1 **Running title: Intraspecific trait variability and ecosystem multifunctionality**

2 **Title: Exploring the relationship between functional structure and ecosystem**
 3 **multifunctionality requires intraspecific trait variability**

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26 **Words:**

27 Abstract: 145; Main text: 4970; Introduction: 1160; Materials and Methods: 1981;

28 Results: 743; Discussion: 1086.

29 References: 47; Tables: 0; Figures: 6; Supplementary Tables and Figures: 6 and 10

Abstract

- Recent studies have shown that intraspecific trait variability is an important source of total trait variation in the face of global change. However, the contribution of intraspecific variability to ecosystem multifunctionality remains unknown.
- We calculated the mean and variability of four functional traits in an alpine meadow under long-term nitrogen addition and experimental warming and split them into interspecific and intraspecific variabilities. We then investigated their net effects and relative importance in determining ecosystem multifunctionality.
- We found that the effect of trait variability on multifunctionality depended not only on the number of functions, but also on the thresholds considered. Trait variability dominating ecosystem multifunctionality switched from interspecific to intraspecific when the thresholds of multifunctionality varied from low to high levels. When more functions were considered to interpret multifunctionality above high threshold levels, the relative contribution of intraspecific variability would be more important.

Keywords: Dominance hypothesis; Ecosystem multifunctionality; Interspecific trait variability; Intraspecific trait variability; Niche complementarity hypothesis; Plant functional structure; Tibetan alpine meadow

Introduction

The Qinghai-Tibetan Plateau is the youngest and highest place on Earth and alpine meadows account for nearly half of this area. These meadows are unique, fragile, and sensitive to global changes¹. Two sources of global change, warming and anthropogenic nitrogen (hereafter N) addition, are especially important in modifying ecosystem processes and functioning in this area¹. However, ecosystems can perform multiple functions simultaneously (e.g. productivity, biochemical cycling), and each function can respond differently to the same disturbance. To study the effects of warming and anthropogenic N addition on multiple ecosystem functions simultaneously, we use the concept of ecosystem multifunctionality, which was put forward to represent the functions of a “whole ecosystem”²⁻⁵.

Changes in temperature and/or N addition can change biodiversity and changes in biodiversity can affect ecosystem multifunctionality^{3-4, 6}. Biodiversity includes both species richness and species composition⁷. However, most studies in this area have concentrated most on species richness. These studies report that communities with higher species richness can maintain multifunctionality at higher levels^{6, 8-10} (Fig. S1). These results are suggestive, but it is community composition, rather than species richness per se, that should account for differences in ecosystem multifunctionality¹¹⁻¹². As Schoolmaster *et al.* (2020) argue, it is essential to correctly account for the cause – effect links between the components of biodiversity and ecosystem functions since community composition would influence ecosystem functions via plant phenotypic traits at small local spatial scales¹³⁻¹⁴. Hence, trait-based approaches

(response/effect traits) quantifying compositional complexity have been proposed as a way of mediating the relationship between global change and ecosystem functions¹²⁻¹⁵. In this paper, we will apply trait-based approaches, and call the pattern of trait values expressed in a community that determined both by the identity and relative abundance of the species possessing these traits, as the community functional structure¹⁶.

Ecosystem multifunctionality can not only be affected by global changes directly, but can also be indirectly affected by changes in community functional structure¹⁵⁻¹⁶ (Fig. 1). The effects of community functional structure (caused by effect traits) on ecosystem multifunctionality can be achieved via at least two mechanisms (Fig. 1 arrow C), i.e. via dominance and niche complementarity hypotheses¹⁵⁻¹⁷. The dominance hypothesis states that the traits of the dominant species have the greatest influence on ecosystem multifunctionality, which can be quantified by community weighted mean (CWM) traits. The niche complementarity hypothesis proposes that differences in species traits can promote the utilization of resources through increasing niche partitioning, and ultimately resulting in high ecosystem multifunctionality. In this case, ecosystem multifunctionality will be positively related to its functional diversity (the variability of traits among species within a community, e.g. Rao's quadratic entropy and functional dispersion).

These two hypotheses are not mutually exclusive. In reality, the importance of these two mechanisms (dominance and niche complementarity hypotheses) for ecosystem multifunctionality varies across ecosystems. For example, Valencia *et al.*

(2015) showed that CWM and functional dispersion were equally important in explaining the variation of multifunctionality in response to both aridity and shrub encroachment along an aridity gradient. Le Bagousse-Pinguet *et al.* (2019) reported that CWM values (the dominance hypothesis) provided limited explanation for multifunctionality, whereas the functional dispersion of SLA and plant height (the niche complementarity hypothesis) was positively related to multifunctionality. However, these studies used the average trait values of species (i.e. only caused by interspecific differences) to measure community functional structure in predicting multifunctionality, which completely ignored the effect of intraspecific variability of traits on ecosystem multifunctionality. Only considering interspecific variability would underestimate CWM and functional dispersion, and thus may misinterpret functional structure-ecosystem functions relationships¹⁸⁻²⁰. We therefore include both interspecific and intraspecific trait variability in our study.

Although interspecific trait variability is often assumed to contribute most to total trait variation within a community, intraspecific trait variability is also an important source of total trait variation for some traits²¹⁻²⁵. For example, Carlucci *et al.* (2015) separated CWM and Rao (strongly positively related to functional dispersion²⁶) within a given community into (i) “fixed value” (i.e. interspecific variability; changes in community functional structure caused solely by species turnover) and (ii) intraspecific variability effect (i.e. changes in community functional structure caused by intraspecific variability of traits), using the variance partitioning method proposed by Lepš *et al.* (2011) for CWM and de Bello *et al.* (2011) for Rao. They reported that

across a canopy openness gradient, intraspecific variability of CWM and Rao of SLA accounted for 19 % and 45 % of the total variation in CWM and Rao, respectively. This suggested that the “mean field approach”, which neglects ubiquitous intraspecific trait variability, underestimated the mean and variation of community functional structure. However, the importance of intraspecific trait variation to total variation (Fig. 1 arrow B) does not necessarily mean that its contribution to ecosystem multifunctionality is equally important (Fig. 1 arrow C). In other words, the relative importance of inter- and intraspecific variability of CWM and Rao of functional traits in explaining the variation in ecosystem multifunctionality remains unclear, which is the core objective of this paper.

As previous studies have reported, multifunctionality is a simple but nebulous concept⁴⁻⁵. The identity and number of selected functions may affect the reliability of the results, because *i*) different functions may differ in their dependence on a specific trait variability; *ii*) the functions can be positively or negatively correlated with each other; *iii*) previous studies have reported conflicting conclusions of the species richness-multifunctionality relationship^{11,27}. Thus, it is necessary to assess the sensitivity of our results to the number of functions, which is the verification of the robustness of the answer to question (*ii*) and (*iii*) below.

In this study, we collected plant functional traits (i.e. maximum adult height, SLA, LDMC, and leaf thickness) of 26 common species in an alpine meadow that has received 8-year's NH_4NO_3 addition (0, 5, 10, and 15 g N m⁻² year⁻¹) and experimental warming in the Tibetan Plateau. To fulfill the knowledge gap of the relative

importance of inter- and intraspecific trait variability in explaining the variation of multifunctionality, we calculated CWM and Rao within each community, and then separated them into a “fixed value” and an intraspecific variability effect as did Carlucci *et al.* (2015). Ecosystem multifunctionality (including 15 functions, i.e. nutrient cycling rates (e.g. enzyme activities related to carbon, nitrogen, phosphorus, and sulfur cycling), insect herbivory and fungal pathogen load) were calculated using both averaging and multi-threshold approaches. Specially, the objectives of this study were to: (i) detect the changes in ecosystem multifunctionality in response to N addition and experimental warming; (ii) assess the net effects of different interspecific and intraspecific trait variability metrics in determining multifunctionality, and the sensitivity of this result to the identity and number of functions; (iii) assess the relative contributions of interspecific and intraspecific trait variability on the relationship between CWM or Rao and multifunctionality, respectively, and the sensitivity of this result to the identity and number of functions. Objectives (ii) and (iii) both work to invest whether could intraspecific variability be ignored when using dominance and niche complementarity hypotheses to explain functional structure-multifunctionality relationship.

Materials and methods

Study site

Our study site is in an alpine meadow (35°58' N, 101°53'E), Maqu, Gansu province, China. It is in the eastern part of the Qinghai-Tibetan Plateau, with high altitudes

(approximately 3500 m), and low temperatures. The mean annual temperature is 1.2 °C , ranging from the average of -10.7°C in January to 11.7°C in July. The mean annual precipitation is 620 mm, which mainly concentrates in the growth season. This typical alpine meadow has high diversity, i.e. more than 30 plant species coexist within one 50×50 cm subplot²⁸. The plant community is dominated by annual and perennial herbaceous species of Poaceae, Cyperaceae, Asteraceae, Fabaceae, and others (e.g. Ranunculaceae, Caryophyllaceae, Umbelliferae), such as *Agrostis hugoniana*, *Kobresia capillifolia*, *Aster diplostephioides*, *Thermopsis lanceolata*, *Thalictrum alpinum*, *Cerastium fontanum*, *Chamaesium paradoxum*. The soil is a typical alpine meadow soil, and classified as Cambosols²⁹.

Experiment design

We fenced a 100×200 m area with a relatively uniform vegetation cover in 2009, and only permitted yak grazing from September to April. A total of 48 5×5 m plots were regularly arranged in June 2011, separated by an interval of 1 m for each plot. All plots were randomly assigned to one of the four concentrations of NH₄NO₃ addition, which were applied at rates of 0, 5, 10, or 15 g N m⁻² year⁻¹. Among the 12 replicates of each N addition treatment, one-half were warmed annually using reinforced-plastic open-top chambers of 1.5 m² basal area at the center of the 5×5 m plots during the growth season from May to August except in 2015 and 2017. Nitrogen was added at the middle of the growing season in each year.

Community data

We recorded the number of species and the abundance of each species within a 50×50 cm randomly selected subplot in each plot at the peak of the growing season (i.e. in August) in 2018.

Trait data

In the middle of August, we measured six plant traits of 26 common plant species (~70 % of relative abundance): maximum adult height (H_m), adult height (H_n), leaf area (LA), dry mass (M_{LD}), mean fresh leaf mass of a leaf (M_{LF}), and leaf thickness (Table S1). We randomly measured the maximum adult height and adult height of up to 10 individuals per species within each subplot. Then we randomly selected up to three mature leaves from the corresponding individuals to measure the other leaf traits. Collected leaves were kept in a cooler, carried to the laboratory immediately, and weighed to 0.0001 g to estimate fresh mass of a leaf. Leaf thickness was measured at the intermediate position to avoid major veins, using thickness gauge push type Digitronic (LR44, Aipu, China) with 8 mm diameter contact points. Leaf area was measured using the LA-S leaf area analysis software (WSeen Detection Technology Co. Ltd., Hangzhou, China). The dry mass of a leaf was weighed to 0.0001 g after dried at 65 °C for 48 h. Then we calculated the specific leaf area (SLA) and leaf dry matter content (LDMC). SLA, LDMC, maximum adult height (H_m), and leaf thickness (Table S2), which generally considered as the functional traits to describe fundamental axes amongst plants¹⁶, were selected to test how functional

traits mediate the influence of global change on ecosystem functioning.

Plant community functional structure calculation

Community weighted mean (CWM) of trait values and Rao quadratic entropy (Rao) were calculated to describe two distinct components of plant community functional structure, i.e. the mean and variability of traits within a community. We then separated CWM and Rao within a given community into a “fixed” interspecific component and an intraspecific variability component respectively using a variance partitioning method²²⁻²³. The “fixed value” only reflects mean interspecific differences in traits, whereas intraspecific trait variability reflects only intraspecific differences in traits around a species’ trait mean.

CWM is the mean of species trait values weighted by their relative abundance, and is calculated as:

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

where a_i and x_i are the relative abundance and the average trait value of the i^{th} species in a given community, respectively.

We then separate CWM into two additive parts: CWM_{fixed} and ITV :

$$CWM_{fixed} = \sum_{i=1}^S a_i x_{ifixed}$$

$$ITV = CWM - CWM_{fixed}$$

where x_{ifixed} is the mean fixed trait value of the i^{th} species over all sampled communities.

Rao is the sum of the distances between species pairs weighted by their relative abundance. The calculation and partitioning are as following:

$$\begin{aligned} \text{Rao} &= \sum_{j=1}^S \sum_{i=1}^S a_i a_j |x_i - x_j| \\ \text{Rao}_{\text{fixed}} &= \sum_{j=1}^S \sum_{i=1}^S a_i a_j |x_{i\text{fixed}} - x_{j\text{fixed}}| \\ \text{ITVR} &= \text{Rao} - \text{Rao}_{\text{fixed}} \end{aligned}$$

where a_j , x_j and $x_{j\text{fixed}}$ are the relative abundance, the average trait value in a given community, and the fixed trait value of the j^{th} species averaged over all sampling communities, respectively.

Ecosystem functions

A total of 15 ecosystem functions were measured in each plot, which include net primary productivity, six enzyme activities (C1, β -XYS, PPO, POD, α -GC, β -GC) related to C cycling, three enzyme activities (LAP, UE, NAG) related to N cycling, two enzyme activities (ACP, AKP/ALP) related to P cycling, and one enzyme activity (ASF) related to S cycling, as well as insect herbivory and fungal disease severity related to nutrient cycling rates (Table S1). Low nutrient cycling rates are considered to be “low” levels of these ecosystem functions. Note that although low levels of herbivory and disease severity can represent a high ecosystem “service”, we assumed that they contribute to a low functioning of nutrient cycling since less nutrients were circulating between trophic levels in the environment.

Before harvesting plants and sampling soils within each plot, we recorded the

herbivory severity and fungal disease severity per species within an area of 50×50 cm.

Six percentage classes were predefined to represent severity: 0%; <5%; 5–10%; 10–20%; 20–50%; >50%. For each species, we examined 25 leaves from at least five individuals. For those species with less than 25 leaves, all available leaves were recorded. Insect herbivory and fungal disease severity were the average proportion of leaves damaged by herbivores³⁰ and covered by fungal lesions, respectively³¹.

Community-level herbivory and pathogen load were calculated as the mean of species' herbivory and fungal disease severity weighted by their relative abundance, respectively. Then all aboveground plant parts were harvested using scissors at the soil surface after recording community composition, and then corresponding belowground soil samples were collected from four soil cores (5 cm diameter, 0-10 cm in depth) and sieved (2 mm). Aboveground biomass (i.e. net primary productivity) was weighed to 0.1 mg after drying at 65 °C for 48 h. Soil enzyme activities were measured through colorimetric methods to obtain a suitable absorption level at a given wavelength (unit: nm) in a cuvette in a spectrophotometer. Corresponding kits were purchased from Comin Biotechnology Co. Ltd., Suzhou, China. In brief, for hydrolytic enzymes, the activities of β -xylosidase (β -XYS), α -glucosidase (α -GC), β -glucosidase (β -GC), N-acetyl- β -D-glucosidase (NAG), acid phosphatase (ACP), alkaline phosphatase (AKP/ALP), aryl sulfatase (ASF) were measured based on the concentration of p-nitrophenol released from enzymes in the soil decomposing enzyme-specific synthetic substrates³². The enzyme activity of leucine aminopeptidase (LAP) was measured based on the concentration of p-nitroaniline

released after leucine aminopeptidase in soil decomposing enzyme-specific synthetic substrates. The activity of polyphenol oxidase (PPO) and peroxidase (POD) were measured by a colorimetric method³². Soil urease (UE) activity was determined using blue-colored complex to quantify the concentration of NH₃-N, which produced by urea hydrolysis. Soil cellulase (C1) activity was determined the concentration total sugar using anthrone-H₂SO₄ method.

Calculation of ecosystem multifunctionality

Before calculating multifunctionality, we checked the correlation among the 15 ecosystem functions to avoid including closely related and highly correlated variables, i.e. possible overweighting of certain aspects of ecosystem functions (Table S3). In our study, we kept all the 15 functions due to the low spearman correlation coefficients (Table S3). Then, we standardized each function using the Z-score transformation:

$$Zscore_{mn} = \frac{EF_{mn} - EF_n}{SD_{EFn}}$$

where EF_{mn} is the value of ecosystem function n in community m, EF_n and SD_{EFn} are the mean and standard deviation of function n across all the 48 communities.

We then calculated ecosystem multifunctionality using both widely used “multi-threshold” and “averaging” approaches for comparison. For the multi-threshold approach, ecosystem multifunctionality was calculated using the *getFuncsMaxed* function in the multifunc library of R⁴:

$$EMF = \sum_{n=0}^{15} \begin{cases} 1 & \text{Zscore}_{mn} \geq \text{Zscoremax}_n \times T \\ 0 & \text{Zscore}_{mn} < \text{Zscoremax}_n \times T \end{cases}$$

290 Zscoremax_n is the top 5% value of function n measured across the 48 plots. T is a
291 given percentages or thresholds. In this study, thresholds between 20 and 80% (every
292 5%) were considered according to Le Bagousse-Pinguet *et al.* (2019). EMF ,
293 calculated for each plot, is therefore the number (0 to 15) of the 15 ecosystem
294 functions in that plot which reach or exceed the chosen threshold.

295 The averaging approach was also used to measure the average effect of trait
296 variability on ecosystem multifunctionality (hereafter EMF_a), which is simply the
297 average Z-score of a plot calculated over the 15 ecosystem functions:
298

$$EMF_a = \frac{\sum_{n=0}^{15} \text{Zscore}_{mn}}{15}$$

301 Statistical Analyses

302 In order to answer the first question, two-way ANOVA and then a Tukey HSD test for
303 multiple comparisons were performed to detect changes in ecosystem
304 multifunctionality in response to N addition and experimental warming.

305 In order to answer the second question, we evaluated the net effect of inter- and
306 intra- specific variability on ecosystem multifunctionality (EMF_a and
307 multifunctionality across multiple thresholds). Model selection (*dredge* function in
308 MuMIn package) and then model averaging (*model.avg* function in MuMIn package)
309 were performed. We conducted model selection from a series of all possible linear
310 models. The full model included treatments (Warming *N addition), interspecific
311 variability of each single trait (CWM_{fixed} and Rao_{fixed} of leaf thickness, Hm, SLA, and

LDMC, respectively), and intraspecific variability of each single trait (ITV and ITVR of each trait). Pearson correlation tests were performed using the *cor.test* function in the stats package to avoid including strongly correlated indices (i.e. 16 single interspecific and intraspecific trait variability metrics) in any one model if $r > 0.6$ (Table S4). The best predictors were obtained based on changes in AICc values (i.e. models with $\Delta AICc < 2$). Then model averaging was conducted to get parameter estimates of the best predictors (i.e. standardized regression coefficients). All interspecific and intraspecific variability metrics and ecosystem functions were standardized using the Z-score transformation to make parameter estimates comparable.

The net effect of interspecific trait variability on EMF_a was calculated as the sum of the standardized regression coefficients of EMF_a on CWM_{fixed} and Rao_{fixed} of each trait respectively. Similarly, the net effect of intraspecific trait variability on EMF_a was calculated as the sum of the standardized regression coefficients of EMF_a on ITV and ITVR of each trait respectively. The corresponding standard error would propagate due to the combination of variables in the additive function. The net effect of trait variability metrics on multifunctionality calculated using multi-threshold approach was calculated as the average standardized regression coefficients over the entire spectrum of thresholds (20–80%).

The relative importance of inter- and intra- specific variability in determining multifunctionality were represented by the relative percentage they explained, which was used to answer question (iii). For example, the relative importance of CWM_{fixed}

of SLA for multifunctionality was measured as the absolute value of its standardized regression coefficients divided by the sum of the absolute value of standardized regression coefficients of all the 16 functional trait variability. The relative importance of interspecific variability was calculated as the sum of relative percentage explained by CWM_{fixed} and Rao_{fixed} of the four functional traits. We repeated this analysis to identify the relative importance of: *i*) intraspecific variability (ITV and ITVR of the four functional traits); *ii*) the dominance effect (CWM_{fixed} and ITV of the four functional traits); and *iii*) the niche complementarity effect (Rao_{fixed} and ITVR of the functional traits).

In order to assess the sensitivity of our results to the number of functions, we therefore calculated multifunctionality over the 500 different combinations of these 15 functions (i.e. $\frac{C_{15}^i}{2^{15}-1} \times 500$, $i \in [1, 15]$) for each of four given thresholds (20%, 40%, 60%, 80%) and average values (i.e. a total of 2500 new multifunctionality measures). For each new multifunctionality measure, data analyses were repeated as above, and then the relationship between the net effect, relative importance of metrics and the number of functions were obtained.

Results

Warming and N addition significantly decreased ecosystem multifunctionality

Among the 15 individual ecosystem functions, N addition significantly increased fungal disease severity, and significantly decreased the activity of LAP, UE, AKP/ALP, and ASF. Seven of the other 10 ecosystem functions showed decreasing trends with N addition. Warming significantly decreased aboveground net primary

productivity, the activity of PPO, and POD. Eight of the other 12 ecosystem functions showed a decreasing trend with warming. The effects of the N addition and warming treatments on individual ecosystem functions were independent on each other (Table S5).

Ecosystem multifunctionality calculated using the averaging approach (i.e. EMF_a) decreased significantly with warming ($F_{1,40}=12.039$, $P=0.001$) and N addition ($F_{3,40}=4.713$, $P=0.007$). The interaction of warming and N addition ($F_{3,40}=0.756$, $P=0.526$) did not affect ecosystem multifunctionality EMF_a (Fig. 2a). For the effect of our treatments on ecosystem multifunctionality across the four thresholds (i.e. 20%, 40%, 60%, 80%), warming and N addition both showed significantly negative effects, and without a significant interaction between (Fig. 2b).

The net effects of interspecific and intraspecific variability on multifunctionality

The net effect of the 16 functional trait variability metrics on ecosystem functions varied among these functions after controlling for the effects of the warming and N addition treatments (Fig. S2). For example, $CWM_{\text{fixed_Hm}}$, $CWM_{\text{fixed_thickness}}$, ITV_{Hm} , ITV_{RSLA} , $Rao_{\text{fixed_Hm}}$, and $Rao_{\text{fixed_thickness}}$ were significantly and positively related to net primary productivity within each experimental treatment. However, only $ITV_{\text{thickness}}$ showed a negative effect, and the other 15 metrics showed weakly positive, weakly negative, or neutral effects on UE activity.

The net effects of different trait variability metrics on multifunctionality depended on not only the thresholds considered (Fig. 3), but also the number of functions (Fig. 4). The number of trait variability metrics included in supported

models decreased with increasing thresholds, and only the intraspecific variability metrics were retained at the 80% threshold (Fig. 3). At a given threshold (e.g. 20%, 40%, 60%, 80%), increasing the number of functions generally increased the strength of the trait variability metrics-multifunctionality relationships (Fig. 4). The steepness of the slope (i.e. trait variability-multifunctionality relationships against the number of functions) decreased with an increase in the thresholds considered, except for the changes in ITV_Hm, ITV_RLDMC, ITV_RSLA, ITV_SLA and ITV_thickness-multifunctionality relationships. When using the highest threshold (i.e. 80%) to calculate multifunctionality, the interspecific trait variability metrics-multifunctionality relationships were nearly neutral irrespective of the number of functions considered. As the number of functions increased, the strength of the trait variability metrics-EMF_a relationships were generally steady (Fig. S3).

Across multiple thresholds (20–80%), all the 16 trait variability metrics except Rao_{fixed}_Hm were included in models with $\Delta AICc < 2$ when explaining the variation in multifunctionality after controlling the effects of treatments (Fig. S4A, Table S6). However, only intraspecific variability of leaf thickness over CWM (i.e. ITV_thickness) showed a significantly negative effect on ecosystem multifunctionality calculated across different thresholds (Fig. S4A). Similar results were found for EMF_a (Fig. S5A).

The relative importance of interspecific and intraspecific variability in determining the functional structure-ecosystem multifunctionality relationship

For ecosystem multifunctionality, the relative importance of intraspecific variability

increased, while the relative importance of interspecific variability decreased, with increasing threshold values (Fig. 5). The relative importance of interspecific and intraspecific variability for ecosystem multifunctionality was similar at a threshold value of 20%, but only intraspecific variability accounted for the variation in multifunctionality at thresholds of 55%, 70%, 75%, and 80%. Meanwhile, only intraspecific variability contributed to the difference in EMF_a, while interspecific variability metrics were not included in the best models (Fig. S6).

At a low threshold (i.e. 20%), increasing the number of functions generally increased the relative importance of interspecific variability on multifunctionality, but decreased relative importance of intraspecific variability (Fig. 6). However, this pattern was reversed at high given thresholds (i.e. 60%, 80%) (Fig. 6). The number of ecosystem functions considered did not consistently affect the variance in EMF_a explained by interspecific and intraspecific variability (Fig. S7), which was similar with the trend at 40% threshold.

The relative importance of CWM_{fixed} and Rao_{fixed} on multifunctionality was identical to the relative importance of dominance effect and niche complementarity effect when ignoring intraspecific trait variability, as we have described above. When taking intraspecific trait variability into account, the variation in multifunctionality explained by CWM was a bit higher than Rao across multi-threshold, except at the threshold of 35% (Fig. S8). At a given threshold, the steepness of the slope (i.e. relative importance of interspecific and intraspecific trait variability against the number of functions) changed very little (Fig. S9).

Discussion

Previous studies have evaluated the relative contributions of interspecific and intraspecific trait variability to total variation in community functional structure along environmental gradients²⁴⁻²⁵. However, few studies have evaluated the relative importance of interspecific and intraspecific trait variability to the relationship between functional structure and ecosystem multifunctionality. In this study, we reached four conclusions. (i) Ecosystem multifunctionality in our study site decreased with N addition and warming. (ii) The net effects of different trait variabilities on multifunctionality depended both on the thresholds considered and on the number of functions included in the calculation. (iii) The relative importance of intraspecific variability in evaluating the functional structure-ecosystem multifunctionality increased with the number of functions considered and the levels of threshold employed. (iv) Neglecting intraspecific variability could underestimate the effect of functional structure on ecosystem multifunctionality.

Warming and N addition significantly decreased ecosystem multifunctionality

Eleven out of 15 individual ecosystem functions were significantly and negatively related to increases in the treatment variables. Hence, the average multifunctionality decreased with N addition and warming. Different from some studies^{6,9,17}, our calculation of multifunctionality captured ecosystem functions related to nutrient cycling rates⁵. Stocks of energy and matter (e.g. soil NH_4^+ , NO_3^- content) were not considered as a component of multifunctionality because they reflect the net balance

of ecosystem processes rather than ecosystem functions as such⁵. For example, a high soil NO₃⁻ content could be considered as reflecting either a low functioning, since it suggests a low plant NO₃⁻ uptake rate, or a high functioning because of high soil nitrification rates. Hence, our results demonstrated that eight-years of N addition and warming decreased nutrient cycling rates of the whole ecosystem. A lower soil community functional complexity³³, or microbial diversity loss (especially rare microbial taxa)³⁴, may partly explained inorganic N addition effect. The effect of warming on multifunctionality vary across ecosystems³⁵⁻³⁷. Further studies about how cascading effects from plants to soil microorganisms explaining experimental warming affect multifunctionality is necessary.

The net effects of trait variability on multifunctionality depended on the thresholds and the number of functions considered

Previous studies found that the species richness-ecosystem multifunctionality relationship depended on the number of functions considered²⁷. Figs. 3 and 4 demonstrated that the effect of trait variability on multifunctionality depended not only on the number of functions, but also on the thresholds considered. In our study, the effects of trait variability on ecosystem functions also depended on both the identity of traits and functions. Among all the traits and functional diversity metrics we considered, only the intraspecific contribution to CWM of leaf thickness (i.e. ITV_thickness) consistently had a significantly negative effect on ecosystem multifunctionality. Stated differently, after controlling for the effects of experimental treatments, those communities having the same species composition and same

interspecific values of height, SLA, LDMC, and leaf thickness, but having plants whose leaves were thinner than typical for their particular species would support a higher multifunctionality. Among 15 individual functions, five soil enzyme activities were significantly negatively related to ITV_thickness. Soil enzyme activities can directly mediate organic matter breakdown and biochemical nutrient cycling through the decomposition of plant litter³⁸⁻³⁹. Thus, plants having thinner leaves within a species might possess higher litter nitrogen, phosphorus and carbon concentration³⁸, and the concentration of substrates influenced soil enzyme activity⁴⁰.

However, that does not mean that the other functional traits we measured were not important in determining ecosystem functions. For example, we found that the mean and variation of community-level height, SLA, and thickness caused by interspecific and intraspecific variability would contribute to the change in productivity¹⁶. This may be because taller individuals can access light more easily, and a more complete filling of space can increase light capture⁴¹⁻⁴². As well, productivity increased with increasing intraspecific variability in plant height and SLA, perhaps due to a “shade-avoidance syndrome”, i.e. all individuals in a light-limited community may share the strategy of allocating a large amount of energy to elongate stem and higher SLA to access more light for growth⁴³. These functional traits are the fundamental dimensions related to plant survival and growth in response to ecological environment⁴⁴⁻⁴⁵ (i.e. response traits). However, when functional traits act as effect traits to drive biochemical nutrient cycling difference, for example, litter quality is necessary since the decomposition of plant litter is a key determinant of

nutrient cycling worldwide^{38,46}.

Intraspecific variability contributed more than interspecific variability in

determining functional structure-multifunctionality relationship

Previous studies reviewed in Garnier *et al.* (2016) found that traits related to light competition (e.g. plant height) and resources acquisition and use (e.g. SLA, LDMC, leaf thickness) are important for ecosystem functioning relevant to rates of nutrient cycling. However, almost all of those studies only took interspecific trait variability into account^{15,17}. We found that neglecting intraspecific variability could underestimate the effect of functional structure on ecosystem multifunctionality. More interestingly, the contribution of intraspecific variability increased, while the contribution of interspecific variability decreased, as thresholds of multifunctionality (i.e. higher level of multifunctionality the community simultaneously achieved) increased. Previous study has proposed “jack-of-all-trades-but-master-of-none” to describe the phenomenon that diverse community would support more functions above low threshold levels, but only few functions above high threshold levels could be maintained⁴⁷ (Fig. S10). As Fig. 5 demonstrated that ecosystems supporting multiple functions simultaneously above low threshold levels were driven more by interspecific differences, but ecosystems supporting multiple functions simultaneously above high threshold levels was driven more by intraspecific difference (Fig. 5). Especially above 70% threshold, only intraspecific difference drives the variation in multifunctionality. After considering both interspecific and intraspecific trait variabilities, evidence for dominance hypothesis became stronger than that for niche

complementarity hypothesis since the relative importance of dominant species was a bit higher than subdominant species. That further confirmed the importance of intraspecific variability. We also confirmed the robustness of this result by testing the sensitivity of the relative importance of intraspecific variability (Fig. 6). The relationship between relative importance of intraspecific variability and the number of functions depends on threshold level we selected. This result supplies one evidence that when more functioning was considered to interpret multifunctionality above high threshold levels, the relative importance of intraspecific variability would be more important.

In conclusion, we found that exploring the relationship between functional structure and ecosystem multifunctionality in response to global change factors should take intraspecific variability of traits into account. A general pattern from regional or even global database related to the importance of intraspecific variability in plant functional traits in determining ecosystem multifunctionality is necessary. Also, the fundamental dimensions of ecosystem functions to supply a guide for measuring variables clearly remains a challenge for future studies⁵.

Acknowledgements

This work was supported by the National Natural Science Foundation of China (31830009 and 31770518), and by a CSC (China Scholarship Council) scholarship to Li Zhang. The work was done in the Research Station of Alpine Meadow and Wetland Ecosystems of Lanzhou University. We thank Liu Xiang, Xiao Yao, Mengjiao Huang,

Seraina Cappelli, and Chen Fei for helping perform the field experiment. We especially thank Noemie Pichon and Françoise Cardou for the suggestions of data analysis and the manuscript.

Author contributions

SZ and LZ designed the experiment. LZ conducted experiments, collected and analyzed data. LZ, SZ, BS developed the hypothesis. LZ, SZ and BS wrote the manuscript and approved the final manuscript.

Data accessibility

All data supporting the manuscript are presented, and additional information is available upon reasonable request.

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699 **Supporting Information**

- 700 Table S1 List of plant traits and ecosystem functions included in data analysis.
- 701 Table S2 Spearman's correlation matrix of eight measured plant traits.
- 702 Table S3 Spearman's correlation matrix of the 15 considered ecosystems functions in
703 our study.
- 704 Table S4 Pearson correlation matrix of the 16 different trait variability metrics.

Table S5 The responses of 15 individual ecosystem functions to N addition gradient

and warming.

Table S6 Standardized regression coefficients of different trait variabilities in

determining multifunctionality at each given threshold.

Fig. S1 Partial residual plots (i.e. deviations of ecosystem multifunctionality after

removing the treatment effect) as a function of species richness.

Fig. S2 Net effects of different trait variabilities in determining individual ecosystem

function.

Fig. S3 Net effects of different trait variabilities in determining average ecosystem

multifunctionality.

Fig. S4 Net effects of different trait variabilities in determining multifunctionality at

four given thresholds (20%, 40%, 60%, 80%).

Fig. S5 The sensitivity of net effects of 16 trait variability metrics on average

ecosystem multifunctionality.

Fig. S6 Relative importance of interspecific and intraspecific trait variability in

determining average ecosystem multifunctionality.

Fig. S7 The sensitivity of the relative importance of interspecific and intraspecific

trait variability in determining average ecosystem multifunctionality.

Fig. S8 The relative importance of dominance hypothesis and niche complementarity

hypothesis in explaining the effects of community functional structure on ecosystem

multifunctionality.

726 Fig. S9 The sensitivity of the relative importance of two mechanisms in explaining
 727 community functional structure and ecosystem multifunctionality relationship.
 728 Fig. S10 The number of functions a community supporting above a given threshold
 729 decreased with thresholds increasing, which was called “Jack-of-all-trades”.

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Figure legend

Fig. 1 Conceptual framework about how N addition and experimental warming affect ecosystem multifunctionality directly (arrow A), and/or mediated by community functional structure (arrow B and C). Arrow B shows plant traits act as response traits, and community functional structure (i.e. distribution of trait values; Mean, and Variability) respond to treatment. Arrow C showed plant traits act as effect traits, and the changes in community functional structure (i.e. CWM, and Rao) promote effects on multifunctionality via two mechanisms, dominance hypothesis and niche complementarity hypothesis. The variation of community functional structure (i.e. CWM and Rao) are due to the plus effects of interspecific difference and intraspecific difference.

Fig. 2 Ecosystem multifunctionality calculated by averaging approach (a) and multi-threshold approach (b). Different letters (a, b, and c) indicate significant differences in ecosystem multifunctionality under N addition (N: 0, 5, 10, and 15 g N m⁻² year⁻¹) and experimental warming (W) (Tukey's HSD test, at $p < 0.05$ level). **a** (Averaging approach): Warming ($F_{1,40}=12.039$, $P=0.001$), N addition ($F_{3,40}=4.713$, $P=0.007$), Warming:N addition ($F_{3,40}=0.756$, $P=0.526$). **b** (Multi-threshold approach): 20%: Warming ($F_{1,40}=3.173$, $P=0.083$), N addition ($F_{3,40}=3.822$, $P=0.017$), Warming:N addition ($F_{3,40}=1.074$, $P=0.371$); 40%: Warming ($F_{1,40}=8.308$, $P=0.006$), N addition ($F_{3,40}=5.487$, $P=0.003$), Warming:N addition ($F_{3,40}=1.145$, $P=0.343$); 60%: Warming ($F_{1,40}=8.825$, $P=0.005$), N addition ($F_{3,40}=5.216$, $P=0.004$), Warming:N addition

($F_{3,40}=2.493$, $P=0.074$); 80%: Warming ($F_{1,40}=9.403$, $P=0.004$), N addition

($F_{3,40}=3.558$, $P=0.023$), Warming:N addition ($F_{3,40}=0.949$, $P=0.426$).

Fig. 3 Parameter estimates (i.e. standardized regression coefficients) of different trait variabilities and treatments (N*Warming) in determining multifunctionality at four given thresholds (20%, 40%, 60%, 80%). Standardized regression coefficients at a given threshold were derived through a model averaging approach (*model.avg* function in MuMIn package) when considering models with changes in $\Delta AICc < 2$ during the model selection procedures (*dredge* function in MuMIn package), shown in Table S6.

Fig. 4 The sensitivity of the effects of 16 trait variability metrics on ecosystem multifunctionality to the number and identity of functions at four given thresholds.

Fig. 5 Relative importance of interspecific trait variability (CWM_{fixed} and Rao_{fixed}) and intraspecific trait variability (ITV and ITV_R) in determining ecosystem multifunctionality across multiple thresholds. Explained variance (%) was based on the percentage of the absolute value of standardized regression coefficients of a certain subset of trait variabilities accounted for the sum of absolute value of standardized regression coefficients of all 16 trait variabilities.

773 Fig. 6 The sensitivity of the relative importance of interspecific trait variability (Inter)
774 and intraspecific trait variability (Intra) in determining ecosystem multifunctionality,
775 i.e. the change of explained variance (%) by Inter or Intra with the number and
776 identity of functions we chosen from 15 ecosystem functions at four given thresholds.
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778 Fig. 1

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Fig. 2

Fig. 3

Fig. 4

790 Fig. 5

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Fig. 6