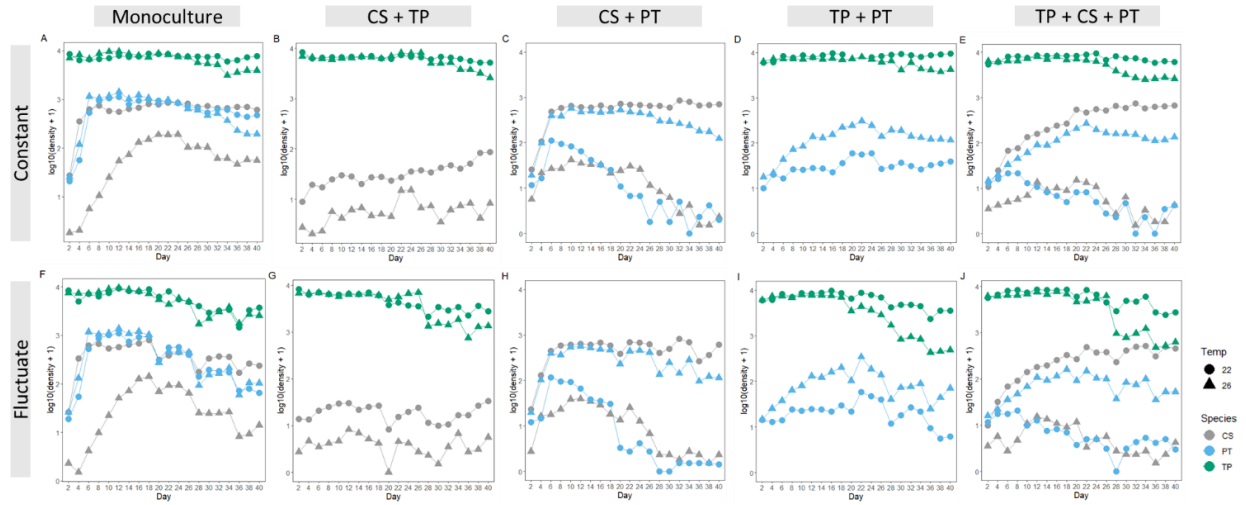
**Figure D1. The *a priori* model considering all plausible pathways through which temperature, environmental fluctuation, ND, and RFD influences ecosystem temporal stability through their impacts on species asynchrony and population temporal stability.**



**Figure D2. Niche difference (a) and relative fitness difference (b) between species pairs under different ambient temperatures.**



**Figure D3. Response of protist species to sonication disturbance at 22°C and 26°C. Error bars represent  $\pm$  SE. Different letters indicate significant differences at  $P = 0.05$  level in a Tukey's HSD test.**



**Figure D4. Population dynamics of *Tetrahymena pyriformis* (TP), *Colpidium striatum* (CS), and *Paramecium tetraurelia* (PT) in monocultures (A and F) and in the presence of competition (B – E and G – J) under constant vs. fluctuating environmental conditions.**