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Intra- and interspecific variability of specific leaf area mitigate the reduction of community stability in response to warming and nitrogen addition

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Global environmental changes are reducing the diversity and affecting the functioning of natural ecosystems as well as their ability to reliably provide ecosystem functions and services to mankind. Many studies have shown that a greater plant diversity can stabilize community productivity against environmental fluctuations. However, most of these studies focused on plant species richness, thus overlooking the potential role of functional traits in stabilizing community productivity against environmental fluctuations. Whether and how functional trait mean and variability influence community stability in response to environmental changes and their relative contributions to community stability are largely unknown. Here, we used a 10-year experiment to investigate the role of species richness, as well as functional mean and intra- and interspecific variability of specific leaf area (SLA) of plants within- and among communities in driving community stability in response to nitrogen (N) addition and warming. We found that both N addition and warming reduced the temporal stability of community productivity by reducing species richness and its contribution to species asynchrony and species stability. In contrast, changes in the mean and variability of SLA in response to N addition and warming mitigated the reduction of community stability. Specifically, N addition reduced variation in SLA both by reducing interspecific differences in SLA within communities and differences in mean values of SLA among communities. Warming increased intraspecific differences in SLA among communities, leading to higher species stability that partly buffered the reduction of community stability. Our study demonstrates the role of trait mean and variability in mitigating the reduction of community stability in response to two pervasive global environmental changes. Gaining a deeper understanding of the processes linking global changes and the stability of our ecosystems requires integrating both trait mean values and trait variability.

Keywords: community stability, experimental warming, intra- and interspecific trait variability, nitrogen addition, species asynchrony, species richness, species stability, specific leaf area

Introduction

Global environmental changes and biodiversity loss are threatening ecosystem stability and the reliable provisioning of ecosystem services to mankind (Cardinale et al. 2012). Understanding the mechanisms by which environmental changes affect the stability of ecosystems functioning has thus become a priority in ecological research (Tilman et al. 1998, Hautier et al. 2015). Ecological stability is a multifaceted concept (e.g. invariability, resilience and resistance) that can be studied at different organizational levels (e.g. population and community) (Lehman and Tilman 2000, Donohue et al. 2016). Here we focus on temporal invariability of community primary productivity, measured as the ratio of the temporal mean of community productivity to its temporal standard deviation (Tilman 1999). Thus, any process that increases the mean, reduces the standard deviation or both can lead to higher community stability.

There is growing evidence from both experimental and observational studies that plant diversity can stabilize community productivity against environmental fluctuations (Tilman et al. 2006, Cardinale et al. 2012, Hautier et al. 2014, 2020). This buffering effect of plant diversity on ecosystem functioning has been formalized by the insurance hypothesis (Yachi and Loreau 1999). That is, declines in the productivity of some species through time are compensated by increases in the productivity of other species (species asynchrony), leading to stable aggregate community productivity. Additionally, community stability can arise from higher average temporal stability of all species in the community (species stability) due to lower variation in individual species productivity from year to year (Tilman et al. 1998).

Most of the studies investigating the link between global environmental changes and stability have focused on changes mediated by plant species richness. Compared to taxonomic species richness, trait differences may improve the prediction of community stability because of a mechanistic link between functional traits and ecological processes (Díaz and Cabido 2001, Sasaki et al. 2019). So far, most studies focused on mean trait values of species and overlooked intraspecific trait variability under the speculation that trait variability among species are greater than those within species (McGill et al. 2006). However, there is growing evidence for the relative importance of intraspecific trait variability in trait-based community studies (Bolnick et al. 2011, Violle et al. 2012, Siefert et al. 2015). While the link between intraspecific trait variability and functional stability has been established theoretically (Wright et al. 2016, de Bello et al. 2021), or tested through virtual experiment (Morin et al. 2014), to our knowledge no study has quantified the impact of changes in intraspecific trait variability on the temporal stability of plant community productivity.

Specific leaf area (SLA) is a crucial functional trait that reflects the expected return on previously captured resources (Westoby 1998). SLA not only responds to environmental changes but also affects productivity (Finegan et al. 2015) and community stability of community productivity (Craven et al. 2018). Within a community, total variability of SLA can be divided into the variability within species (intraspecific trait variability within communities, $wITV_{intra}$; Table 1) and between species (interspecific trait variability within communities; $wITV_{inter}$) (Lepš et al. 2006). Species or populations with different SLA in response to environmental changes can fluctuate asynchronously or compensate each other for light use (de Bello et al. 2021). However, it was also reported that large trait variability among species can either increase community stability through increasing species asynchrony due to negative covariation among species or decreasing community stability due to strong asymmetry in interspecific competitive traits (Morin et al. 2014). For example, Morin et al. (2014) reported that higher community-weighted variance of shade tolerance (usually higher

Table 1. Functional trait indices and description.

Abbreviations	Description	Links to community stability
$wITV_{inter}$	Interspecific trait variability within communities	Higher $wITV_{inter}$ can either lead to higher community stability through increasing species asynchrony due to compensating for resources or negative covariation among species, or lower species asynchrony and community stability due to strong asymmetry in interspecific competitive traits.
$wITV_{intra}$	Intraspecific trait variability within communities	Higher $wITV_{intra}$ can either lead to higher community stability through increasing species stability due to compensating for resources or negative covariation among individuals, or lower species stability and community stability due to strong asymmetry in intraspecific competitive traits.
CWM_{fixed}	Species turnover among communities	Higher CWM_{fixed} of SLA (community dominated by fast species) can lead to higher species stability and community stability because species recover fast against environmental disturbance, or lower species stability and community stability because species are less resistant. Larger CWM_{fixed} of SLA can also lead to higher species asynchrony.
$aITV_{intra}$	Intraspecific trait variability among communities	Higher or lower $aITV_{intra}$ SLA may reduce community stability by reducing species asynchrony as species productivity will respond more synchronously in response to environmental changes. The same species may have larger SLA and become fast species under N addition or warming, thus less stable due to lower resistance or more stable due to higher recovery.
$CWM_{specific}$	Total trait variability among communities	–

SLA) in the community (the same as wITV$_{inter}$) can decrease community stability by decreasing species asynchrony in their responses to environmental fluctuations. Similarly, large variability of SLA within species may either increase or decrease species stability and community stability by increasing or decreasing asynchrony among individuals within species against environmental fluctuations (Supporting information).

Among communities, the variation of community weighted mean of SLA along environmental gradients can be caused by species turnover (CWM$_{fixed}$; i.e. changes in species occurrence and relative abundance) and intraspecific trait variability (aITV$_{intra}$) of SLA due to phenotypic plasticity along environmental gradients (Lepš et al. 2011). Species turnover of SLA can impact community stability through a tradeoff between resource acquisition (fast) and conservation (slow) strategy (Reich 2014). Specifically, communities dominated by slow-growing species with low SLA can be more resistant and thus more stable because they can tolerate low-resource conditions and maintain high survival due to the resource conservation strategy (Majeková et al. 2014, Craven et al. 2018), or less stable because they recover slowly against environmental disturbance (Craven et al. 2018, Li et al. 2021). Species turnover of SLA can also impact community stability by altering species asynchrony or species stability. For example, Morin et al. (2014) reported that virtual forest communities dominated by shade tolerant species had higher species asynchrony and community stability. Functional traits linked to conservative strategy may also predict community stability through increasing stability of plant populations under fertilization (Majeková et al. 2014). aITV$_{intra}$ SLA can reflect the direction of changes in community-level mean SLA. The same species may have larger SLA and become fast species under N addition (Knops and Reinhart 2000) or warming (Bjorkman et al. 2018), and these populations may become less stable due to lower resistance or more stable due to higher recovery. In addition, higher or lower aITV$_{intra}$ SLA may reduce community stability by reducing species asynchrony as species productivity will respond more synchronously in response to environmental changes.

Previous studies have demonstrated that global environmental changes can affect community stability via changes in plant diversity (Hautier et al. 2015) or independently of changes in plant diversity via changes in species asynchrony and/or species stability (Hautier et al. 2014, Xu et al. 2015). Nitrogen addition and warming are two major drivers of ecosystem functioning and community stability. Nitrogen addition usually reduces community stability by reducing plant species richness, species asynchrony (Hautier et al. 2014, 2020) or species stability (Zhang et al. 2016). Warming can also decrease community stability by reducing species asynchrony (Ma et al. 2017, Huang et al. 2020), but studies report little evidence for the role of species stability (Quan et al. 2021) and mixed evidence for the role of plant species richness (Post 2013, Shi et al. 2016, Wu et al. 2020) as mediators of the impact of warming on community stability. In addition, whether and how intra- and interspecific trait variability influences community stability in response to nitrogen addition and warming via changes in species asynchrony and species stability and the relative contribution of intra- and interspecific trait variability to community stability remain unknown.

Based on a 10-year warming and N addition experiment in an alpine meadow of the Qinghai-Tibetan Plateau, China, we quantified plant SLA and partitioned total variability of SLA into intra- and interspecific trait variability both within and among communities. Previous analyses at this study site demonstrated that N addition and warming impact community stability differently by impacting asynchrony among species or functional groups after four-year of treatment (Huang et al. 2020). Here, combining plant trait, we explore the following questions: (a) do warming and N addition impact temporal stability of community productivity through changes in species richness, trait mean and variability? (b) Do species richness, trait mean and variability impact community stability through species stability and species asynchrony?

Methods

Study sites and experimental design

Our study site is located in the eastern part of the Qinghai-Tibetan Plateau in Maqu County, Gansu Province, China (101°53′E, 35°58′N; 3500 m a.s.l.). The annual mean temperature is 1.2°C and the annual mean precipitation is 620 mm, most of which falls in summer (Luo et al. 2006). The soil is classified as Cambosols in the Chinese Soil Taxonomy, with an average depth of 80 cm (Gong et al. 1999). The vegetation is typical alpine meadow with high plant species richness dominated by perennial herbaceous species like Poaceae, Asteraceae and Ranunculaceae.

A permanent study area of 100 × 200 m was fenced in July 2009, where grazing was only permitted outside the growing season (from October to April). In June 2011, forty-eight 5 × 5 m plots were regularly arranged at intervals of 1 m within the fenced area. With a completely randomized experimental design, these 48 plots were randomly assigned four levels of nitrogen addition (NH$_4$NO$_3$): 0, 5, 10 or 15 g m^{-2} year^{-1}, which is the typical concentration range of anthropogenic nutrient deposition in alpine meadows (Li et al. 2014). Half of the plots within each nitrogen addition level were also randomly assigned to warming by transparent open-top chambers (OTCs) with 1.5 m^2 basal area at the centre of the plots (Liu et al. 2016), resulting in eight treatments with six replicates for each treatment. Each OTC increased the air temperature by about 0.77°C at night and by 1.80°C during the day (Liu et al. 2016). The OTCs were kept in place from May to October each year except the year of 2015 and 2017 in order to minimize the disturbance of ants under warming. As global warming is not continuous but with large fluctuations across years (Hansen et al. 2006), we used both 10-year (2011–2020)

and 8-year (2011–2020 excluding 2015 and 2017) data for the following analysis. Because the results are similar, we only showed the results of 10-year analysis in the main text.

Sampling and data collection

In August of each year (the peak of the growing season) from 2011 to 2020, we recorded species richness and individual number of each species (abundance) in 50 × 50 cm quadrats randomly placed in the plots (within OTCs in warming plots). Above-ground materials of each species were clipped at ground level, dried to constant weight at 70°C and weighed to 0.1 mg for species above-ground biomass estimation.

In August 2018, we selected 26 plant species of different life-forms (grass, Asteraceae, legume and forb) covering nine plant families, whose accumulated relative abundance is more than 70% across all species and all plots in 2017 (Supporting information). In each plot, we randomly selected up to 10 individuals for each of the 26 species for specific leaf area (SLA) measurements. We selected up to three mature and healthy leaves of each individual to measure leaf area (LA, mm^2, using the LA-S Leaf Area Analysis software, WSeen Detection Technology Co. Ltd., Hangzhou, China) within 24 h. Leaves were then dried at 65°C and measured to 0.001 g. SLA was calculated as leaf area divided by its dry mass (m^2 kg^{-1}) (Cornelissen et al. 2003).

Community stability and species asynchrony

We calculated community temporal stability as μ/σ, which is the ratio of temporal mean biomass of all species in a plot (μ) to its temporal standard deviation (σ) over the 10-year period (2011–2020) (Tilman 1999, Lehman and Tilman 2000). We calculated species stability as the temporal stability of species biomass averaged across all species in the community. We also calculated species asynchrony (Loreau and de Mazancourt 2008) for each community as:

$$1 - \varphi = 1 - \frac{\sigma^2}{\left(\sum_{i=1}^{S} \sigma_i \right)^2}$$

where φ is species synchrony, σ^2 is the variance in community temporal biomass, σ$_i$ is the standard deviation in temporal biomass of species i in a community with S species across the 10 years.

Trait variability within communities

According to the method proposed by Lepš et al. (2006), we partitioned the total trait variation within a specific community into intra- (wITV$_{intra}$) and interspecific trait variability (wITV$_{inter}$) as abundance-weighted within-species and between-species variability respectively based on SLA collected in 2018 and the relative biomass of each species in each year as:

$$\text{wITV}_{\text{intra}} = \sum_{i=1}^{S} a_i \times \frac{1}{\text{Nind}_i} \sum_{j=1}^{\text{Nind}_i} (x_{ji} - x_i)^2$$

$$\text{wITV}_{\text{inter}} = \sum_{i=1}^{S} a_i \times \left(x_i - \sum_{i=1}^{S} a_i x_i \right)^2$$

where a_i is the relative biomass of species i in the community (among the 26 trait-sampled species), Nind$_i$ is the number of sampling individuals of species i, x_{ji} is the SLA of individual j of species i and x_i is the average SLA of species i in the given community. Small values suggest intra- or interspecific trait convergence within communities. That is, individuals within species or among different species within a community have similar SLA.

Trait variability among communities

We calculate total among-community trait variability in response to different treatments as specific community weighted mean (CWM$_{specific}$), and its causes by species turnover (change in species composition; CWM$_{fixed}$), and intraspecific trait variability (aITV$_{intra}$) of SLA for each community following Lepš et al. (2011):

$$\text{CWM}_{\text{specific}} = \sum_{i=1}^{S} a_i x_i$$

$$\text{CWM}_{\text{fixed}} = \sum_{i=1}^{S} a_i x_{\text{average}}$$

$$\text{aITV}_{\text{intra}} = \text{CWM}_{\text{specific}} - \text{CWM}_{\text{fixed}}$$

where x_{average} is the average SLA of species i over all individuals across all 48 communities. Trait variability and CWM values were calculated annually for each plot using trait collected in 2018 and biomass collected every year, and then averaged across years. Different from wITV$_{intra}$, aITV$_{intra}$ reflects changes in mean trait rather than variance of individuals within species in response to treatments. Larger aITV$_{intra}$ SLA in N addition or warming plots suggest that the individuals of the species have larger SLA in N addition or warming habitats. To improve the normality, stability, asynchrony and trait variability measures were logarithm transformed.

Analyses

We used analysis of covariance (ANCOVA) to assess the effects of N addition, warming and their interaction on community stability, species asynchrony, species stability, species richness, intra- (wITV$_{intra}$) and interspecific trait variability of SLA within communities (wITV$_{inter}$), as well as intraspecific variability

(aITV$_{intra}$) and differences in species composition (CWM$_{fixed}$) of SLA among communities. N addition was treated as a continuous variable and warming as a categorical variable. We considered models in which N addition was a linear and quadratic function of the response variable in ANCOVA. If the quadratic term was not significant at the p = 0.1 level, we dropped it and fit a model containing only the linear term. We fitted linear models to assess the relationship of species richness, wITV$_{intra}$ and wITV$_{inter}$ SLA, as well as CWM$_{fixed}$ among communities and aITV$_{intra}$ SLA on community stability, species stability and species asynchrony, as well as the relationship of species stability and species asynchrony with community stability.

To assess the pathways by which N addition, warming and their interaction impact community stability, we constructed piecewise structural equation model (SEM) with the quadratic model with both the first and quadratic terms of N addition if it was better supported than the linear one. Based on our hypothesis, we related intraspecific variability of SLA within communities (wITV$_{intra}$), as well as CWM$_{fixed}$ and intraspecific variability of SLA among communities (aITV$_{intra}$) to species stability. Similarly, we related interspecific variability of SLA within communities (wITV$_{inter}$), as well as CWM$_{fixed}$ and intraspecific variability of SLA among communities (aITV$_{intra}$) to species asynchrony (Supporting information). We improved the model fit by eliminating non-significant pathways to obtain the final models. The goodness-of-fit test of the models

were assessed by Fisher's C and p-value. All analyses were conducted in R, using piecewiseSEM (Lefcheck 2016).

Results

Treatment effects on richness, asynchrony and stability

N addition and warming both reduced community stability (Fig. 1a). N addition had no effect on species asynchrony, while warming reduced it (Fig. 1b). Both N addition and warming reduced species stability (Fig. 1c) and species richness (Fig. 1d). The impact of N addition on species stability and species richness was nonlinear such that the effect became weaker at higher N levels. N addition and warming did not interact to affect the temporal stability of community productivity (Fig. 1a, Supporting information) or species asynchrony (Fig. 1b), but interacted to impact species stability (Fig. 1c) and species richness (Fig. 1d). Specifically, the negative impact of N addition on species stability and species richness were stronger under warming conditions.

Treatment effects on trait variability within communities

N addition decreased interspecific variability of SLA within communities (wITV$_{inter}$; Fig. 2b, Supporting information),
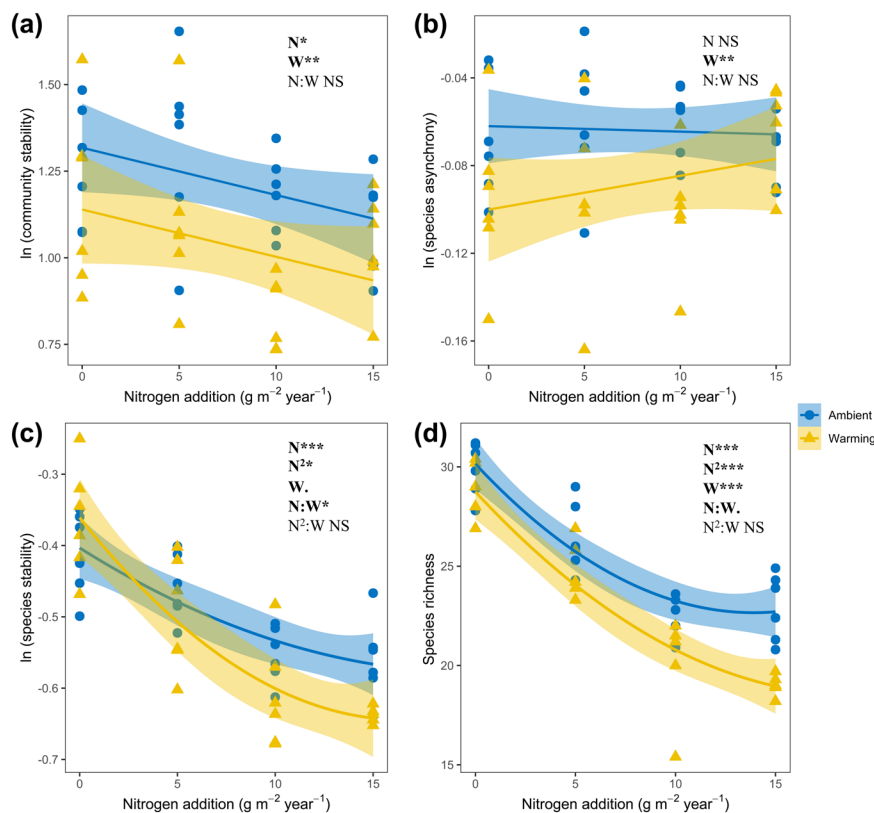
Figure 1. Impact of nitrogen (N) addition and warming on (a) community stability, (b) species asynchrony, (c) species stability and (d) mean species richness across 10 years (2011–2020). ***p < 0.001, **p < 0.01, *p < 0.05, ·p < 0.1, NS = non-significant.
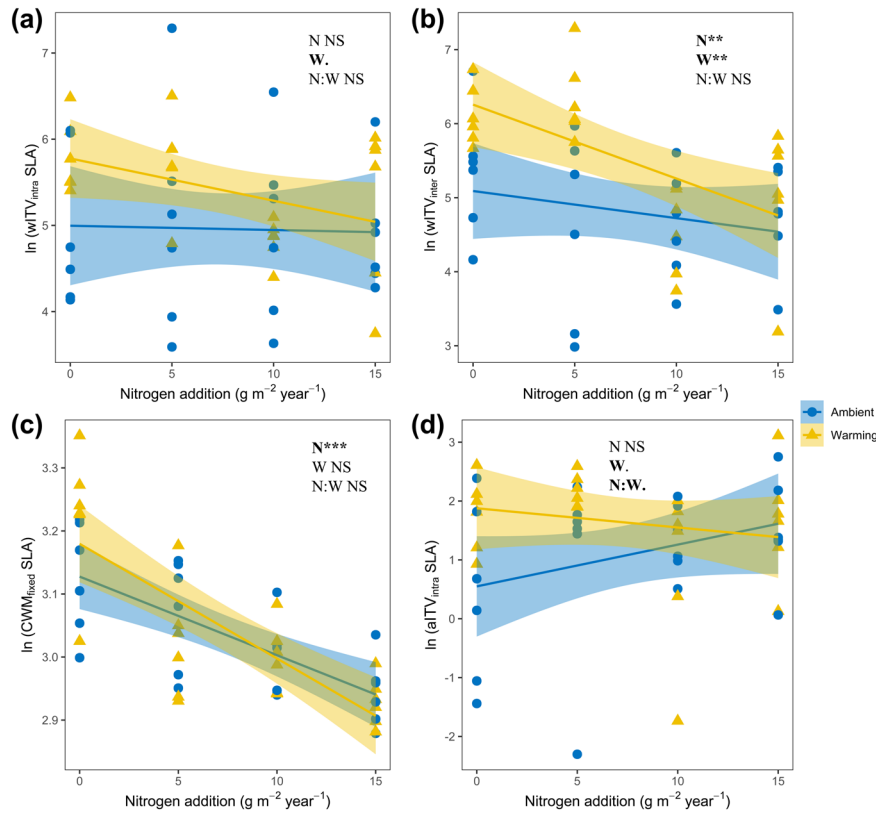
Figure 2. Impact of nitrogen (N) addition and warming on (a) intraspecific (wITV$_{intra}$) and (b) interspecific variability of specific leaf area (SLA) within communities (wITV$_{inter}$) and (c) species turnover (CWM$_{fixed}$) and (d) intraspecific variability of SLA among communities (aITV$_{intra}$) averaged across 10 years. ***$p < 0.001$, **$p < 0.01$, *$p < 0.05$, ·$p < 0.1$, NS = non-significant.

indicating a convergence of SLA among species in the communities with N addition. Warming increased both intra- (wITV$_{intra}$) and interspecific variability of SLA (wITV$_{inter}$) (Fig. 2a–b), which indicates a divergence of SLA within and among species under warming. N addition and warming did not interact to affect wITV$_{intra}$ (Fig. 2a) or wITV$_{inter}$ (Fig. 2b).

Treatment effects on trait variability among communities

N addition decreased species turnover (CWM$_{fixed}$) of SLA (Fig. 2c), and had no effect on intraspecific variability of SLA among communities (aITV$_{intra}$, Fig. 2d). Warming increased aITV$_{intra}$ SLA, and the impact of N addition on aITV$_{intra}$ SLA changed from non-significant to negative under warming (Fig. 2d). This indicates that communities were dominated by species with low SLA under N addition and that individuals of the same species had higher SLA under warming, but this latter effect decreased with increased N addition. N addition and warming did not interact to affect CWM$_{fixed}$ SLA (Fig. 2c), but interacted marginally to impact aITV$_{intra}$ (Fig. 2d).

Bivariate relationships

Species richness was positively related to temporal stability of community productivity (Fig. 3a). This relationship was

mainly attributed to the positive relationship between species richness and species stability (Fig. 3b), while species richness was not related to species asynchrony (Fig. 3c). Species stability (Fig. 3d) and species asynchrony (Fig. 3e) were both positively related to community stability.

wITV$_{intra}$ was negatively related to species asynchrony (Fig. 4b), but not related to community stability (Fig. 4a) or species stability (Fig. 4c). wITV$_{inter}$ SLA was negatively related to species asynchrony (Fig. 4e), but positively related to species stability (Fig. 4f), and not related to community stability (Fig. 4d). CWM$_{fixed}$ SLA was positively related to community stability (Fig. 5a) and species stability (Fig. 5c), but not related to species asynchrony (Fig. 5b). aITV$_{intra}$ SLA was not related to community stability (Fig. 5d), species asynchrony (Fig. 5e) or species stability (Fig. 5f).

SEM

Our SEM revealed that N addition alone reduced temporal stability of community productivity through two pathways (Fig. 6). First, N addition reduced species asynchrony and thus community stability by decreasing species richness, an effect that became weaker at higher N levels as revealed by the inclusion of the quadratic N term (Fig. 1d, 6). However, this effect was counteracted by a positive effect of N addition on species asynchrony through decreasing CWM$_{fixed}$
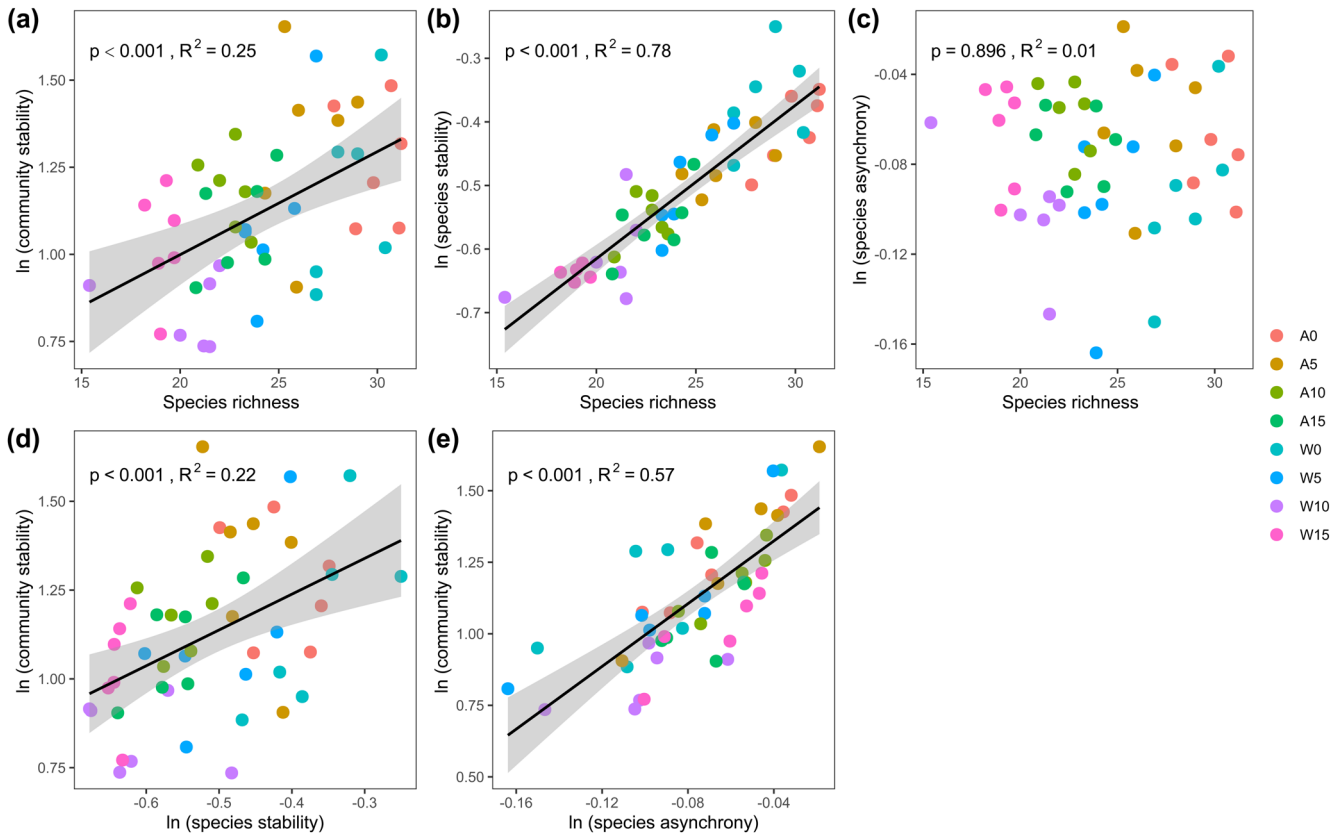
Figure 3. Relationships of (a) community stability, (b) species stability and (c) species asynchrony with species richness, and of community stability and (d) species stability with (e) species asynchrony across 10 years. Fitted lines were added when p < 0.05. Colored points represent different treatments. A = ambient; W = warming; 0 = no nitrogen addition; 5 = 5 g N m^{-2} year^{-1}; 10 = 10 g N m^{-2} year^{-1}; 15 = 15 g N m^{-2} year^{-1}.

and wITV$_{inter}$ SLA. These counteracting effects led to overall no impact of N addition on species asynchrony (Fig. 1b, 6). Second, N addition reduced species stability and thus community stability by decreasing species richness and CWM$_{fixed}$ SLA (Fig. 6). The lack of overall impact of N addition on species asynchrony and the negative impact on species stability explained the negative effect of N addition on community stability (Fig. 1a).

Warming alone also reduced community stability through two pathways (Fig. 6). First, warming reduced species asynchrony and community stability by decreasing species richness and increasing wITV$_{inter}$ SLA (Fig. 1b, 6). Second, warming reduced species stability and community stability by decreasing species richness, but this effect was partly counteracted by a marginally positive impact of warming on species stability by increasing aITV$_{intra}$ SLA, resulting in an overall marginally negative impact on species stability (Fig. 1c). The negative impact of warming on species asynchrony and the marginal negative impact on species stability explained the negative effect of warming on community stability (Fig. 1a).

N addition and warming interacted marginally to impact aITV$_{intra}$ SLA and thereby species stability and community stability. That is, the positive impact of N addition on aITV$_{intra}$ SLA decreased with warming, resulting in lower species stability and community stability (Fig. 2d, 6).

Discussion

Our study shows that N addition and warming had additive negative effects on the temporal stability of community productivity. Previous studies have shown that N addition can decrease community stability by decreasing species asynchrony and species stability (Zhang et al. 2016), and that these effects can be driven by N-induced loss of plant species richness (Liu et al. 2019, Wu et al. 2020) or independent of changes in richness (Zhang et al. 2016). Similarly, warming can decrease community stability by decreasing species asynchrony and species stability via warming-induced loss of plant species richness (Zhou et al. 2018) or independently of changes in richness (Ma et al. 2017, Wu et al. 2020). Our results support the idea that the decrease in community stability with N addition and warming is linked to a reduction in species asynchrony and species stability driven by a loss of species richness.

Importantly, our study provides new insights by demonstrating that changes in trait mean as well as intra- and inter-specific trait variability can mitigate the reduction of community stability in response to N addition and warming. Specifically, N addition decreased both interspecific variability of SLA within communities (wITV$_{inter}$ SLA) and differences in mean values of SLA among communities (CWM$_{fixed}$ SLA).
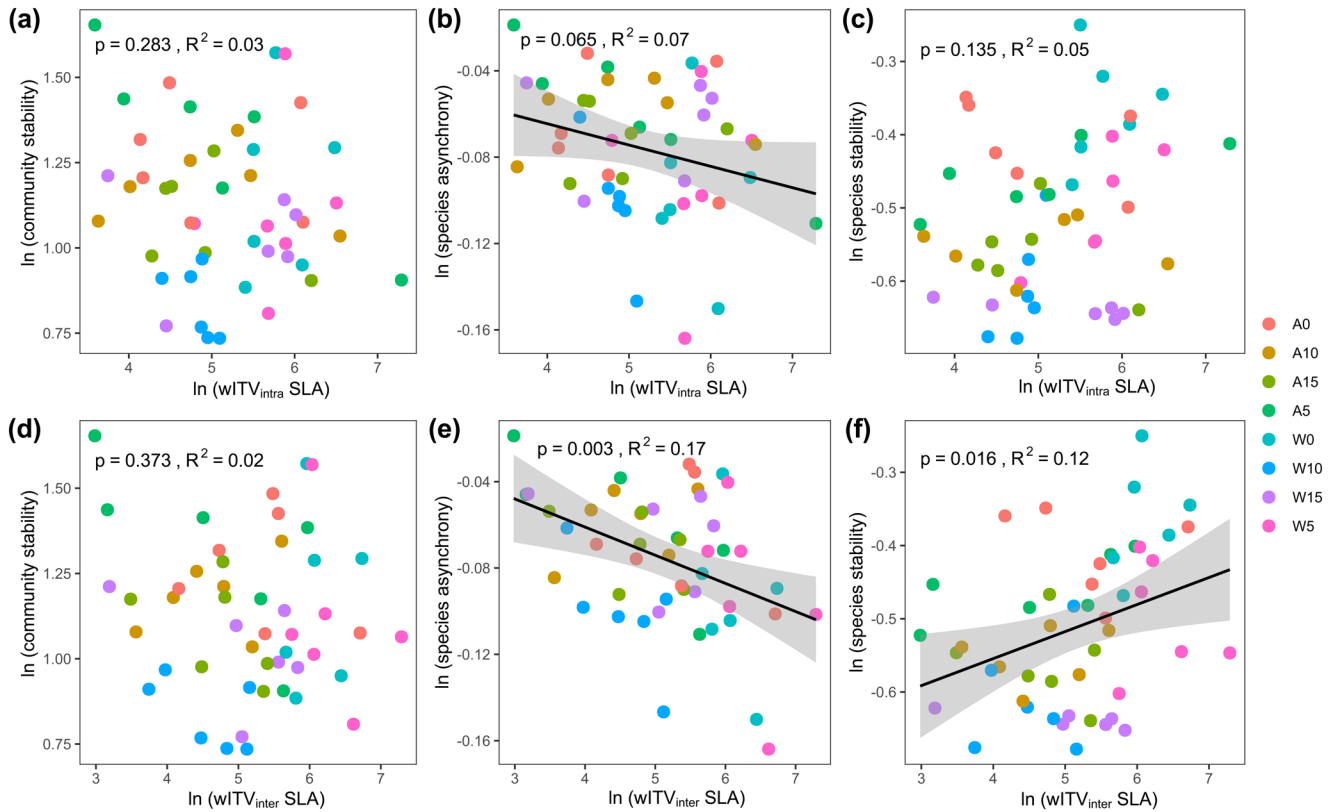
Figure 4. Within communities trait variance. Effect of (a–c) intraspecific (wITV$_{intra}$) and (d–f) interspecific variability of specific leaf area (SLA) within communities (wITV$_{inter}$) on community stability, species asynchrony and species stability across 10 years. Fitted lines were added when p < 0.1. Colored points represent different treatments. A = ambient; W = warming; 0 = no nitrogen addition; 5 = 5 g N m^{-2} year^{-1}; 10 = 10 g N m^{-2} year^{-1}; 15 = 15 g N m^{-2} year^{-1}.

That is, N addition led to communities dominated by species with low or similar SLA values. This reduction in community mean trait value and variability of SLA led to higher species asynchrony and thereby mitigated the decrease in community stability because large variations in SLA among communities and among species within communities were negatively associated with species asynchrony. Warming increased intraspecific variability of SLA among communities (aITV$_{intra}$ SLA). This increased trait variability led higher species stability and partly buffered the decrease in community stability.

Our results show that large variations in SLA among communities and among species within communities were negatively associated with species asynchrony are counterintuitive but can be explained as follow. In our study, dominant graminoids species were taller and had lower SLA values with larger biomass after nitrogen addition concentrated in the upper layers (Supporting information) compared to e.g. subordinated legumes species that occurred in the lower layers under low-light conditions with higher SLA, light-capture efficiency and photosynthetic rates. Such changes in community composition with N addition may have increased asynchrony among dominant species or between dominant species and other species to maintain community temporal stability. This result is in contrast to a recent study showing that avian communities dominated by 'fast' species exhibited

higher species asynchrony compared with those dominated by 'slow' species (Li et al. 2021). Additionally, Morin et al. (2014) showed that community dominated by species with larger variability of shade tolerance led to lower species asynchrony in response to environmental fluctuations (but higher species asynchrony in response to competition between species). Morin et al. (2014) suggested that the stabilising effect promoted by trait variability may arise from interactions between species rather than from their different responses to environmental conditions. This may be because trait variability of shade-tolerant species is more likely to compensate with shade-intolerant species at different canopy layers (Morin et al. 2014).

The positive contribution of differences in mean values of SLA among communities on species stability suggests that communities dominated by fast species are more stable in populations. Our result is consistent with Li et al. (2021) showing high recovery rate of fast species, but in contrast to Majeková et al. (2014) showing that slow species responded less rapidly to environment changes thus larger species stability. Intraspecific variability of SLA among communities also showed a positive contribution to species stability. This suggests that individuals with larger SLA may improve light-capture efficiency and photosynthetic rates and may exhibit larger species stability.
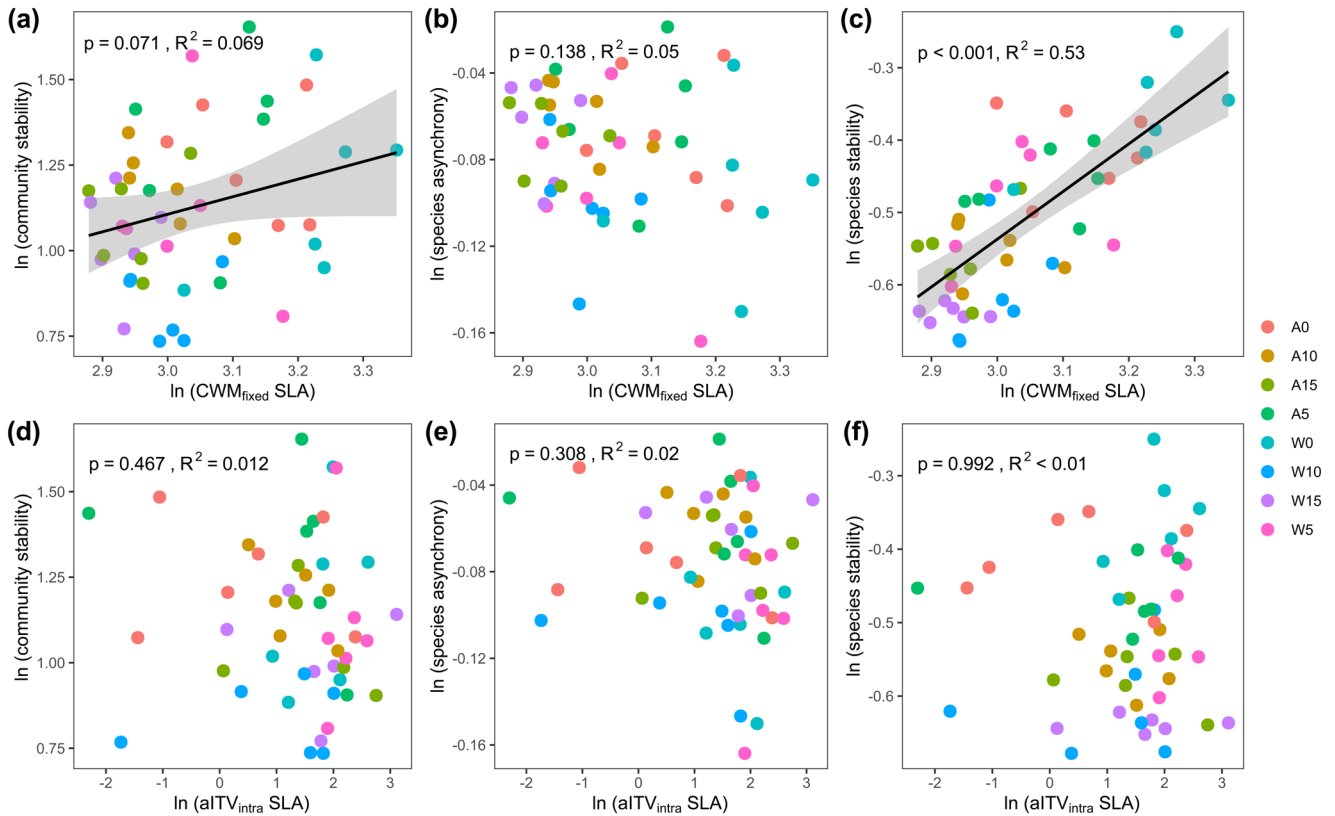
Figure 5. Among communities trait variance. Effect of (a–c) species turnover (CWM_{fixed}) and (d–f) intraspecific variability of SLA among communities ($aITV_{intra}$) on community stability, species asynchrony and species stability across 10 years. Fitted lines were added when p < 0.1. Points in different colors represent different treatments. A = ambient; W = warming; 0 = no nitrogen addition; 5 = 5 g N m^{-2} year^{-1}; 10 = 10 g N m^{-2} year^{-1}; 15 = 15 g N m^{-2} year^{-1}.
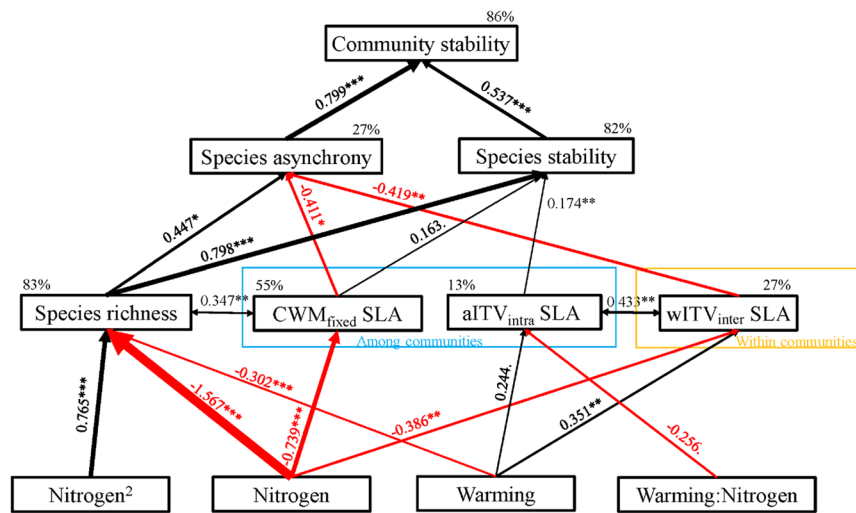

Figure 6. Piecewise structural equation model (SEM) for the relative contributions of species richness, intra- and interspecific trait variability of specific leaf area (SLA) within and among communities on community stability across 10 years. CWM_{fixed} = species turnover; $aITV_{intra}$ = intraspecific trait variability among communities; $wITV_{inter}$ = interspecific trait variability within communities. Red and solid lines: significant negative; Black and solid lines: significant positive. Numbers on arrows are standardized path coefficients (scaled by their mean and standard deviation), and asterisks indicate statistical significance (***p < 0.001; **p < 0.01; *p < 0.05, ·p < 0.1). Percentages next to endogenous variables indicate the variance explained by the model (R^2). Overall model Fisher's C = 37.433, p = 0.864, AIC = 99.433, df = 48.

In our study, N addition pushed the communities to be dominated by species with low SLA values (low differences in mean values of SLA among communities) and by species with similar SLA values (low interspecific variability of SLA within communities). The fact that N addition pushed the communities to be dominated by species with low SLA values in our study is inconsistent with previous studies (Tatarko and Knops 2018, Xu et al. 2018). In our study, many species with large SLA were either lost or decreased in biomass while many species with small SLA increased in biomass with nitrogen addition and dominated the community (Supporting information). Additionally, changes in SLA among species with N addition were larger than changes in biomass. Together, this led to low differences in mean values of SLA among communities in N addition plots because the metric biases towards dominant species. The fact that N addition pushed the communities to be dominated by species with similar SLA values in our study is inconsistent with previous studies (Sonnier et al. 2010). Our study showed that species with higher SLA are more likely to be lost under N addition (Supporting information), leading to communities dominated by species with similarly low SLA values. However, consistent with a previous study (Liu et al. 2021), interspecific variability of SLA within communities was divergent under warming, which suggested that the changes of interspecific variability of SLA within communities may depend on the type of perturbations. Because communities dominated by species with low or similar SLA values had reduced asynchronous dynamics, the resulting effect of N addition via functional traits was to increase species asynchrony.

Intraspecific variability of SLA among communities was increased by warming. That is, individuals had larger SLA in warmer plots. Bjorkman et al. (2018) also reported that intraspecific variability of SLA among communities was related to winter temperature in tundra biomes. Since our system is situated at the Tibetan Pleateu with low temperature, this suggests that resource-economics traits reflect plant tolerance to cold-stress (Bjorkman et al. 2018). However, the increased intraspecific variability of SLA among communities under warming shifted to decreasing at high N addition level. It suggestd that N addition may supress the positive effect of warming on intraspecific variability of SLA among communities due to species loss under N addition. Because intraspecific variability of SLA among communities had increased species stability, the resulting effect of warming via functional traits was to increase species stability.

Interspecific variability of SLA within and among communities under N addition buffered the decreased in species asynchrony, and the intraspecific variability of SLA among communities under warming buffered the decreased in species stability and community stability due to reduction in species richness. This suggests that the buffering effect of trait variability on species asynchrony is more related to trait difference among species, while the buffering effect of trait variability on species stability is more related to trait difference within species. Although growing studies consider intraspecific trait variability in response to environmental changes and its impact on ecosystem function, the relative extent of interspecific trait variability was still larger than intraspecific trait variability (Siefert et al. 2015). Variability of SLA can be the result of both phenotypic plasticity and genetic variability, two individuals from the different species are usually more different in both phenotypic plasticity and genetic variability than that of two individuals from the same species, thus leading to larger compensatory dynamics between them. However, the stability of population is more likely determined by the correlations of trait among individuals within species rather than between species.

Overall, N addition primarily reduced community stability by decreasing species stability, while warming primarily decreased community stability by decreasing species asynchrony through different pathways via species richness and trait variability of SLA. This suggests that different global change drivers may impact community stability by different pathways with N addition primarily leading to species loss and changes in trait variability, and warming primarily changing between-species interactions.

We measured SLA in one of the ten years used in this study due to prohibitively laborious work for individual trait measurement. However, in contrast to most previous studies, this allowed us to measure in addition to mean trait values, intra- and inter-specific trait variation and to assess its contribution to community stability under warming and N addition. We acknowledge that SLA values are likely to change both within and among species during the course of the study. Integrating such variation should help clarify the variability in ecosystem functioning. Our results are thus likely to be conservative and underestimate the contribution of trait variation caused by changing environmental conditions. Future studies should thrive to integrate the full temporal changes in trait variation and their contribution to ecosystem functioning.

In conclusion, our study considered the impact of intra- and inter-specific trait variability of SLA within and among communities on community stability of productivity through time in response to N addition and warming. Although N addition and warming reduced community stability by decreasing species richness, such effects are buffered by the simultaneous changes in trait distributions. Specifically, the positive effect of N addition on species asynchrony by decreasing interspecific variability of SLA within communities and differences in species composition among communities buffered the reduction of community stability, while the positive effect of warming on species stability by increasing intraspecific variability of SLA among communities partly buffered the reduction of community stability. Our study highlights the important role of both intra-and interspecific variability of SLA within and among communities in modulating temporal stability of community productivity, and provides a deeper understanding of the pathway linking intra- and interspecific trait variability on community stability through species stability and species asynchrony.

Author contributions

Mengjiao Huang: Formal analysis (lead); Investigation (equal); Methodology (equal); Writing – original draft (lead); Writing – review and editing (equal). **Shaopeng Wang**: Methodology (supporting); Writing – review and editing (equal). **Xiang Liu**: Investigation (equal); Writing – review and editing (supporting). **Ming Nie**: Supervision (supporting); Writing – review and editing (supporting). **Shurong Zhou**: Conceptualization (lead); Formal analysis (supporting); Funding acquisition (lead); Methodology (equal); Project administration (lead); Supervision (equal); Writing – original draft (supporting); Writing – review and editing (equal). **Yann Hautier**: Formal analysis (supporting); Methodology (supporting); Supervision (equal); Writing – original draft (supporting); Writing – review and editing (equal).

Data availability statement

Data are available from the Dryad Digital Repository: <https://doi.org/10.5061/dryad.kprr4xh57> (Huang et al. 2022).

Supporting information

The Supporting information associated with this article is available with the online version.

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