

Species Richness Interacts with Drought to Affect Litter Decomposition via its Effect on Litter Nitrogen Concentration

Jiang Wang (✉ wangjiang@tzc.edu.cn)

School of Life Science; Zhejiang Provincial Key Laboratory of Plant Evolutionary Ecology and Conservation, Taizhou University, Taizhou 318000, China <https://orcid.org/0000-0001-9269-0894>

Yuan Ge

State Key Laboratory of Urban and Regional Ecology, Research Center for Eco-Environmental Sciences, Chinese Academy of Sciences, Beijing 100038, China

J. Hans C. Cornelissen

System Ecology, Department of Ecological Science, Vrije Universiteit, 1081 HV Amsterdam, The Netherlands

Xiaoyan Wang

School of Life Science; Zhejiang Provincial Key Laboratory of Plant Evolutionary Ecology and Conservation, Taizhou University, Taizhou 318000, China

Song Gao

School of Life Science; Zhejiang Provincial Key Laboratory of Plant Evolutionary Ecology and Conservation, Taizhou University, Taizhou 318000, China

Yi Bai

School of Life Science; Zhejiang Provincial Key Laboratory of Plant Evolutionary Ecology and Conservation, Taizhou University, Taizhou 318000, China

Tong Chen

School of Life Science; Zhejiang Provincial Key Laboratory of Plant Evolutionary Ecology and Conservation, Taizhou University, Taizhou 318000, China

Zhongwang Jing

State Key Laboratory of Urban and Regional Ecology, Research Center for Eco-Environmental Sciences, Chinese Academy of Sciences, Beijing 100038, China

Chongbang Zhang

School of Life Science; Zhejiang Provincial Key Laboratory of Plant Evolutionary Ecology and Conservation, Taizhou University, Taizhou 318000, China

Wenli Liu

School of Life Science; Zhejiang Provincial Key Laboratory of Plant Evolutionary Ecology and Conservation, Taizhou University, Taizhou 318000, China

Junmin Li

School of Life Science; Zhejiang Provincial Key Laboratory of Plant Evolutionary Ecology and Conservation, Taizhou University, Taizhou 318000, China

Feihai Yu

Zhejiang Provincial Key Laboratory of Plant Evolutionary Ecology and Conservation, Taizhou University, Taizhou 318000, China; Institute of Wetland Ecology & Clone Ecology, Taizhou University, Taizhou 318000, China

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Species richness interacts with drought to affect litter decomposition via its effect on litter nitrogen concentration¹

Jiang Wang¹, Yuan Ge^{2#}, Johannes H.C. Cornelissen³, Xiao-Yan Wang¹, Song Gao¹, Yi Bai¹, Tong Chen¹,
Zhong-Wang Jing², Chong-Bang Zhang¹, Wen-Li Liu¹, Jun-Min Li¹, Fei-Hai Yu^{1,4*},

¹ School of Life Science; Zhejiang Provincial Key Laboratory of Plant Evolutionary Ecology and Conservation, Taizhou University, Taizhou 318000, China

² State Key Laboratory of Urban and Regional Ecology, Research Center for Eco-Environmental Sciences, Chinese Academy of Sciences, Beijing 100038, China

³ System Ecology, Department of Ecological Science, Vrije Universiteit, 1081 HV Amsterdam, The Netherlands

⁴ Institute of Wetland Ecology & Clone Ecology, Taizhou University, Taizhou 318000, China

[#] Co-first author

^{*} Corresponding author

E-mail address: feihaiyu@126.com (F.-H. Yu)

Short title: Richness-drought interactions on litter decay

¹ JW, YG and FHY designed the experiment; JW, YG, SG, BY, XYW, TC, CBZ, WLL and JML performed the experiment; YB collected data of fauna; JW, YG, FHY and ZWJ conducted data analysis; JW drafted the manuscript; FHY and JHCC contributed substantially to revision.

Abstract

Biodiversity loss, exotic plant invasions and climatic change are currently the three major challenges to our globe and can each affect various ecological processes, including litter composition. To gain a better understanding of global change impacts on ecological processes, these three global change components need to be considered simultaneously. Here we assembled experimental plant communities with species richness levels (1, 2, 4, 8 or 16) and subjected them to drought (no, moderate or intensive drought) and invasion (invasion by the exotic annual plant *Symphyotrichum subulatum* or not). We collected litter of the native plant communities and let it decompose for nine months within the communities. Drought decreased litter decomposition, while the exotic plant invasion had no impact. Increasing species richness decreased litter decomposition under the mesic condition (no drought), but had little impact under moderate and intensive drought. A structural equation model showed that drought and species richness affected litter decomposition mainly via influencing litter nitrogen concentration, but not via altering the quantity and diversity of soil meso-fauna or soil physio-chemical properties. The negative impact of species diversity on litter decomposition under the mesic condition was mainly ascribed to a sampling effect, i.e. via particularly low litter nitrogen concentrations in the two dominant species. Our results indicate that species richness can interact with drought to affect litter decomposition via effect on litter nitrogen. We conclude that nitrogen-dependent litter decomposition should be a mechanism to predict integrated effects of plant diversity loss, exotic plant invasions and climatic change on litter decomposition.

Keywords: Invasion, exotic plant, global change, litter traits, dominant species

Introduction

Climatic change, biodiversity loss and biological invasions are currently the three major challenges to the health of our globe (Venezia et al. 2018; Chan et al. 2019), and can each have tremendous impacts on various ecological processes (Palmer et al. 2017; Haim et al. 2018). A large body of literature has evaluated the ecological impacts of each of these three global change factors (Clark et al. 2016; Haeuser et al. 2017; Korell et al. 2020). However, to gain a better understanding of global change impacts on ecological processes, these three global change components need to be considered simultaneously, accounting for their possible interactions (Flombaum et al. 2016; Pires et al. 2018; Rillig et al. 2019).

Litter decomposition is a fundamental process of nutrient and carbon cycling and influences soil fertility, species composition, carbon storage and plant productivity (Parker et al. 2018; McBride et al. 2020; Yang et al. 2020). The impacts of native plant diversity loss and exotic plant invasions on aboveground–belowground interactions and feedbacks, especially for litter decomposition, have received great concern (Helsen et al. 2018; Lin and Zeng 2018; Bueno de Mesquita et al. 2019). When a native or an exotic plant has particular traits deviating from that of the community studied, the loss of this native plant or the invasion of this exotic plant is likely to change the chemical composition of community-level litter and thus affect the decomposition process (Finerty et al. 2016; Mutshekwa et al. 2020). In nature, the invasion of exotic plants and the loss of native plants commonly occur simultaneously, but how they interact to affect litter decomposition has not been reported.

Many studies have examined effects of either plant species diversity (Hector et al. 2000; Barantal et al. 2011; Joly et al. 2017) or exotic plant invasions (Prescott and Zukswert 2015; Broadbent et al. 2017) on litter decomposition. Unlike the predominantly positive effects of plant species diversity on primary productivity (Loreau et al. 2001; Liang et al. 2016), it is difficult to predict effects of plant species diversity

on litter decomposition (Liu et al. 2020), even though a strong positive overall effect has been shown for forest and wetland ecosystems recently (Mori et al. 2020). Higher plant diversity can promote (Barantal et al. 2011; Huang et al. 2017), have no effect on (Hector et al. 2000; Lin and Zeng 2018; Porre et al. 2020) and even restrain (Seidelmann et al. 2016) litter decomposition. Similarly, plant invasions can also have different impacts on litter decomposition, and positive, neutral and negative effects have all been reported (Ehrenfeld 2003; Godoy et al. 2010; Broadbent et al. 2017). In addition, different stages of plant invasions (e.g. early vs. late stages) may impose different impacts on litter decomposition (Zeng et al. 2020). While plant species diversity and exotic plant invasions may affect litter decomposition via influencing various biotic and abiotic factors, especially soil physio-chemical properties and decomposer quantity and diversity, their effects on litter traits may be more critical in litter decomposition (Finerty et al. 2016; Setiawan et al. 2016; Helsen et al. 2018; Lin and Zeng 2018; López-Rojo et al. 2020), as some litter traits such as litter nitrogen (N) concentration are generally correlated with litter decomposition rate across species (Aerts et al. 2012; Szefer et al. 2017; Guillaume et al. 2020; Hong et al. 2020; Pichon et al. 2020).

Climate change is projected to result in more intensive drought in some regions in the world (Peltier and Ogle 2019; da Silva et al. 2020). Drought can not only affect litter traits such as litter N concentration (Sanaullah et al. 2012; Xie et al. 2020), but also influence soil physio-chemical properties (e.g. soil moisture, temperature and pH) and diversity, quantity and activities of decomposers (e.g. meso- and micro-fauna; Duarte et al. 2017; Kheir et al. 2019), all of which can result in altered litter decomposition (Allison et al. 2013; Santonja et al. 2015). Exotic plant invasions occur more frequently in regions where precipitation is high and thus species diversity is high (i.e. subtropics and tropics; Pysek et al. 2017; Panda and Behera 2018; Camarero 2019), but less frequently in regions where drought is intensive and thus species diversity is low (i.e. arid and semi-arid areas; Pysek et al. 2017; Tripathi et al. 2019). Such

phenomena suggest that drought, species diversity and exotic plant invasions may interact to affect various ecological processes, including litter decomposition. These suggested interactions in turn lead to the hypothesis that the effects of species diversity and exotic plant invasions on litter decomposition would be moderated by an increased intensity of drought.

To test this hypothesis, we constructed experimental native plant communities with different species richness and subjected them to no, moderate or intensive drought and to the invasion by the exotic annual plant *Symphyotrichum subulatum* or not. We collected litter of the native plant communities and let it decompose for nine months. Previous studies have tested the effect of the middle or later stage of exotic plant invasions on litter decomposition, and these studies have generally shown that mixing with high-quality litter from invasive plants can accelerate litter decomposition of the whole community (Castro-Díez et al. 2019; Bush et al. 2020). However, little litter is produced at the early stage of exotic plant invasions, and how litter decomposition is influenced by exotic plant invasions at this stage is still unclear. Therefore, we placed the collected litter within the communities during the early stage of the invasion by *S. subulatum*. We measured litter decomposition rate and various biotic and abiotic factors, including litter N and P concentrations, quantity and diversity of soil meso-fauna and soil moisture, temperature and pH. Specifically, we addressed the following questions: (1) Do native species richness, exotic plant invasions and drought have interactive effects on litter decomposition? (2) What are the main drivers underlying these (interactive) effects on litter decomposition?

Materials and methods

Community assembly and richness levels

In Mar-2013, the experimental plant communities were constructed in plastic containers (72 cm long × 64 cm wide × 42 cm deep) with five draining holes at the bottom. Each container was first filled with a 27 cm

layer of a soil (total N: $0.763 \pm 0.104 \text{ g kg}^{-1}$, total P: $0.216 \pm 0.047 \text{ g kg}^{-1}$, mean $\pm$ SE, $n = 10$) and then a 10 cm layer of a mixture of the soil and a nutrient-rich potting compost (Table S1) at a volume ratio of 1:1 (total N: $4.612 \pm 0.456 \text{ g kg}^{-1}$, total P: $0.802 \pm 0.189 \text{ g kg}^{-1}$, mean $\pm$ SE, $n = 10$). The soil was collected in a mountain area near Taizhou city in Zhejiang province, China, and it was classified as the fine loamy mixed semiativie mosaic humic hapludults soil (Chinese Soil Taxonomy Cooperative Research Group 1995). The potting compost was brought from Shanghai Kuheng Company, China. The soil-compost mixture layer was added to facilitate seed germination and seedling establishment.

The species pool used in this experiment consisted of 16 native herbaceous species that commonly occur in local plant communities around Taizhou city (Table S2). For species richness treatments, we selected 46 communities consisting of one, two, four, eight and 16 species, including all 16 monocultures for each species, 10 two-species mixtures, 10 four-species mixtures, 9 eight-species mixtures and the only 16-species mixture (Table S3). Each of the two-, four- or eight-species mixtures had a different species composition (Table S3). In the two, four- and eight-species mixtures, the species were randomly chosen from the species pool and no mixtures had exactly the same species composition.

All the 45 communities of the one-, two-, four- and eight-species mixture were replicated six times, and the community of the 16-species mixture was replicated 30 times, resulting in a total of 300 communities (containers; Fig. S1). The six replicates of the 45 communities of the one-, two-, four- and eight-species mixture were randomly assigned to the six combinations of three drought intensity treatments (no, moderate and intensive drought) and two invasion treatments (with or without an exotic plant invasion; as described in the next two sections); the 30 replicates of the 16-species mixture were also randomly assigned to the six treatment combinations of drought and invasion, with five replicates each (Fig. S1).

In Dec-2013, we sowed a total of 800 seeds in each container and determined seed number of a

species in a container by dividing 800 by species number. One month after germination, 32 vigorous seedlings were retained and excess seedlings were removed. Thus, at the start of the experiment, plant density was maintained at 32 seedlings per container, and each species was represented by the same number of seedlings (e.g. for four-species mixtures, there were eight seedlings for each of the four species in a container). The 32 seedlings were spatially evenly distributed in the container, and seedlings of the same species were not adjacent. In each container, we also removed undesired seedlings, i.e. those not belonging to the originally sown species. All the containers were randomly placed inside a plastic rain shelter in Taizhou University, Zhejiang Province, China, which was open at the bottom sides to allow air to be ventilated.

Drought manipulation

Using automatic drip irrigation systems, we set up three drought intensity treatments (no, moderate and intensive drought) via the control of the irrigated time. To account for seasonal variation of trans-evaporation, 20 containers with different species compositions in each of the six treatment combinations of drought and invasion were randomly selected every other week and their volumetric soil water content was measured with a ProCheck analyzer (Decagon, Pullman, Washington, USA). Data collected using this ProCheck analyzer were adjusted based on the traditional way of measuring gravimetric soil water content (Fig. S2). The irrigated time was adjusted based on the data of these measurements. For the treatment of no drought, the irrigated time was set to 20-35 minutes, and gravimetric soil water content (15.5–19.8%) was maintained similar to that of plant communities of the mountain areas (Wugui mountain, E121.383°, N28.652°; Baiyun mountain, E121.419°, N28.667°; Beigu mountain, E121.112°, N28.856°) around Taizhou city, Zhejiang Province, China. For the treatments of moderate and intensive drought, the irrigated time was 50% (gravimetric soil water content ranging from 12.4-15.4%)

and 25% (gravimetric soil water content ranging from 10.0-12.6%) of that in the no drought treatment, respectively. Depending on the weather conditions, plant communities in the containers were irrigated once a day between May and September, once every other day between March and April and between October and December, and once every week between January and February.

The six replicates of the 50 communities of different richness levels were randomly assigned to one of the three drought treatments, so that each drought treatment had two replicates. The drought treatments started on 12-Mar-2015.

Invasive species and invasion introduction

Symphyotrichum subulatum (Michx.) G. L. Nesom is an annual herb of Asteraceae. It is native to South America, but now widespread in warm regions of the world (Zhuge et al. 2011). In China, *S. subulatum* is listed as an invasive exotic plant species as it has invaded many areas (Zhuge et al. 2011). This species often forms a mono-dominant community and displaces native plant species. It grows 16-150 cm tall with erect stems. It reproduces sexually and each plant can produce profuse viable seeds. Seeds are dispersed by wind. In Dec-2015, for half (150) of the experimental communities, 50 seeds of *S. subulatum* were evenly sown in each container. For the other half, no seeds of *S. subulatum* were sown.

Litter decomposition experiment

In Nov-2015, about one month before the invasion treatment was started and when most leaves shed, we collected freshly produced litter (mainly leaves) of each community (in each container). Then we thoroughly mixed the litter collected from the two communities with exactly the same species composition and subjected to the same drought treatment, i.e. one was later used for the invasion treatment and the other for the corresponding control treatment (no invasion). The mixed litter (about 40 g) was treated as one litter sample. The litter samples were cleaned and dried at *ca.* 40°C in the oven. The litter samples were not

170 air-dried to avoid pretreatment decomposition as the air at this time was quite humid.

171 For each litter sample, a subsample of 3 g was ground and used for analyzing initial concentration of
172 total nitrogen (Autoanalyzer 3, BRAN+LUEBBE, Germany, measured with three replicates). Ten
173 subsamples, each about 2 g (range: 1.997–2.003 g), of each litter sample were placed in ten plastic
174 litterbags (6 cm × 8 cm) with a mesh size of 2 mm, which permits entry of both microfauna and mesofauna
175 (Smith and Bradford 2003). Larger leaf litter was cut into pieces of 2 cm × 2 cm before being placed into
176 the litterbags.

177 In Dec-2015, we placed the ten litterbags of each litter sample into the litter layers of the two
178 communities where it had been collected, with five litterbags in the community invaded by the exotic
179 species (*A. subulatus*) and the other five in the corresponding community not invaded by the exotic species.
180 Caution was taken not to cause excessive disturbance during litterbag placement.

181 Three litterbags in each community were collected three, six and nine months after the litterbags had
182 been placed into the communities. After cleaning, the litter from each litterbag was dried in the oven at
183 60°C for three days and weighed. Then, the litter was ground into powder and used to measure the
184 concentration of nitrogen (Autoanalyzer 3, BRAN+LUEBBE, Germany).

185 On 18-Jun-2016, two litterbags from each community (container) were collected. One litterbag was
186 used for quantifying mesofauna directly or indirectly involved in decomposition. Mesofauna are highly
187 active in June and thus measurement at this stage can well catch decomposer composition. Each litterbag
188 collected was put into a plastic bag to avoid residue loss and then transported to the laboratory for
189 measurement of mesofauna. The litter remaining in the litterbag was processed in Berlese funnels during 10
190 days to extract mesofauna. The organisms obtained were stored in 70% alcohol and identified to family
191 level (with double-tube anatomical lens); they mainly belonged to Acari and Collembola, which are

involved in decomposition directly or by consuming the microbial decomposers growing on the litter. Species richness and number of mesofauna individuals in each litterbag were recorded. The other litterbag was used for analyzing microbial activity. Due to logistics reasons, the litter of only the lowest (monoculture) and the highest (16-species mixture) richness levels were analyzed.

Plant community harvest and measurements

We harvested the communities in all containers in Oct-2016. In each container, aboveground parts of living plants were sorted to species, dried to constant mass at 80°C and weighed. Additional soil volumetric water content and temperature were measured four times on 4-May, 16-Jun, 14-Jul and 24-Aug-2016, respectively, and the average value of the four times of measurements was used for data analysis.

Statistical analysis

The monocultures of *Medicago sativa* did not have any living plants, resulting in a final sample of 49 communities for each of six treatment combinations of drought and invasion. For each community, we calculated the coefficient of litter decomposition rate (k , unit: month⁻¹) by fitting data of litter mass and the time of litter decomposition to the equation where litter mass at day 0 and t , respectively (Olson 1963). Each k value was based on litter mass of the four sampling times (0, 3, 6 and 9 months).

We used ANOVA to assess the effects of species richness, drought, invasion and their interactions on k . In this model, species richness, drought and invasion were treated as fixed factors and species composition was included as a random factor nested within species richness. We also used linear regressions to explore the relationships of k with species richness in each of the six treatment combinations of drought and invasion.

We employed linear regressions to explore the relationships between k and litter initial N concentration in each of the six treatment combinations of drought and invasion. We also used linear

regressions to examine the relationships between litter initial N concentration and species richness in each of the three drought treatments (invasion and un-invasion treatments were not considered separately as the litter was a mixture from the invaded and uninvaded plot of the same species composition so that the initial litter composition of these two plots were the same).

A functional diversity index was also calculated following the method of Rao (1982) using the Euclidean distance based on litter N and P and abundance (aboveground biomass) of each species. However, there were no significant relationships between the functional diversity index and litter decomposition (Fig. S3).

We built a structural equation model in AMOS (SPSS 2006), hypothesizing the relationships among direct effects of treatments (drought, species richness and invasion) and indirect effects of treatments through influencing biotic and abiotic factors (number of mesofauna individuals, number of mesofauna species, soil microbial activity, litter N, aboveground biomass of plant communities, soil temperature and soil pH) in order to partition the variance among possible causal influences (Table S4). Drought, species richness and invasion were modeled as treatment variables, and number of mesofauna individuals, number of mesofauna species, soil microbial activity, litter N, community aboveground biomass, soil temperature and soil pH were modeled as response variables whose effects on k were mediated by these treatments. Because data on soil microbial activity was only available for the monocultures and the 16-species mixtures (total $n = 120$) and random numbers that have the same mean and standard deviation of the measured microbial activity data were used for other mixtures. The direct, indirect and total effects of each treatment and response variable on all downstream variables can be calculated by path coefficients, which are mathematically equivalent to partial correlation coefficients (Grace 2006). The maximum likelihood χ^2 , goodness-of-fit test (GFI) and root mean square error of approximation (RMSEA; Steiger 1990) were used

to evaluate the model fit (Grace and Pugsek 1998). A high P -value indicates a better model fit.

As in the treatments with no drought we found a significant effect of species richness on litter decomposition (see Results), we further explored the traits of dominant species to assess whether the sampling effect of species diversity played a role. Under no drought, *Patrinia scabiosaefolia* and *Artemisia migoana* were the dominant species, contributing to over 90.04% (uninvaded) and 90.53% (invaded) aboveground biomass of the communities in the plots with one or both of them. To analyze how dominant species might affect litter decomposition via influencing litter N concentration, we used t-tests to compare litter N concentration and litter decomposition in plots in the presence vs. in the absence of *P. scabiosaefolia* and/or *A. migoana* under no, moderate and intensive drought.

Results

Effects of drought, invasion and species richness on litter decomposition

Drought significantly affected litter decomposition rate (k ; Table 1). Average across species richness and invasion treatments, k decreased from 0.148 with no drought, via 0.103 under moderate drought, to 0.080 under intensive drought (Fig. 1). There was a significant interaction of drought $\times$ species richness on k (Table 1): species richness showed a negative relationship with k under no-drought treatment, but not under moderate or intensive drought treatments (Fig. 1). Invasion had no significant effect on k (Table 1). There were no further two-way or three-way interactions on k .

Relationships of litter nitrogen with litter decomposition and species richness

Litter N concentration had a significant positive relationship with k value in all the six treatment combinations of drought and invasion ($r = 0.308 - 0.683$, all $P < 0.05$, $n = 49$; Fig. 2). Also, litter N concentration was significantly negatively related to species richness under no drought ($r = -0.411$, $n = 49$, $P = 0.003$; Fig. 2), but had no significant relationship with species richness under moderate or intensive

drought (Fig. 2).

Direct and indirect effects on litter decomposition

The structural equation model fitted the data well (GFI, $P = 0.986$; Maximum likelihood $\chi^2 = 22.664$, $P = 0.161$; RMSEA = 0.034, $P = 0.759$; Fig. 3, Table S4). The parameters included in the model explained 41.1% of the variation in litter decomposition (Fig. 3).

The strongest predictors of k were drought (negative) and litter nitrogen (positive; Fig. 3). Drought could directly affect k and could also indirectly affect k via its direct effect on litter N concentration and soil microbial activity (Fig. 3). While drought could also directly affect community aboveground biomass, number of mesofauna individuals, number of mesofauna species, soil temperature and pH, it could not indirectly affect k via influencing these biotic and abiotic factors (Fig. 3).

Species richness could not directly affect k , but could indirectly affect k via altering litter N concentration (Fig. 3). Species richness could directly positively affect community aboveground biomass and number of mesofauna species, but could not indirectly affect k via influencing these two factors (Fig. 3). Invasion had neither direct nor indirect effect on litter decomposition, although it could directly affect number of mesofauna species (Fig. 3).

Effects of dominant species on litter nitrogen

The presence of *P. scabiosaefolia* and/or *A. migoana* significantly decreased litter N concentration of the whole communities under no drought (Fig. 4) and led to lower litter decomposition rate (Fig. 5A, D). As these two species occurred more often in more diverse communities, litter decomposition rate of these more diverse communities had lower values and lower variance (Fig. 5A, D), suggesting a significant sampling effect. The less diverse communities had a very large variance in k , where all the high k values corresponded with high litter N concentration and the absence of the two dominants. However, the

decreased effect of the presence of *P. scabiosaefolia* and/or *A. migoana* on litter N concentration gradually disappeared from moderate to intensive drought (Fig. 4). Accordingly, the presence of *P. scabiosaefolia* and/or *A. migoana* had no effect (Fig. 5B, E, F) and even increased the litter decomposition rate somewhat (Fig. 5C), which led to the negative relationship between species richness and litter decomposition rate disappearing under moderate and intensive drought.

Discussion

We tested the effects of three major global change factors (plant species diversity, exotic plant invasion and drought) on litter decomposition of native plant communities. Our results revealed that plant species richness interacted with drought to affect litter decomposition via influencing litter N concentration, and that drought could decrease litter decomposition also via its impact on litter quality (particularly litter N) and soil microbial activity. However, we found no effect of exotic plant invasion on litter decomposition.

Effects of plant richness on litter decomposition

The effect of plant species diversity on litter decomposition is difficult to predict and the results are also inconsistent among studies (Hector et al. 2000; Barantal et al. 2011; Seidelmann et al. 2016; Huang et al. 2017; Lin and Zeng 2018; Liu et al. 2020). We found that under the mesic condition (no drought) increasing species richness decreased the decomposition rate of litter of native plant communities, but such a diversity effect disappeared under moderate or intensive drought (Fig. 1). The diversity effect on litter decomposition corresponded well to the diversity effect on litter initial N concentration (Fig. 2), and also litter decomposition rate was significantly positively correlated with litter initial N concentration (Fig. 2). These results suggest that under mesic conditions species diversity affected litter decomposition mainly via its effect on litter N concentration. Under moderate or intensive drought conditions, species richness had no impact on litter N concentration and thus failed to affect litter decomposition.

The mass-ratio hypothesis predicts that the most abundant species determines litter quality and controls litter decomposition (Grime 1998; Koukoura et al. 2003; Bílá et al. 2014; Tardif et al. 2014; López-Rojo et al. 2020). Our results showed that the diversity effect on litter decomposition under the mesic condition was due to the two dominant plant species (*P. scabiosaefolia* and/or *A. migoana*), supporting the mass-ratio hypothesis (Grime 1998) and, between the two main reported mechanisms of the species diversity effect, pointing strongly to a sampling effect as opposed to a complementarity effect (Huston et al. 1997). As the two dominant species had very low litter N concentration, communities that had one or both of these two dominant species (more in the more diverse communities) had on average low values of litter N concentration. Such a sampling effect on litter N concentration resulted in litter of species-richer communities decomposing more slowly under the mesic condition. Consistent with our results, Lin and Zeng (2018) found that functional identity related to dominant species rather than functional diversity or species richness determined litter mixture decomposition. Also, Ball et al. (2008) found that the presence or absence of dominant species exerted a great impact effect on litter mixture decomposition. Moreover, the effect of dominant species on litter mixture decomposition was previously found to vary with abiotic environments (Dickson and Wilsey 2009; Tardif et al. 2014). Similarly, we found that the effect of the two dominant species on litter N concentration varied with the drought gradient. Therefore, the sampling effect plays an important role in the effect of plant species richness on litter decomposition, and this role is dependent on the environment.

We collected mixed litter from native plant communities and put them back in the communities where it had been collected. Thus, our diversity effect on litter decomposition was a combined effect of the diversity of litters from communities with different species diversity and the diversity of habitats created by communities of different species diversity. Many previous studies used litter mixtures to

examine the effect of plant diversity on litter decomposition (Gartner and Cardon 2004; Lecerf et al. 2007; Swan et al. 2009; Dimitrakopoulos 2010; Duan et al. 2013; Setiawan et al. 2016; Lin and Zeng 2018). In most of these experiments, total litter biomass was held constant and litter mixtures were made up of equal biomass of the component species (Gartner and Cardon 2004; Lecerf et al. 2007; Duan et al. 2013; Setiawan et al. 2016; Lin and Zeng 2018), and only a few studies controlled the evenness of litter (Swan et al. 2009; Dimitrakopoulos 2010). However, not only quality but also quantity of litter from different species could play a role in litter decomposition (Chapman et al. 1988). In our study, litter collected in each community better reflected the effect of plant diversity (richness, evenness and composition) on litter quality and quantity. Apart from the direct effect on litter quality and quantity, plant diversity can also affect the decomposition process indirectly via changes in microenvironments and soil biota (Hector 2000; Wardle 2002). Litter was put back to each of its own community could thus better reflect the effect of plant diversity on litter decomposition via modifying microenvironments. In our study, species richness was also found to promote soil fauna diversity (Fig. 3), but it influenced litter decomposition mainly via influencing litter nitrogen rather than modifying microenvironments (promoting soil fauna diversity). However, it is not inconceivable that, as for the litter quality effects reported above, a relatively small number of detritivorous species could have a disproportionately large effect of decomposition. Such effects may not be captured by mesofauna richness or abundance *per se*.

Effects of drought on litter decomposition

Drought can affect litter decomposition in multiple ways (Allison et al. 2013; Santonja et al. 2015). For instance, drought can decrease litter decomposition via decreasing litter quality (Sanaullah et al. 2012; Xie et al. 2020), reducing quantity, diversity and activities of decomposers (Kheir et al. 2019; da Silva

et al. 2020) and altering soil physio-chemical properties (Duarte et al. 2017). We found that drought directly decreased litter decomposition (Fig. 3, Table S4b), which may be related to the low soil moisture and associated lower microbial activity in the drought treatment (Zhang and Zak 1995; Walse et al. 1998).

Apart from the direct effect, drought also indirectly affected litter decomposition of native plant communities mainly via its impact on litter N concentration and soil microbial activity (Fig. 3). Thus, the drought-mediated changes in litter quality and soil microbial activity are also two of the mechanisms underlying the drought effect on litter decomposition. We also found that drought significantly decreased quantity and diversity of soil mesofauna. However, different from our expectation (Table S4a), such impacts failed to translate to affect litter decomposition. Several factors may explain why diversity of mesofauna (involved in decomposition) *per se* may not be the best predictor of litter decomposition. These factors include (1) complex trophic interactions and high functional redundancy in decomposer food webs (Mikola et al. 2001, Wardle 2002), (2) some taxa having a disproportionately large effect (see above) or (3) an indirect effect via feeding on the decomposing microbes (see above), and (4) changes in the decomposing microbial community (fungi, bacteria) having effects that outweigh those of mesofauna. In future studies other parameters representing the detritivorous fauna and the microbial community should be explored to get a better handle on indirect effect of drought via soil decomposers on litter decomposition.

Effects of exotic plant invasions on litter decomposition

Different from our expectation (Table S4a), we observed no effect of invasion by the exotic annual forb *S. subulatum* on litter decomposition of native plant communities. In this study, we mimicked the initial stage (i.e. first year) of exotic plant invasion, aiming to test its effect on litter decomposition. Thus, litter that we

used was only from native plant species, but not from invasive species which usually contains a high concentration of nitrogen and thus can accelerate litter decomposition of the whole community (Wolkovich et al. 2010; Castro-Díez et al. 2014).

Impacts of invaders on litter decomposition are usually determined by their litter trait difference from native species and/or its abundance (Finerty et al. 2016; Mutshekwa et al. 2020). In our study, during the litter decomposition experiment, the invader (*S. subulatum*) had not much litter input (deciduous leaves) to the litter of plant communities. Also, at the end of the litter decomposition experiment, the invasion of *S. subulatum* did not significantly affect the nitrogen concentration of litter out of litterbags compared to the uninvaded treatment (Fig. S4). We thus speculate that the lack of effect of *S. subulatum* invasion on litter decomposition may be because there was little litter input from the invader or because there was little difference in litter nitrogen between the invader and native plants in this experiment. Moreover, in theory, there could also have been an indirect effect of invaders changing the microclimate, e.g. via enhanced shading and associated soil moisture. However, in our experiment the invader did evidently not produce enough foliage to have such effects via the abiotic regime. Thus, in the very early stage of exotic plant invasion, community litter decomposition may not be affected by plant invasion and play little role in the invasion success of exotic plants.

Conclusions

No matter to which combination of drought intensity and invasion treatments our experimental plant communities were exposed, nitrogen-dependent litter decomposition was always found in plant communities irrespective of species richness. The effect of plant richness on litter decomposition changed with drought intensity, which could be ascribed to a change in the sampling effect on litter nitrogen in response to the increase in drought intensity. While nitrogen was the main limiting element in our system,

and in most ecosystems in the world, we need to be aware that phosphorous is the main limiting element in several other ecosystems such as some wetlands (Saaltink et al. 2016; Saaltink et al. 2017) and drylands (Lambers et al. 2020). In such systems the dependence of litter decomposition on phosphorus should be put central studies of this kind. Together, our findings indicate that, in the face of global climate change, human-induced declines in biodiversity and invasions of exotic species, nitrogen-dependent (or phosphorus-dependent) litter decomposition may provide an integrated method to look for how these global change drivers influence litter decomposition of communities.

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Declarations

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Code availability (Not applicable)

Authors' contributions

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644 **Table 1** Results of ANOVA for the effects of species richness, drought, invasion and their interactions on
645 litter decomposition rate (k)

Effect ^a	df	F	<i>p</i>
Richness (R)	4, 44	1.83	0.141
Drought (D)	2, 220	41.22	<0.001
Invasion (I)	1, 220	0.17	0.682
R × D	8, 220	6.38	<0.001
R × I	4, 220	0.94	0.439
D × I	2, 220	0.09	0.912
R × D × I	8, 220	0.10	0.999

646 ^aSpecies composition was included as a random factor nested within species richness.

Figure legends

Figure 1 Relationships between litter decomposition rate (k) and species richness in plots unininvaded or invaded by the exotic species *Symphyotrichum subulatum* under (A and D) no, (B and E) moderate or (C and F) intensive drought. Filled circles and error bars are mean and SE. $n = 49$ for all regressions.

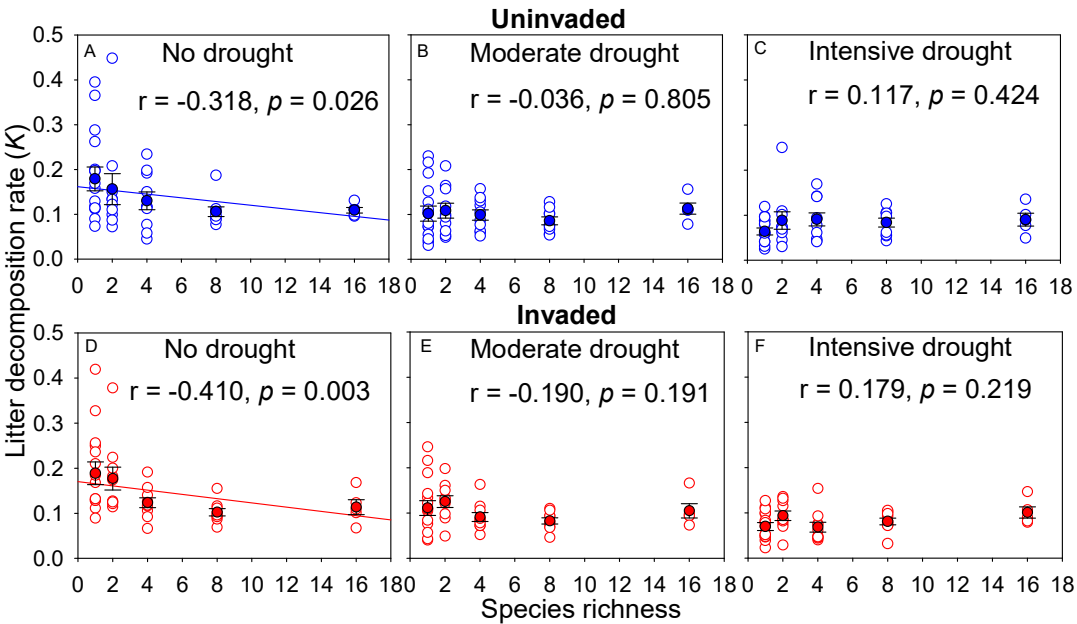
Figure 2 Relationships of litter nitrogen concentration with litter decomposition rate (k) in plots unininvaded or invaded by the exotic species *Symphyotrichum subulatum* under (A, D) no, (B, E) moderate or (C, F) intensive drought. $n = 49$ for all regressions. The gradient of blue color and size of scatter points denotes species richness levels.

Figure 3 A structural equation model (SEM) showing the causal effects of treatments (green rectangles) and biotic and abiotic factors mediated by treatments (yellow hexagon) on litter decomposition rate (k ; blue rectangles). Thickness of solid lines indicates the strength of the causal influence. Numbers on solid lines indicate path coefficients, a measure of the strength of causal relationships that are mathematically equivalent to either partial regression coefficients or correlation coefficients. Nonsignificant pathways are represented with gray dotted lines. R^2 values represent the proportion of variance explained for each variable.

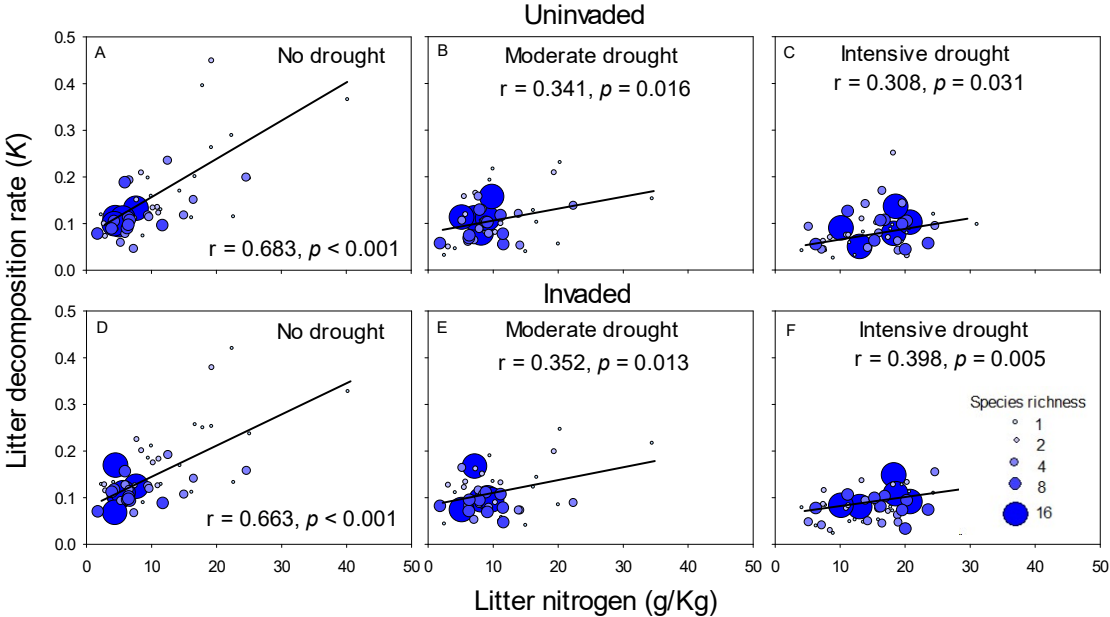
Figure 4 Litter nitrogen concentration in plots in the presence or absence of the dominant species (*Patrinia scabiosaefolia* and/or *Artemisia migoana*) under no, moderate and intensive drought. Results of t-tests and the significance levels (** $P < 0.01$; ^{ns} $P > 0.05$) are also given.

Figure 5 Litter decomposition rate (k) in plots unininvaded or invaded by the exotic species *Symphyotrichum subulatum* under (A, D) no, (B, E) moderate or (C, F) intensive drought. Red, blue, purple and white rectangles respectively denote the plots with *P. scabiosaefolia*, *A. migoana*, both *P. scabiosaefolia* and *A. migoana*, and neither *P. scabiosaefolia* nor *A. migoana*, respectively. The size gradient of scatter points denotes litter nitrogen level. Results of t-tests and the significance levels (** $P < 0.01$; ^{ns} $P > 0.05$) are also given.

673 **Figure 1**

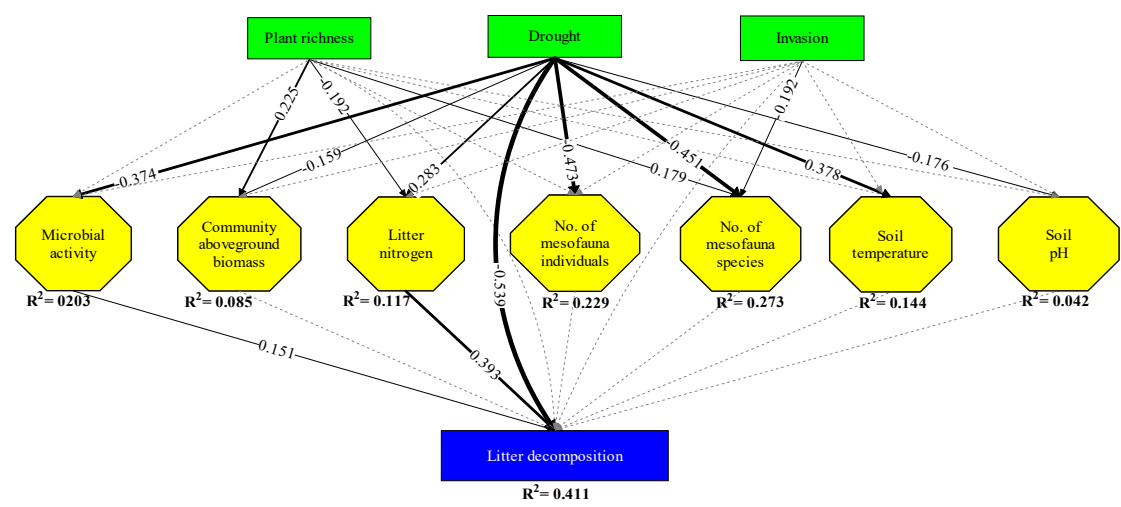


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679 **Figure 3**

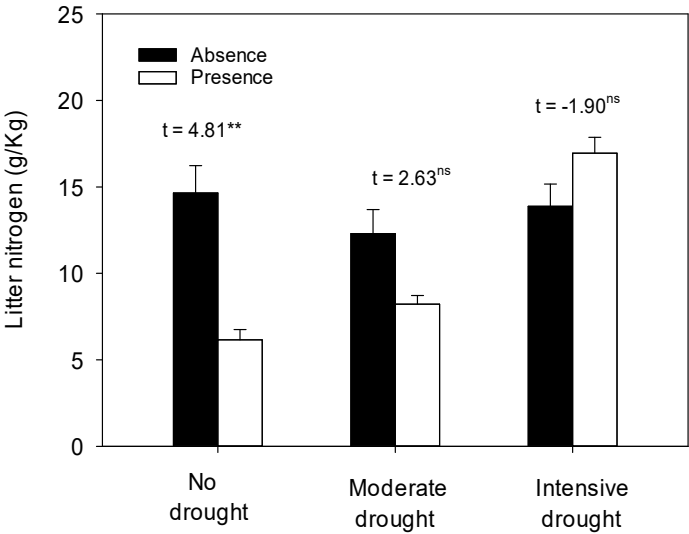


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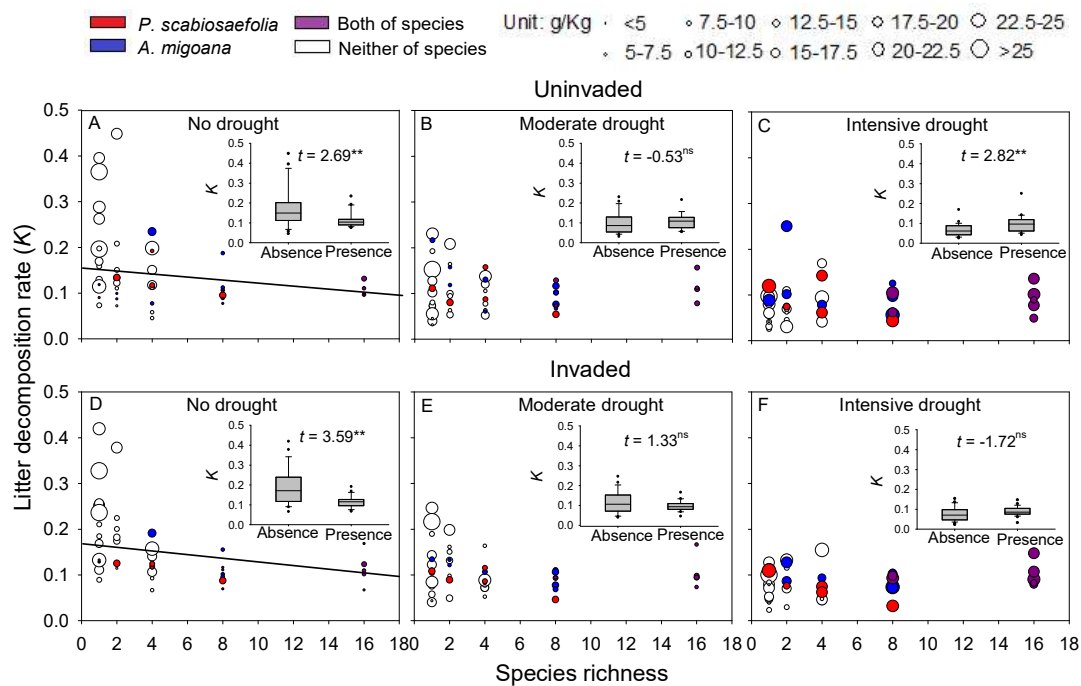
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683 **Figure 4**



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Figures

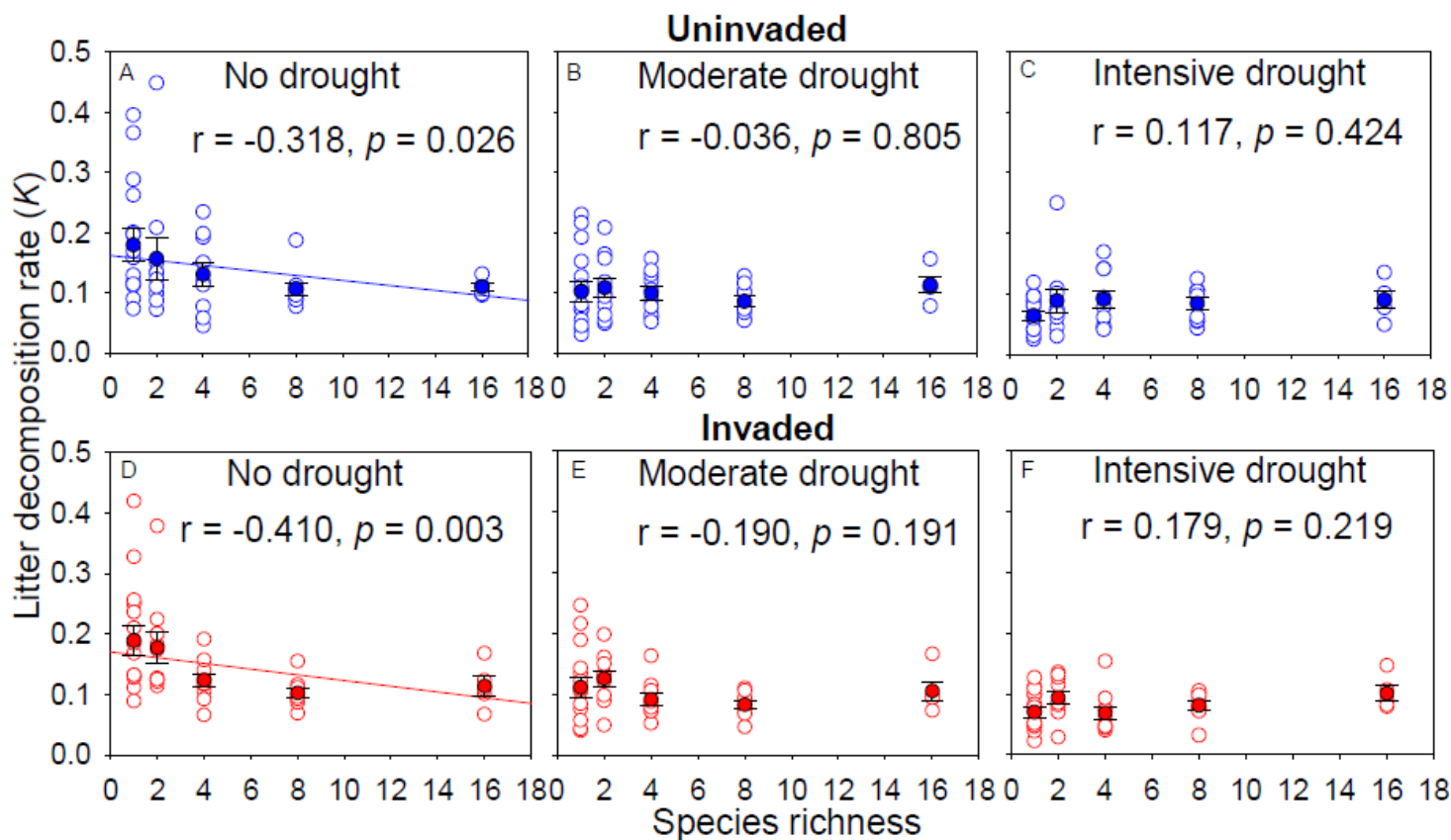


Figure 1

Relationships between litter decomposition rate (k) and species richness in plots uninvaded or invaded by the exotic species *Symphyotrichum subulatum* under (A and D) no, (B and E) moderate or (C and F) intensive drought. Filled circles and error bars are mean and SE. $n = 49$ for all regressions.

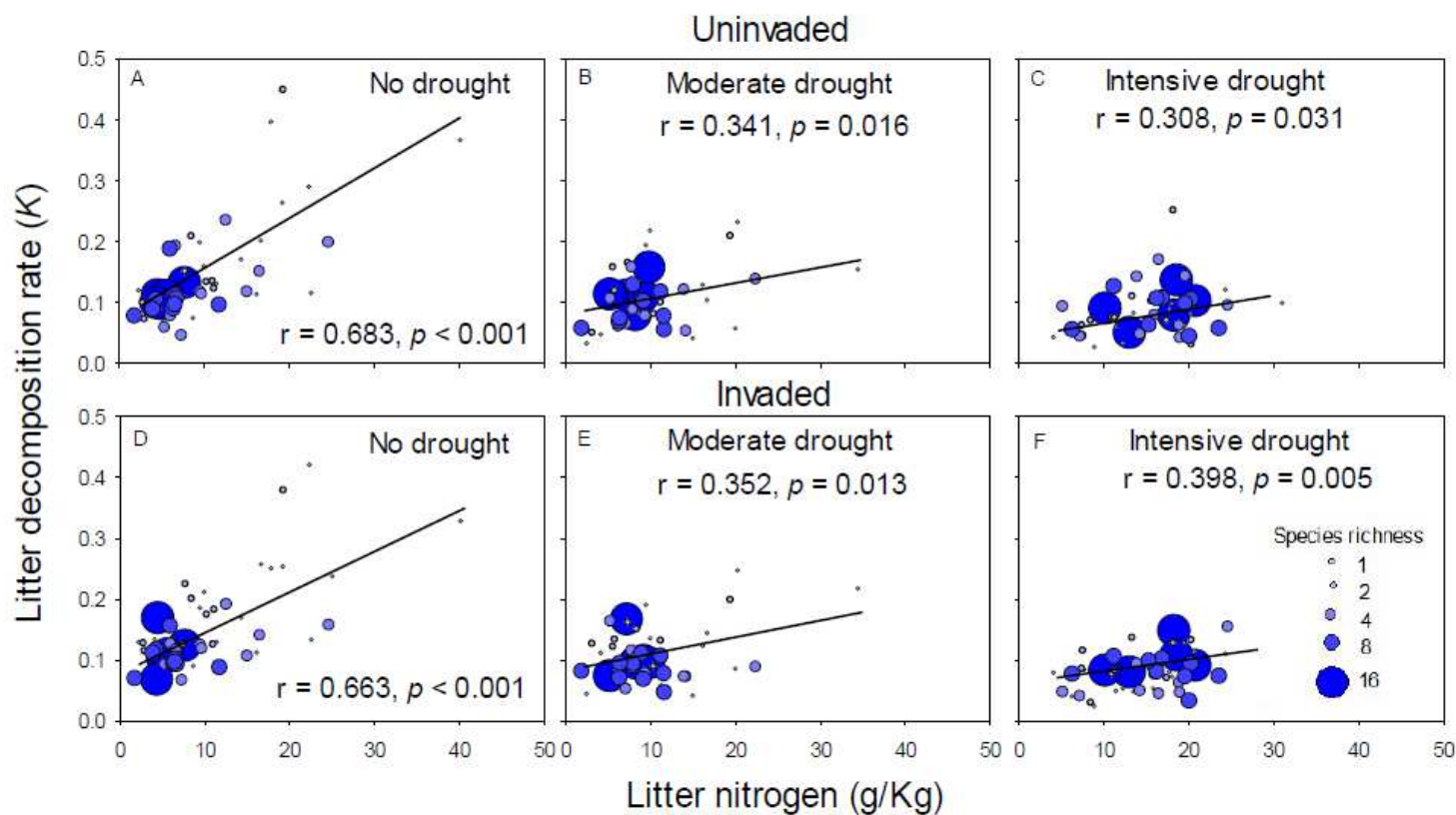


Figure 2

Relationships of litter nitrogen concentration with litter decomposition rate (k) in plots uninvaded or invaded by the exotic species *Symphytotrichum subulatum* under (A, D) no, (B, E) moderate or (C, F) intensive drought. $n = 49$ for all regressions. The gradient of blue color and size of scatter points denotes species richness levels.

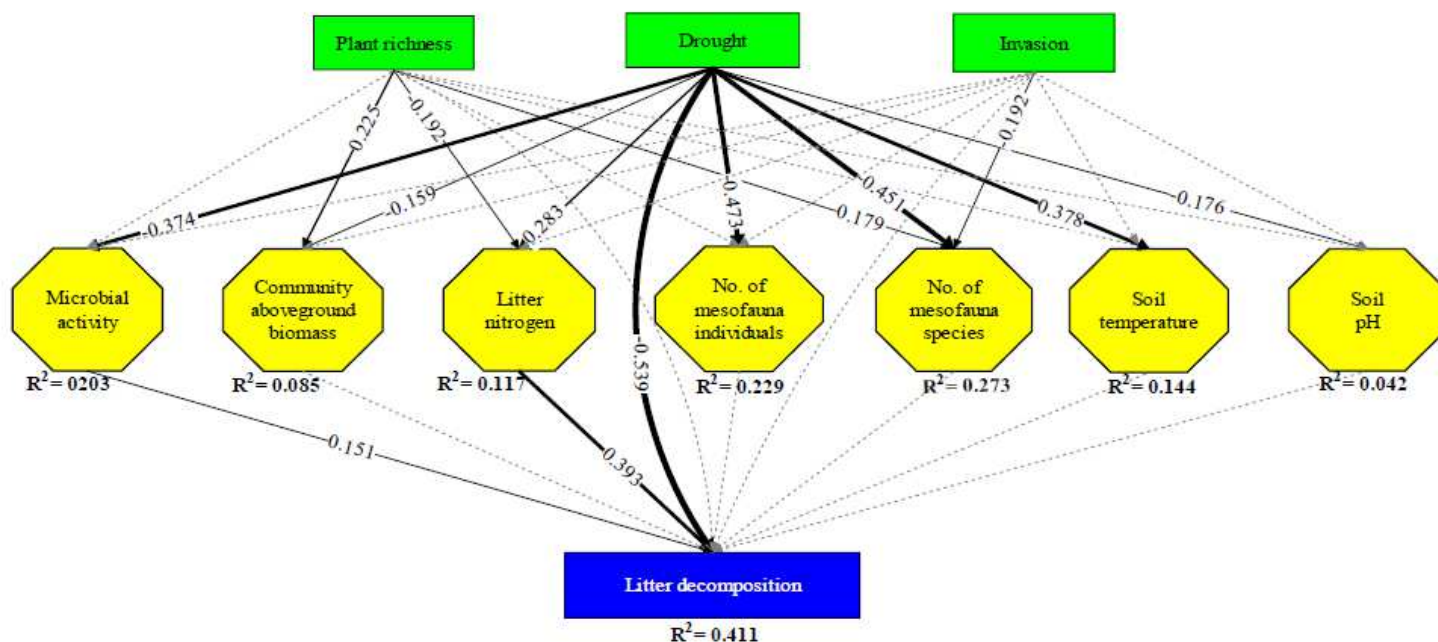


Figure 3

A structural equation model (SEM) showing the causal effects of treatments (green rectangles) and biotic and abiotic factors mediated by treatments (yellow hexagon) on litter decomposition rate (k; blue rectangles). Thickness of solid lines indicates the strength of the causal influence. Numbers on solid lines indicate path coefficients, a measure of the strength of causal relationships that are mathematically equivalent to either partial regression coefficients or correlation coefficients. Nonsignificant pathways are represented with gray dotted lines. R2 values represent the proportion of variance explained for each variable.

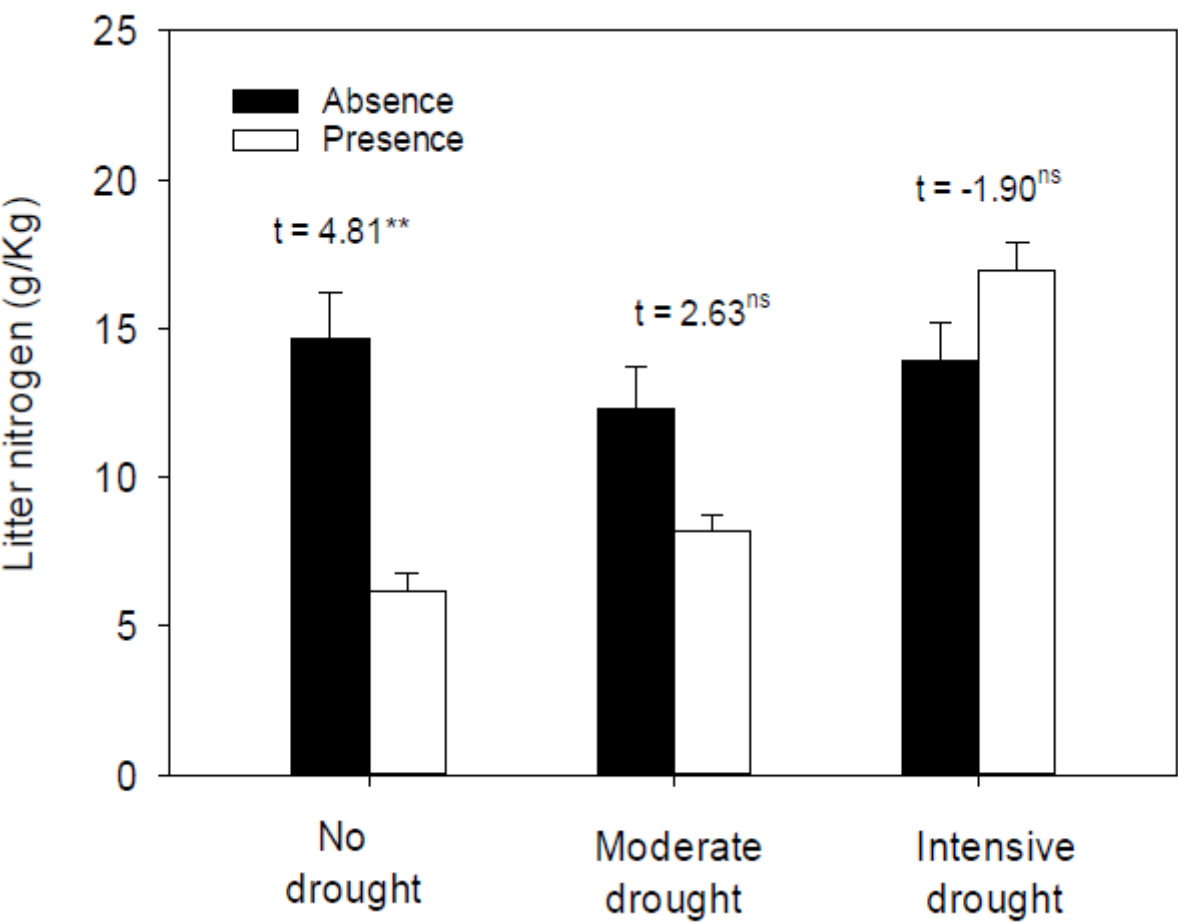


Figure 4

Litter nitrogen concentration in plots in the presence or absence of the dominant species (*Patrinia scabiosaefolia* and/or *Artemisia migoana*) under no, moderate and intensive drought. Results of t-tests and the significance levels (** $P < 0.01$; ns $P > 0.05$) are also given.

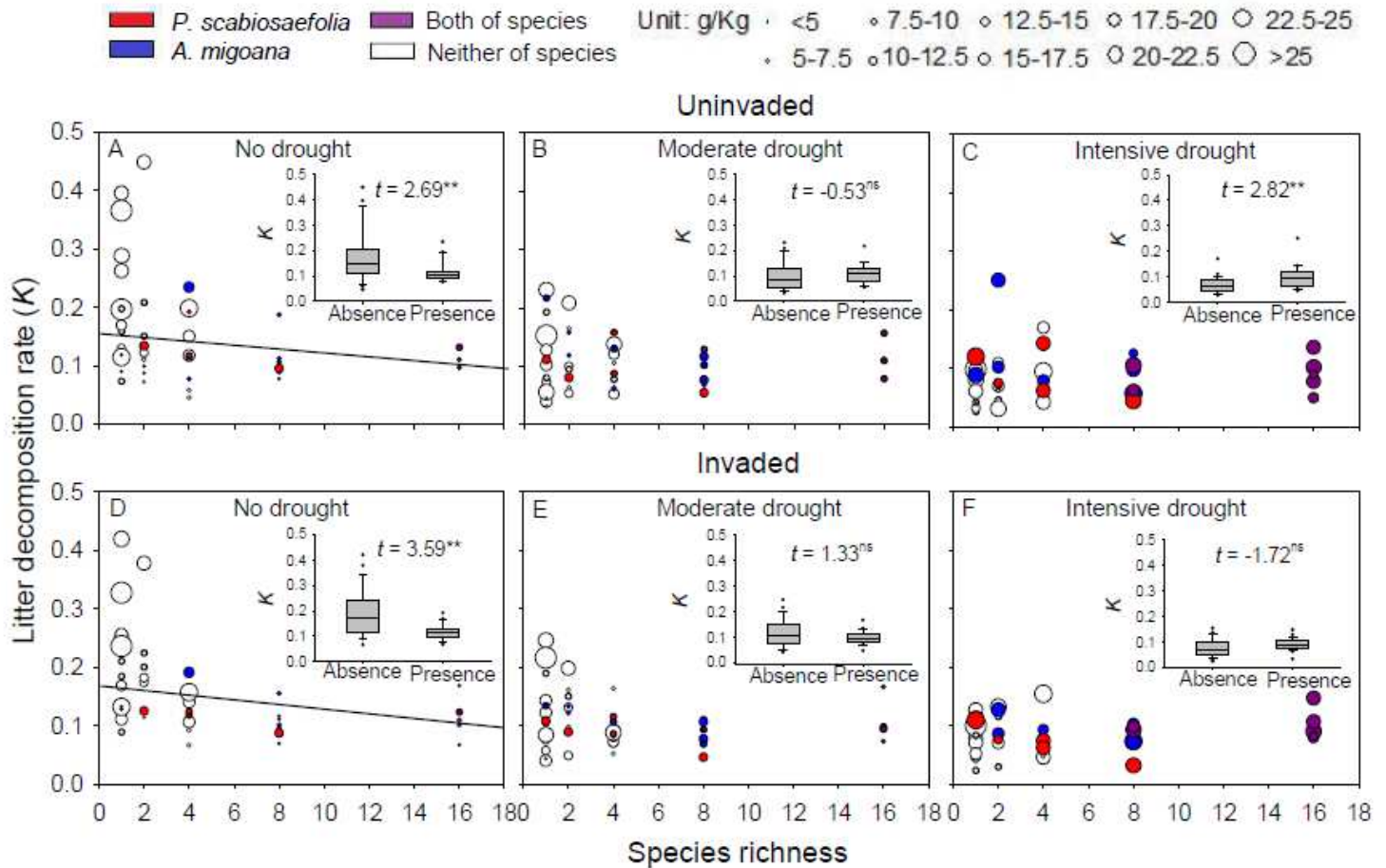


Figure 5

Litter decomposition rate (k) in plots uninverted or inverted by the exotic species *Symphyotrichum subulatum* under (A, D) no, (B, E) moderate or (C, F) intensive drought. Red, blue, purple and white rectangles respectively denote the plots with *P. scabiosaefolia*, *A. migoana*, both *P. scabiosaefolia* and *A. migoana*, and neither *P. scabiosaefolia* nor *A. migoana*, respectively. The size gradient of scatter points denotes litter nitrogen level. Results of t-tests and the significance levels (** $P < 0.01$; ns $P > 0.05$) are also given.

Supplementary Files

This is a list of supplementary files associated with this preprint. Click to download.

- [supplementarymaterials.pdf](#)