

Interannual climatic variability outweighs microhabitat effects on ground-active arthropod diversity in a semi-arid sandy ecosystem

Rentao Liu^{a,*}, Zhixia Guo^b, Josep Penuelas^{c,d}, Marcelo Sternberg^e

^a School of Ecology and Environment, Ningxia University, Yinchuan 750021, China

^b School of Agriculture, Ningxia University, Yinchuan 750021, China

^c CSIC, Global Ecology Unit, CREAF-CSIC-UAB, Bellaterra, Catalonia E08193, Spain

^d CREAF, Cerdanyola del Vallès, Barcelona, Catalonia E08193, Spain

^e School of Plant Sciences and Food Security, The George S. Wise Faculty of Life Sciences, Tel-Aviv University, Ramat Aviv, Tel Aviv 69978, Israel

ARTICLE INFO

Handling Editor: Dr. M Liu

Keywords:

Interannual climatic variability
Shrub microhabitats
Trophic structure
Biodiversity recovery
Ground-active arthropods
Sandy ecosystem

ABSTRACT

Understanding how interannual climatic variability shapes the trophic structure and diversity of ground-active arthropods across shrub microhabitats remains limited, particularly in desertified ecosystems. Here, we examine the abundance and taxa richness of phytophages and predators, and the diversity index of ground-active arthropods using pitfall traps in *Caragana korshinskii* and *Artemisia ordosica* shrub canopy microhabitats, with adjacent open spaces as control, in the Mu Us sandy land. These observations captured a seasonal moisture gradient from wet to exceptionally dry summers over three consecutive years. Our results revealed no significant differences at the microhabitat scale in trophic structure between interannual seasons, indicating a stable quantitative distribution of phytophagous and predatory arthropods between microhabitats. However, arthropod abundance and taxonomic richness exhibited pronounced unimodal seasonal patterns across all microhabitats, including phytophagous groups (except for taxa richness beneath the *C. korshinskii* canopy), with peaks occurring under moderately moist conditions following a previous wet year. Microhabitats beneath the *C. korshinskii* canopy consistently maintained stable soil arthropod richness across contrasting seasons, likely due to herbaceous height performances and stronger buffering of soil moisture-thermal conditions. On the contrary, *A. ordosica* shrubs provided comparatively weaker facilitative effects, highlighting the importance of species-specific functional traits, particularly during extremely dry summers. Overall, interannual climatic conditions exerted a stronger influence than the type of microhabitats on ground-active arthropod communities in this semi-arid sandy ecosystem. These findings underscore the necessity of integrating climatic context and shrub functional identity into revegetation strategies to enhance biodiversity conservation and ecosystem functioning in dryland restoration.

1. Introduction

In desertified regions, shrubs are widely recognized as ecosystem engineers that create small-scale microhabitats beneath their canopies (Li et al., 2025). By forming “fertile islands”, they can enhance microhabitat heterogeneity through improved microclimatic conditions, increased litter accumulation and soil moisture, and enhanced soil structure and fertility (Garner and Steinberger, 1989). These shrub-induced modifications play a crucial role in the maintenance of biodiversity under harsh environmental conditions, particularly by supporting soil biota in arid and semiarid ecosystems (Chen et al., 2019; Liu

et al., 2016a,b; Zhao and Liu, 2013). Under ongoing climatic changes, disentangling the relative roles of biotic filters imposed by shrubs and abiotic constraints driven by rainfall seasonality is essential to understand biodiversity persistence in desertified landscapes.

Increasing evidence suggests that vegetation cover, such as shrubs, can modulate the ecological impacts of changing precipitation regimes. For example, vegetation buffering has been shown to stabilize soil arthropod abundance under shifting seasonal rainfall patterns (Ball et al., 2023). On the contrary, extreme seasonal droughts may reduce arthropod biomass regardless of vegetation structure, with cascading consequences for higher trophic levels (Newell et al., 2023). These

* Corresponding author at: School of Ecology and Environment, Ningxia University, Helanshan West Road 489, Yinchuan 750021, China.

E-mail addresses: nxuli2012@126.com (R. Liu), guo202100@126.com (Z. Guo), josep.penuelas@creaf.cat (J. Penuelas), marcelos@tauex.tau.ac.il (M. Sternberg).

<https://doi.org/10.1016/j.geoderma.2026.117794>

Received 4 July 2025; Received in revised form 20 March 2026; Accepted 23 March 2026

Available online 27 March 2026

0016-7061/© 2026 The Author(s). Published by Elsevier B.V. This is an open access article under the CC BY license (<http://creativecommons.org/licenses/by/4.0/>).

contrasting findings indicate that the effects of precipitation seasonality on soil biodiversity are climatically contingent and can be modulated by local variables including shrub cover and microhabitat conditions (Martins et al., 2024). Despite growing recognition that shrub patches can mediate ecological processes under variable precipitation regimes (Yela et al., 2023), how shrub microhabitat effects interact with seasonal and interannual precipitation variability to shape soil arthropod diversity and trophic structure remains largely unresolved.

Particularly in drought-prone regions, shrub-based afforestation and reforestation have been widely adopted as key strategies to combat desertification and mitigate climate change, as exemplified by China's Three-North Shelter Forest Program (Mongil-Manso et al., 2022; Xu, 2011). Once established, shrub plantations can fundamentally alter local microclimates and soil conditions, modifying temperature regimes, nutrient cycling, and water availability (Butt et al., 2011). These changes allow shrub plantations to act as functional mediators, capable of amplifying, buffering, or shifting broader ecological seasonality and associated biodiversity patterns under climate change (Hernández-Carasco et al., 2025). Critically, by influencing the timing and magnitude of key ecological processes on the microhabitat scale, shrub-mediated effects have profound implications for biodiversity maintenance in arid regional landscapes. However, how soil arthropod diversity and trophic structure respond to shrub-induced microhabitats across interannual climatic fluctuations in seasonal precipitation remains poorly understood, especially in afforested sandy ecosystems vulnerable to desertification (Ball et al., 2023).

Importantly, shrub effects on soil communities are not uniform but are strongly mediated by divergence in shrub functional traits. In shrub-dominated sandy lands, key traits such as nitrogen-fixing capacity, rooting depth, litter quality, and allelochemical production generate contrasting soil environments, with cascading consequences for soil arthropod biodiversity (Kang et al., 2025; Liu et al., 2015). These functional traits determine both the direction and magnitude of shrub effects on soil biota, shaping adaptive strategies that allow species to anticipate periodic changes in seasonally fluctuating environments (Rudolf, 2019; Varpe, 2017), through both immediate and carryover responses to biotic and abiotic conditions across the annual cycle (Koons et al., 2009; Lian et al., 2021). For instance, leguminous shrubs such as *Caragana* species often facilitate understory vegetation via nitrogen enrichment and microclimatic buffering (Xie et al., 2017; Zhai et al., 2023). In contrast, nonleguminous xerophytic shrubs such as *Artemisia* species can exert inhibitory effects through intense competition for water or the release of allelopathic compounds (Tojić et al., 2025). Such trait-mediated contrasts between facilitative and inhibitory shrubs are likely to create divergent ecological templates for associated soil arthropod communities. However, how interannual climate-driven changes in seasonality influence biodiversity across shrubs with contrasting functional traits remains poorly understood.

The present study was to examine the distribution of arthropod diversity and trophic structure across leguminous and nonleguminous shrub microhabitats under alternating wet and dry seasonal years. Specifically, we address two questions: (1) how do shrub–arthropod interactions vary among trophic groups under contrasting seasonal rainfall patterns? and (2) Do shrub patches buffer soil arthropod diversity against the impacts of interannual precipitation seasonality? By addressing these questions, our objective is to clarify how functional divergence of plants and climatic variability jointly shape belowground biodiversity, thus forming the ecological design and adaptive management of shrub-based afforestation in arid and semiarid regions.

2. Materials and Methods

2.1. Study area

The present study was conducted in the southeastern Mu Us Sandy Land (38°19'12" N, 109°40'39" E; 1109 m a.s.l.), near Yulin City in

Shaanxi Province, northwest China. This region lies within the arid and semi-arid transition zone (Fig. S1), experiencing a temperate continental climate characterized by cold winters and hot summers. The mean annual temperature is 8.7 °C, and the mean annual precipitation is approximately 410 mm, with the majority falling between June and September (Fig. S2; National Meteorological Center of China). The growing season spans from May to October. Soils are classified as Calcic Cambisols (WRB) and are predominantly sandy, with a sand content reaching approximately 90%.

The region exhibits pronounced interannual variability in precipitation, with rainy years receiving two to four times more rainfall than dry years. Droughts are frequent, particularly during summer (Wang et al., 2022). Seasonal amplitude, timing, and predictability fluctuate markedly, making this an ecologically sensitive and highly desertification-prone area (Li et al., 2022; Zhang et al., 2023). As part of China's "Three-North Shelter Forest Program" initiated in the 1970 s, afforestation has been a major strategy for combating desertification. The current landscape is dominated by shrub plantations combined with naturally restored grasslands on stabilized sandy dunes under long-term exclusion without ongoing anthropogenic disturbance (i.e., grazing). Dominant plant species include *Leymus secalinus*, *Lespedeza potaninii*, *Salsola collina*, *Artemisia ordosica*, and planted shrubs such as *Salix cheilophila* and *Caragana korshinskii*.

2.2. Experimental design

Five replicate plots (30 × 30 m² each) were established, each containing cooccurring leguminous (*C. korshinskii*) and nonleguminous (*A. ordosica*) shrubs. Here, the leguminous shrub *C. korshinskii* represents the predominant afforested species (that is, the shrub belt apart from 7 m with plant spacing at 1 m) widely used in the study area for desertification control. Similarly, the nonleguminous shrub *A. ordosica*, a widely distributed native xerophyte, demonstrates a strong capacity for the stabilization of mobile sandy soils, a trait associated with its allometric growth strategy. The plots were spaced 50 m apart to ensure spatial independence and minimize spatial autocorrelation, guaranteeing the independent replicates, given the reconfigured sand dune topography following shrub-based afforestation.

Within each plot, four individuals of each shrub species were randomly selected for sampling beneath the canopy. That is, *C. korshinskii* shrubs were spaced 7 m apart, according to the afforested arrangement described above, whereas *A. ordosica* shrubs were spaced 5 m to 7 m apart according to their natural spatial configuration. In addition, four open areas lacking shrub cover were designated as control microhabitats, each separated by 10 m. Based on previous observations and published literatures (Liu et al., 2016a,b), ground-active arthropods (e.g., Carabidae and Tenebrionidae) typically wander up to approximately 10 m, thereby supporting the spatial independence among microhabitats.

In total, 60 sampling points were established (4 points × 3 microhabitat types × 5 replicates). Sampling was carried out at eight time points over three consecutive years: July and September of 2019; May, July and September of 2020; and May, July and September of 2021. Summer rain (June–August) was 337.7 mm in 2019, 225 mm in 2020, and 118.7 mm in 2021 (Fig. S2). In May 2019, we completed the experimental design and site selection; To reduce anthropogenic disturbance, field sampling was deferred until July and September that year.

2.3. Ground-active arthropod sampling and identification

At each sampling point, four pitfall traps consisting of plastic cups (7 cm inner diameter, 10 cm depth) were installed at the four cardinal directions: east, south, west, and north. Each trap contained ~ 20 ml of antifreeze mixed with 98% ethanol. A 1 cm mesh metal screen was installed above the traps to protect from vertebrate disturbances (Brown

and Matthews, 2016). Traps were operated continuously for 14 days and emptied every three days to preserve specimen quality.

Collected arthropods were stored in 75% ethanol and identified to the family or genus level using standard taxonomic keys (Yin, 2000; Zheng and Gui, 1999). Flying insects were excluded. Ground-active arthropods were categorized into two trophic groups based on their family-level feeding traits: phytophages (plant feeder) and predators (arthropod feeder) (Bröcher et al., 2025). Although this classification simplifies trophic complexity, it enables broad community-level analysis on trophic structure (Table S1).

2.4. Sampling of plant performance

Shrub traits, including plant height (m) and canopy area (m²), were measured in situ. Leaf area index (LAI, %) was estimated using a portable canopy analyzer (ADC Sunscan, China) (see Fig. S3).

Herbaceous vegetation was surveyed within 50 × 50 cm quadrats centered at each sampling point. Within each quadrat, plant density (HD, individuals m⁻²), species richness (HR), and mean plant height (HH, cm) were recorded (see Table S2).

2.5. Soil sampling and analysis

At each sampling point, soil samples were collected from four directions (N, S, E, W) and combined into one composite sample (Qu et al., 2025). Soil was collected from the depths of 0 cm to 15 cm using a 100 cm³ metal corer. Samples were sieved to 2 mm and air dried prior to laboratory analysis.

Soil pH and electrical conductivity (EC, μS·cm⁻¹) were measured in a 1:5 soil to water suspension. Total nitrogen (TN, g·kg⁻¹) was determined by Kjeldahl digestion (UDK 140 and Titroline 96, Italy), and soil organic carbon (OC, g·kg⁻¹) via the Walkley-Black method. Soil moisture (SM, %) was measured gravimetrically after drying at 105 °C for 24 h. Soil temperature (ST, °C) was averaged for three consecutive days using a portable field thermometer. Soil texture (sand, silt and clay contents; %) was determined by laser diffraction (Mastersizer 3000, Malvern Instruments, UK).

2.6. Data analysis

Arthropod diversity was quantified using (1) abundance (individuals trap⁻¹), (2) taxonomic richness (taxa trap⁻¹), and (3) the Shannon diversity index. The abundance and richness at the trophic group-level were also assessed.

We primarily used linear mixed effects models (LMMs) with a plot as a random intercept to analyze the effects of microhabitat, season, and their interaction on all diversity metrics, accounting for repeated measures across seasons. For comparison and where design permitted, a complementary two-way analysis of variance (ANOVA) was also applied. Model assumptions were verified, with data log-transformed when necessary. Significant fixed effects were further examined using Tukey's HSD post hoc tests. To detect unimodal seasonal responses, we fitted separate LMMs that included a quadratic term for season.

To assess the direct and indirect effects of soil and plant variables on arthropod diversity, we employed piecewise structural equation modeling (pSEM). Three pSEMs were constructed: (1) examining the direct and indirect effects of microhabitats on the trophic structure across seasonal periods; (2) examining the direct and indirect effects of microhabitats on the diversity of ground-active arthropods across seasonal periods; and (3) examining the direct and indirect effects of microhabitats on the diversity of ground-active arthropods specifically in July 2021. In model (3), climatic variables were excluded to isolate the effects of microhabitat-induced environmental factors, as significant differences among microhabitats were detected only in July 2021.

Before pSEM, we used correlation analysis to select herbaceous and soil variables that correlated with diversity indices (see Figs. S7–S9).

Principal Component Analysis (PCA) was then applied to reduce the multicollinearity among the selected soil variables. The first two PCA axes (PCA1 and PCA2) were retained and used as composite predictors in the pSEM (Fig. S4–S6; Table S3). All analyses were performed in R 4.1.0 using the packages *vegan*, *car*, *nlme*, *emmeans*, *piecewiseSEM*, and *ggplot2* (R Core Team 2019).

3. Results

3.1. Trophic structure of ground-active arthropods

The abundance of phytophagous arthropods was significantly influenced by seasonal timing ($F = 13.29, p < 0.001$) and by the interaction between microhabitat and season ($F = 3.19, p < 0.001$). In contrast, the abundance of predators ($F = 11.08, p < 0.001$), and the taxonomic richness of phytophages ($F = 7.04, p < 0.001$) and predators ($F = 3.08, p = 0.006$) were significantly affected by season alone, with no significant ($p > 0.05$) effects of microhabitat or the interaction term.

Across all seasons, no significant ($p > 0.05$) differences in the abundance or taxonomic richness of phytophages or predators were detected between shrub microhabitats. However, both the abundance and richness of phytophages showed pronounced seasonal fluctuations (Fig. 1). Phytophagous abundance exhibited a unimodal seasonal pattern in all microhabitats, peaking in September 2020 (Fig. 1). Similarly, the taxonomic richness of phytophages in both *Artemisia* canopy microhabitats (AT) and open spaces (OP) also peaked in September 2020. However, phytophagous richness in *Caragana* canopy microhabitats (CA) remained relatively stable, with no significant ($p > 0.05$) seasonal variation. Noticeably, predator abundance and richness showed no significant ($p > 0.05$) seasonal variation across any separate microhabitat (Fig. 1).

3.2. Abundance, taxa richness and Shannon index of ground-active arthropods

Arthropod abundance was significantly influenced by seasonal timing ($F = 10.64, p < 0.001$) and the microhabitat × season interaction ($F = 3.19, p < 0.001$). In contrast, both taxonomic richness ($F = 3.30, p = 0.003$) and the Shannon diversity index ($F = 5.94, p < 0.001$) were affected by season alone.

For most seasons, no significant ($p > 0.05$) differences in arthropod abundance, richness, or Shannon index were observed between microhabitats (Fig. 2). However, in July 2021, it exhibited significantly ($p < 0.05$) higher abundance, taxonomic richness, and Shannon diversity of ground-active arthropods in *Caragana* canopy microhabitat (CA) compared to *Artemisia* canopy microhabitat (AT) and open spaces (OP) (Fig. 2).

Across seasons, arthropod abundance and richness were found to generally follow unimodal seasonal trends, peaking approximately in September 2020. For example, arthropod abundance showed significant seasonal trends in the OP ($R^2 = 0.22, p = 0.010$), and marginally in AT ($R^2 = 0.19, p = 0.073$) and CA ($R^2 = 0.15, p = 0.052$). Taxonomic richness followed similar patterns in OP ($R^2 = 0.08, p = 0.092$) and AT ($R^2 = 0.09, p = 0.071$), but remained constant in CA ($R^2 = 0.04, p = 0.86$). Noticeably, no significant ($p > 0.05$) seasonal effects were observed for the Shannon index in any separate microhabitats (Fig. 2).

3.3. Drivers of trophic structure and diversity distribution of ground-active arthropods

As the microhabitat had no significant ($p > 0.05$) effect on trophic diversity, we applied pSEM to data pooled from the three microhabitats at all time points (Fig. 3a). Phytophagous abundance responded positively to herbaceous plant density and was indirectly regulated by microhabitat-driven variation along the soil silt gradient (Soil PC2; Table S3). In contrast, phytophagous richness was directly affected by

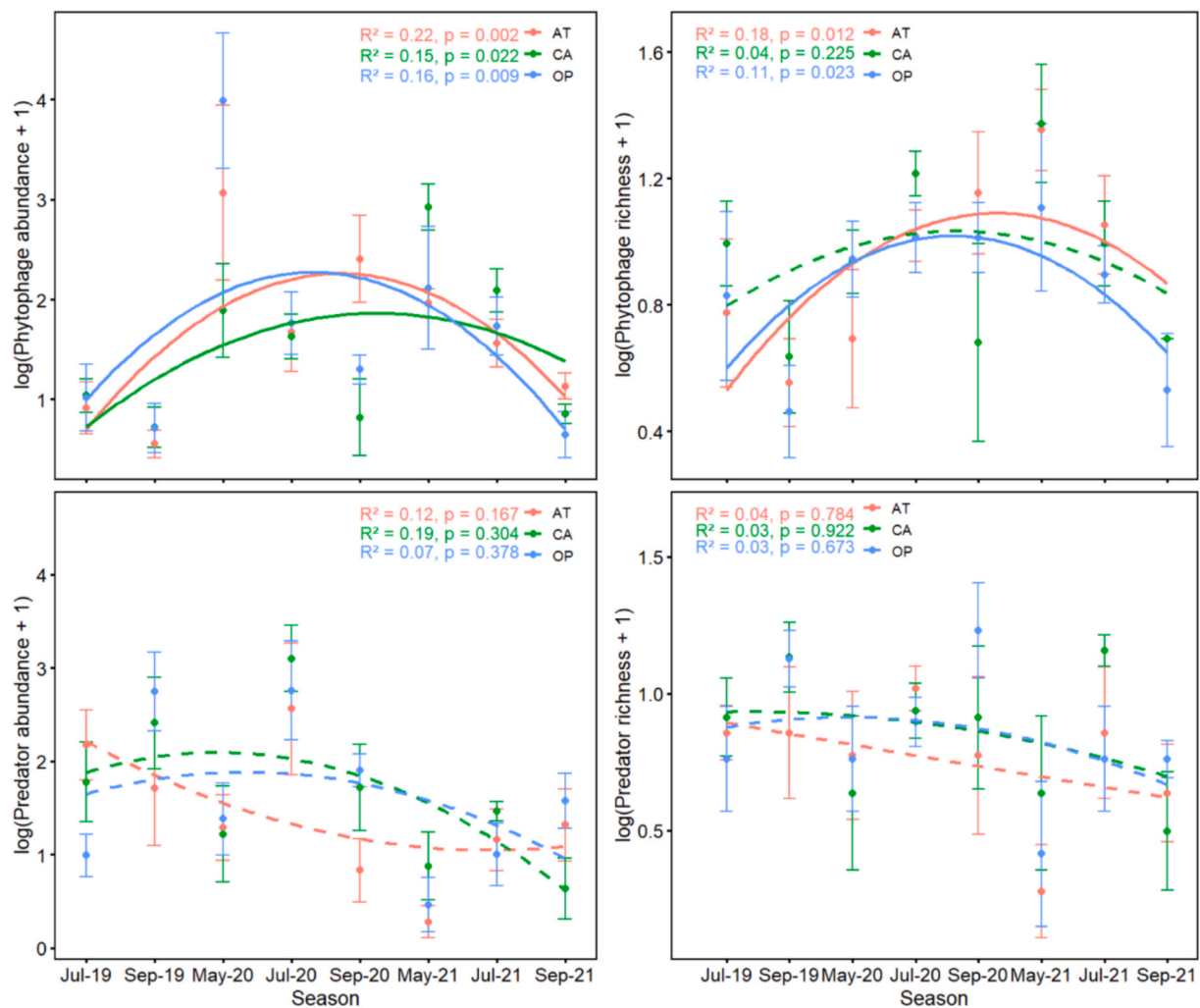


Fig.1. LMMs modes for seasonal variation in the abundance and taxonomic richness of phytophagous and predatory arthropods across three shrub microhabitats. Different letters indicate significant differences among sampling times within each microhabitat. Values are log-transformed and presented as means \pm SE. R^2 and p -values indicate the goodness of fit of seasonal trends within each microhabitat. Solid lines denote significant trends ($p < 0.05$); dashed lines indicate non-significant trends ($p > 0.05$). AT: *Artemisia* canopy microhabitat, red; CA: *Caragana* canopy microhabitat, green; OP: open spaces, blue. Jul-19 = July 2019, Sep-19 = September 2019, May-20 = May 2020, Jul-20 = July 2020, Sep-20 = September 2020, May-21 = May 2021, Jul-21 = July 2021, Sep-21 = September 2021.

microhabitat type. Predator abundance was positively associated with herbaceous density and soil silt (Soil PC2), but showed negative relationships with phytophagous abundance and the soil clay-carbon-nitrogen gradient (soil PC1). Predator richness increased with its abundance but declined along the soil silt gradient (Soil PC2). Herbaceous plant density was negatively related to the soil clay-carbon-nitrogen gradient (Soil PC1), while being positively influenced by microhabitat (Fig. 3a).

Because shrub microhabitat existed no significant effects on arthropod diversity across most seasons, we applied pSEM to diversity data pooled across the three microhabitats over all seasonal sampling periods (Fig. 3b). Arthropod abundance was positively associated with herbaceous plant density and the soil silt gradient (Soil PC2), but negatively related to the soil clay-carbon-nitrogen gradient (Soil PC1) and seasonal rainfall. Taxonomic richness was positively related to herbaceous plant height. The Shannon diversity index increased with taxonomic richness but declined with increasing arthropod abundance. Herbaceous plant density was positively influenced by microhabitat-mediated variation along the soil clay-carbon-nitrogen gradient (Soil PC1), whereas plant height was negatively affected by the soil silt gradient (Soil PC2). In turn, both soil gradients were strongly driven by seasonal rainfall variability.

Given the strong microhabitat effects observed in July 2021, we constructed a separate pSEM for this sampling period (Fig. 3c). In this model, arthropod abundance and richness were directly influenced by microhabitat. Taxonomic richness was positively associated with herbaceous height, which was also regulated by microhabitat. The Shannon index was positively related to taxa richness but negatively related to soil moisture, with both herbaceous height and soil moisture positively affected by microhabitat.

4. Discussion

4.1. Shrub-microhabitat effects on arthropod trophic structure across seasonal climatic variability

Although shrubs are widely regarded as facilitators of soil fauna (Liu et al., 2015; Zhao and Liu, 2013), our results revealed no significant effects of shrub microhabitats on the trophic structure of ground-active arthropods across seasons. This spatial consistency likely reflects the high mobility and ecological plasticity of phytophagous and predatory arthropods at fine spatial scales (De Boer et al., 2011), allowing a rapid redistribution among microhabitats in response to fluctuating environmental conditions (Mestre et al., 2020). Consequently, dominant

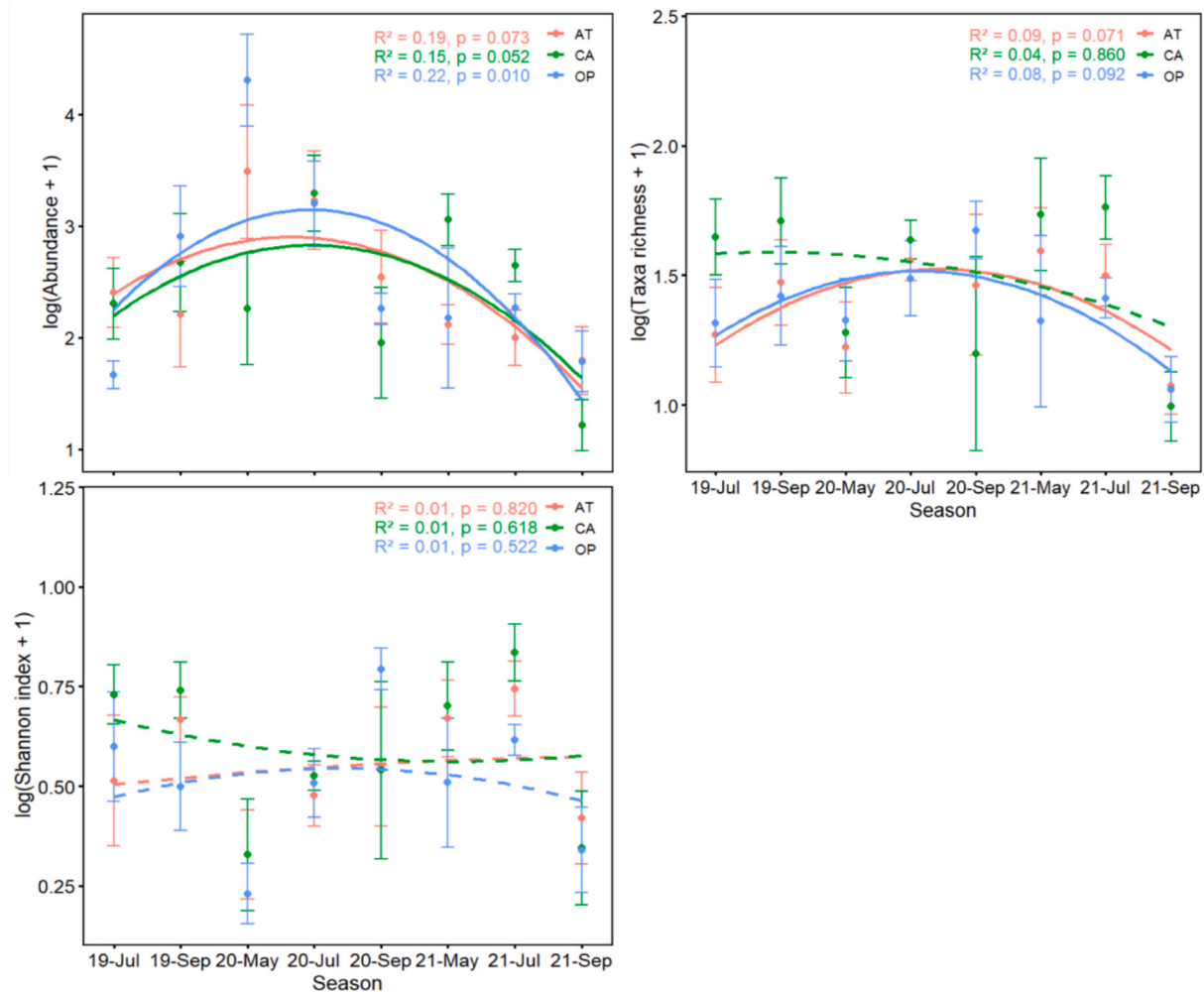


Fig. 2. Seasonal variation modeled by linear mixed-effects models (LMMs) for abundance, taxonomic richness, and Shannon index across three shrub microhabitats. Different letters indicate significant differences among sampling times within each microhabitat. Values are log-transformed and presented as means \pm SE. R^2 and p -values indicate the goodness of fit of seasonal trends within each microhabitat. Solid lines represent statistically significant trends ($p < 0.05$), including marginally significant trends ($0.05 \leq p < 0.1$); dashed lines indicate non-significant trends ($p > 0.05$). AT: *Artemisia shrub* microhabitat, red; CA: *Caragana shrub* microhabitat, green; OP: open spaces, blue. Jul-19 = July 2019, Sep-19 = September 2019, May-20 = May 2020, Jul-20 = July 2020, Sep-20 = September 2020, May-21 = May 2021, Jul-21 = July 2021, Sep-21 = September 2021.

phytophagous (Geometroidea, Cicadelloidea) and predatory (Gnaphosidae, Lycosidae, Carabidae) families were consistently detected across shrub canopy and open spaces without shrubs, generally exhibiting higher abundances beneath shrub canopies across seasons. In addition, the observed stability of trophic structure across microhabitats may stem from trait-mediated resistance to microscale environmental variability, reflecting arthropod ecological and life-history traits (Adje et al., 2023), thereby supporting stable trophic interactions and ecosystem functioning in shrub-restored landscapes (Hernández Matías et al., 2025).

Despite this stability at the microhabitat level, pronounced seasonal dynamics were evident in the arthropod trophic structure, characterized by a unimodal pattern peaking in September 2020 (Fig. 1). This seasonal pattern links herbivore activity to pulses of plant productivity, particularly herbaceous density, in semi-arid systems, consistent with the resource availability hypothesis (Ball et al., 2023; Endara and Coley, 2011). Structural equation modeling (Fig. 3a) further indicated that this pattern was primarily driven by herbaceous vegetation dynamics, especially plant density (Fig. 3a). Such responses align with theories of nonlinear demographic regulation in which arthropod performance peaks under intermediate environmental conditions due to convex-shaped physiological response curves (Hernández-Carrasco et al., 2025).

On the contrary, predator assemblages consistently occupied higher

trophic positions across seasons (Fig. 1), a pattern commonly associated with greater demographic stability (Svanbäck et al., 2015). The SEM results (Fig. 3a) revealed that predator abundance was jointly regulated by bottom-up facilitative effects of herbaceous plant density – likely reflecting refuge provision – and by top-down constraints, as indicated by negative associations with phytophagous abundance (Fig. 3a). This dual regulation suggests a partial decoupling of predator dynamics from primary production pulses (Mougi, 2024). Moreover, the lack of significant effects of the microhabitat on predatory trophic structure indicates that shrubs, despite modifying local environmental conditions (Table S2), do not differentially filter arthropod trophic groups at the functional level. Instead, this stability likely reflects the buffering capacity of shrub microhabitats, which mitigates the impacts of seasonal climatic variability on predatory arthropods (Martin-Chave et al., 2019).

Collectively, these findings underscore the divergent sensitivities of trophic guilds to seasonal drivers: phytophagous arthropods respond rapidly to fluctuations in plant performance, whereas predators maintain comparatively stable dynamics (Bauer and Hoye, 2014; Svanbäck et al., 2015). These contrasting responses support the framework of seasonal impact propagation across trophic levels (Hernández-Carrasco et al., 2025), whereby shrub-mediated environmental modification modulates plant–arthropod interactions under variable climatic

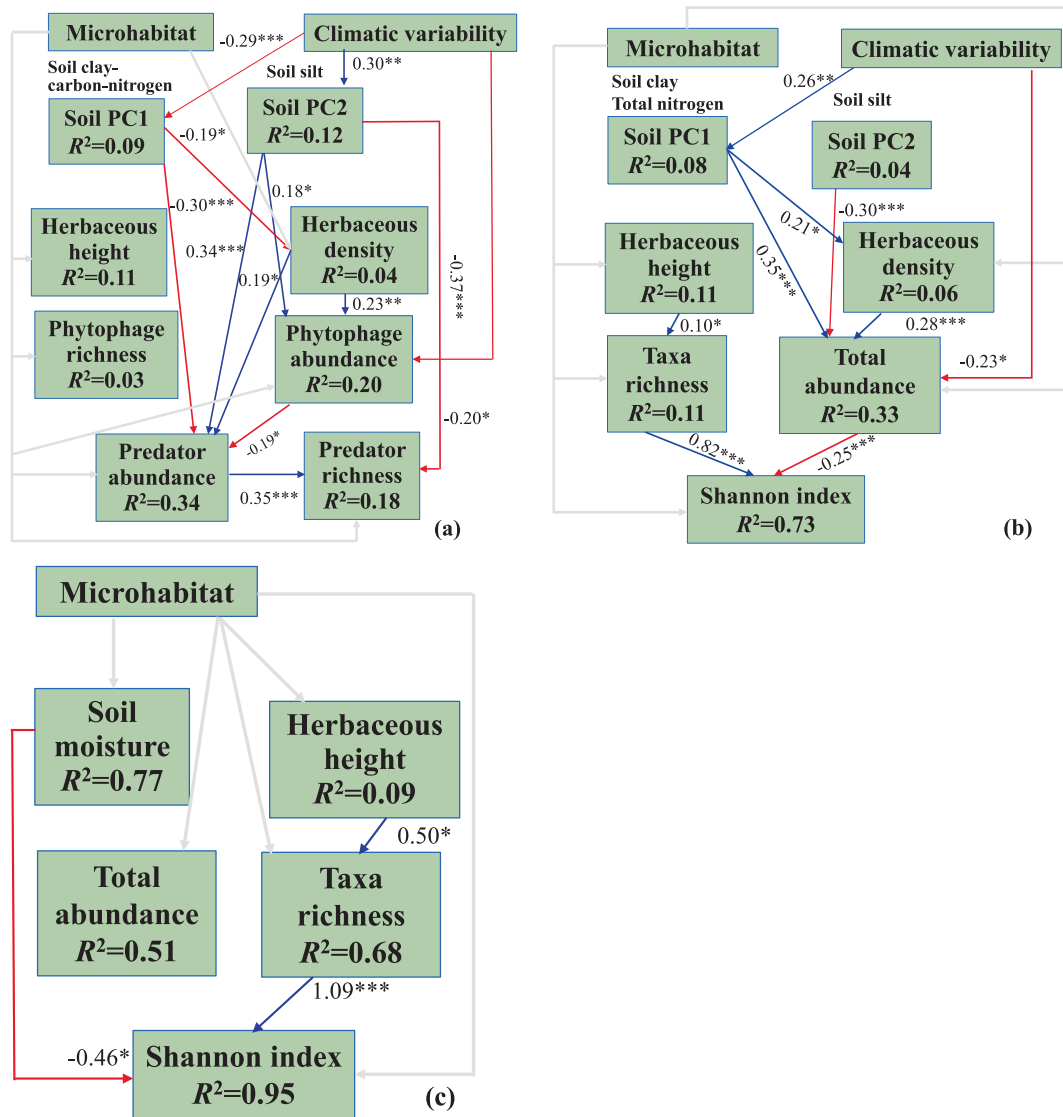


Fig. 3. Piecewise structural equation model (pSEM) depicting the direct and indirect effects of microhabitats on the trophic structure ((a) Fisher's $C = 3.07$, $df = 12$, $p = 0.995$, $AIC = 4274.87$; $\chi^2 = 0.615$, $df = 6$, $p = 0.996$) and diversity ((b) Fisher's $C = 3.07$, $df = 12$, $p = 0.995$, $AIC = 4274.87$; $\chi^2 = 0.615$, $df = 6$, $p = 0.996$) of ground-active arthropods across seasonal sampling timing, and in July 2021 ((c) Fisher's $C = 2.81$, $df = 2$, $p = 0.245$, $AIC = 205.17$; $\chi^2 = 0.253$, $df = 1$, $p = 0.111$). Standardized path coefficients are shown for significant continuous pathways only. The categorical predictor (Microhabitat) was included in the model but was not assigned standardized coefficients. Red and blue arrows indicate negative and positive relationships, respectively, while gray lines denote paths involving the categorical predictor. * $p < 0.05$; ** $p < 0.01$; *** $p < 0.001$. The results of soil PC1 and PC2 see Table S3 and Fig. S4–S6. The selected environmental variables come from Fig. S7–S9.

conditions. Consequently, accurately forecasting climate-driven changes in the trophic structure of ground-active arthropod communities within shrub microhabitats remains a substantial challenge (Torode et al., 2016).

4.2. Shrub-microhabitat effects on arthropod abundance and diversity across seasonal climatic variability

Regarding arthropod diversity, no significant differences were detected between shrub microhabitats across most seasons. However, facilitative effects emerged in July 2021, a year characterized by below-average precipitation and summer drought (Fig. S2). This drought-specific response contrasts with the largely stable trophic structure of ground-active arthropods across seasons (Fig. 1), highlighting interactive effects between climatic variability and shrub microhabitats on arthropod abundance and diversity (Fig. 2). Collectively, these findings emphasize the context-dependent nature of shrub facilitation across

seasonal climatic variability (Liu et al., 2020), likely mediated by plant functional traits and their capacity to buffer environmental stress (Martin-Chave et al., 2019).

During most interannual seasons, ground-active arthropods were evenly distributed among microhabitats, probably reflecting their high mobility (Fitzgerald et al., 2021) and the relatively mild and homogeneous living conditions during growth periods (i.e., herbaceous height and texture soil conditions; Fig. 3b, Table S2), which allowed free movement and resulted in similar capture probabilities across microhabitats (Braun et al., 2021). However, during the extreme drought year of 2021, arthropod abundance, taxonomic richness, and diversity were found to be greater in *Caragana* canopy microhabitats relative to *Artemisia* canopy microhabitats and open spaces (Fig. 2; Table S1). Structural equation modeling (Fig. 3c) indicated that this pattern was primarily mediated by increased herbaceous height beneath *Caragana* canopies, highlighting the role of shrub-induced microhabitat modification in buffering drought stress, consistent with documented

microclimatic amelioration effects of shrubs under water limitation (Prévosto et al., 2020). This facilitative effect likely arises from the denser canopy structure and higher LAI of *Caragana* shrubs (Fig. S3), which promote herbaceous growth and vertical structural complexity while moderating thermal and moisture stress (Jiang et al., 2024; Zhang et al., 2020).

However, shrub facilitation is inherently context dependent (Pichon et al., 2024). Under severe drought, *Caragana* shrubs can impose strong competitive effects through their extensive root system and high water demand (Jiang et al., 2024), potentially suppressing herbaceous performance when soil moisture becomes critically limited (Miriti, 2006). By contrast, *Artemisia* shrubs provided weaker abiotic buffering and were associated with lower arthropod diversity, likely due to their lower canopy density combined with allelopathic and belowground competitive effects that constrain herbaceous establishment and structural complexity (Tojić et al., 2025). Together, these results indicate that the microhabitat effects on arthropod communities are shaped not only by passive microclimatic filtering but also by species-specific biotic interactions, with facilitation–competition balances shifting under extreme drought conditions (Lai et al., 2023).

More importantly, we found unimodal seasonal patterns of both abundance and taxonomic richness, despite the notable exception of stable richness in *Caragana* canopy (CA) microhabitats. One possible explanation is a legacy effect of the preceding wet year (2019), which may have promoted peak arthropod abundance and richness in the current year, i.e., 2020 (Lian et al., 2021). Elevated herbaceous plant density, higher soil nitrogen content, and lower soil pH (Table S2) likely enhanced resource availability (Fig. 3b), supporting arthropod communities in line with the resource availability hypothesis (Endara and Coley, 2011). The positive associations observed between arthropod abundance and herbaceous density and soil nitrogen (Fig. S8) confirmed this point.

Conversely, arthropod abundance and richness declined sharply in the dry summer of 2021, particularly in the *Artemisia* canopy microhabitats (AT) and open spaces (OP) exposed to harsher climatic conditions. On the one hand, this decline highlights the vulnerability of ground-active arthropods to drought, which can substantially limit their populations under moisture-deficient conditions (Newell et al., 2023). Moreover, it was suggested that the legacy effects of seasonal vegetation growth conditions appear to persist into the following year, but may be diminished or overridden by extreme climatic events (Lian et al., 2021).

Furthermore, greater temporal variability was observed in *Artemisia* canopy microhabitats (AT) and in open spaces (OP), indicating a lower capacity to buffer climatic stressors and a higher susceptibility to seasonal drought. In contrast, *Caragana* canopy microhabitats (CA) consistently maintained more stable arthropod taxonomic richness across both seasonal and interannual moisture fluctuations. This stability is likely to be attributable to the leguminous nature of *Caragana* shrubs (Martinez Almoyna et al., 2024), which promote microenvironmental buffering through increased herbaceous height and structural complexity (Fig. 3b; Table S2). These features can help mitigate the impact of precipitation variability (Braun et al., 2021), positioning CA microhabitats as potential ecological refuges (Sun et al., 2025; Zhang et al., 2022). Such distinctive buffering capacity may reflect bet-hedging strategies (Wilbur and Rudolf, 2006). Specifically, *Caragana* canopy microhabitats may support both “conservative bet-hedging” and “diversifying bet hedging” (Kivela et al., 2016). Collectively, these findings underscore the functional importance of shrub species identity in modulating arthropod community responses under increasing climatic unpredictability (Adje et al., 2023). Therefore, leguminous shrubs such as the *Caragana* canopy can play a critical role in enhancing the resilience of arthropod communities in arid landscapes.

Interestingly, the Shannon diversity of ground-active arthropods remained stable across seasonal transitions in all three microhabitats. This temporal constancy suggests that present microhabitats induced by

shrub cover can buffer environmental variability (Brandon-Mong et al., 2018), maintaining overall community evenness despite shifts in species abundance or richness (Braun et al., 2021). The lack of consistent diversity enhancement by microhabitats in terms of shrub species may be explained by antagonistic interactions between abiotic facilitation (e.g., shading, moderated temperature) (Zhao and Liu, 2013) and biotic interference (e.g., water competition) (Wang et al., 2008). These opposing forces may offset each other, depending on species composition and environmental context. Collectively, these results further highlight the complex and context-dependent roles of shrub microhabitats in structuring ground-active arthropod diversity under both seasonal and interannual climate variability (Nielsen and Ball, 2015).

5. Conclusions and implications

Our study demonstrates that in semi-arid ecosystems, climatic variability is a stronger regulator of trophic structure and diversity of ground-active arthropods than shrub microhabitat differences. We observed a unimodal seasonal peak in arthropod metrics (i.e., abundance and taxonomic richness) under moderate moisture following a wet year with high rainfall, underscoring the critical legacy effects of precipitation. In particular, *C. korshinskii* shrubs maintained greater cross-seasonal stability in arthropod richness, a benefit likely derived from their ability to enhance resources and buffer the microclimate stress. This contrasts with the weaker facilitative effect of shrubs like *A. ordosica*, highlighting the pivotal role of species-specific functional traits. From a restoration perspective, these findings underscore the importance of aligning revegetation strategies with climatic context and shrub functional traits for effectively enhancing biodiversity conservation and ecosystem resilience in semi-arid sandy landscapes.

CRedit authorship contribution statement

Rentao Liu: Writing – review & editing, Writing – original draft, Visualization, Validation, Software, Resources, Project administration, Funding acquisition, Formal analysis, Data curation, Conceptualization. **Zhixia Guo:** Resources, Methodology, Investigation, Data curation. **Josep Penuelas:** Writing – review & editing, Supervision. **Marcelo Sternberg:** Writing – review & editing, Writing – original draft, Supervision.

Declaration of competing interest

The authors declare that they have no known competing financial interests or personal relationships that could have appeared to influence the work reported in this paper.

Acknowledgements

This work was supported by the National Natural Science Foundation of China (U25A20765; 32360318), the Natural Science Foundation of Ningxia (2023AAC01002; 2026AAC02624); the Central Government-Guided Special Fund for Local Science and Technology Development (2024FRD05049), and the Ningxia Leading Talent Program in Science and Technology (2024GKLRXL15). We are very grateful for the support from China Scholarship Council Program (CSC).

Appendix A. Supplementary data

Supplementary data to this article can be found online at <https://doi.org/10.1016/j.geoderma.2026.117794>.

Data availability

Data will be made available on request.

References

- Adje, G., Wojcik, L.A., Gaedke, U., 2023. Functional diversity increases the resistance of a tritrophic food web to environmental changes. *Theor. Ecol.* 16 (2), 131–150. <https://doi.org/10.1007/s12080-023-00558-0>.
- Ball, B.A., Bergin, K., Morrison, A., 2023. Vegetation influences desert soil arthropods and their response to altered precipitation. *J. Arid Environ.* 208, 104873. <https://doi.org/10.1016/j.jaridenv.2022.104873>.
- Bauer, S., Hoye, B.J., 2014. Migratory animals couple biodiversity and ecosystem functioning worldwide. *Science* 344 (6179), 1242552. <https://doi.org/10.1126/science.1242552>.
- Brandon-Mong, G.J., Littlefair, J.E., Sing, K.W., Lee, Y.P., Gan, H.M., Clare, E.L., Wilson, J.J., 2018. Temporal changes in arthropod activity in tropical anthropogenic forests. *Bull. Entomol. Res.* 108 (6), 792–799. <https://doi.org/10.1017/S000748531800010X>.
- Braun, J., Westphal, M., Lortie, C.J., 2021. The shrub *Ephedra californica* facilitates arthropod communities along a regional desert climatic gradient. *Ecosphere* 12 (9), e03760. <https://doi.org/10.1002/ecs2.3760>.
- Bröcher, M., Meyer, S.T., Leher, A.G., Ebeling, A., 2025. Ecological traits for 1374 arthropod species collected in a German grassland. *Ecology* 106 (4), e70077. <https://doi.org/10.1002/ecy.70077>.
- Brown, G.R., Matthews, L.M., 2016. A review of extensive variation in the design of pitfall traps and a proposal for a standard pitfall trap design for monitoring ground-active arthropod biodiversity. *Ecol. Evol.* 6 (12), 3953–3964. <https://doi.org/10.1002/ece3.2176>.
- Butt, N., de Oliveira, P.A., Costa, M.H., 2011. Evidence that deforestation affects the onset of the rainy season in Rondônia, Brazil. *J. Geophys. Res.* 116 (D11), D11120. <https://doi.org/10.1029/2010JD015174>.
- Chen, J.G., He, X.F., Wang, S.W., Yang, Y., Sun, H., 2019. Cushion and shrub ecosystem engineers contribute differently to diversity and functions in alpine ecosystems. *J. Veg. Sci.* 30 (2), 362–374. <https://doi.org/10.1111/jvs.12725>.
- De Boer, T.E., Birlutiu, A., Bochdanovits, Z., Timmermans, M.J.T.N., Dijkstra, T.M.H., Van Straalen, N.M., Ylstra, B., Roelofs, D., 2011. Transcriptional plasticity of a soil arthropod across different ecological conditions. *Mol. Ecol.* 20 (6), 1144–1154. <https://doi.org/10.1111/j.1365-294X.2010.04985.x>.
- Endara, M.J., Coley, P.D., 2011. The resource availability hypothesis revisited: a meta-analysis. *Funct. Ecol.* 25 (2), 389–398. <https://doi.org/10.1111/j.1365-2435.2010.01803.x>.
- Fitzgerald, J.L., Stubble, K.L., Nichols, L.M., Diamond, S.E., Wentworth, T.R., Pelini, S.L., Gotelli, N.J., Sanders, N.J., Dunn, R.R., Penick, C.A., 2021. Abundance of spring- and winter-active arthropods declines with warming. *Ecosphere* 12 (4), e03473. <https://doi.org/10.1002/ecs2.3473>.
- Garner, W., Steinberger, Y., 1989. A proposed mechanism for the formation of 'fertile islands' in the desert ecosystem. *J. Arid Environ.* 16 (3), 257–262.
- Hernández Matías, A., Peragón, I., Resano Mayor, J., Moleón, M., Virgós, E., Real, J., 2025. Temporal and spatial variation in trophic cascades affects population demographic heterogeneity in Bonelli's Eagle (*Aquila fasciata*). *Ibis* 167 (1), 179–195. <https://doi.org/10.1111/ibi.13351>.
- Hernández-Carrasco, D., Tylilanakis, J.M., Lytle, D.A., Tonkin, J.D., 2025. Ecological and evolutionary consequences of changing seasonality. *Science* 388 (6750), eads4880. <https://doi.org/10.1126/science.ads4880>.
- Jiang, P., Yuan, Y., Li, Q., 2024. Advanced precipitation enhances vegetation primary productivity in central Asia. *Ecol. Ind.* 166, 112276. <https://doi.org/10.1016/j.ecolind.2024.112276>.
- Kang, X., Wu, X., Liu, Y., Zhang, A., Duan, L., Zhou, J., Zhan, Z., Qi, W., 2025. Shrub effect on grassland community assembly depends on plant functional traits and shrub morphology. *Oecologia* 207 (5), 77. <https://doi.org/10.1007/s00442-025-05716-1>.
- Kivela, S.M., Valimaki, P., Gotthard, K., 2016. Evolution of alternative insect life histories in stochastic seasonal environments. *Ecol. Evol.* 6 (16), 5596–5613. <https://doi.org/10.1002/ece3.2310>.
- Koons, D.N., Pavard, S., Baudisch, A., Jessica, E., Metcalf, C., 2009. Is life-history buffering or liability adaptive in stochastic environments? *Oikos* 118 (7), 972–980. <https://doi.org/10.1111/j.1600-0706.2009.16399.x>.
- Lai, Z.R., Sun, Y.F., Yu, Y., Liu, Z., Bai, Y.X., Qiao, Y.G., Miao, L., She, W.W., Qin, S.G., Feng, W., 2023. Plant selection and ecological microhabitat drive the shrub-associated microbiome selection in revegetated shrub ecosystems. *Appl. Soil Ecol.* 190, 105023. <https://doi.org/10.1016/j.apsoil.2023.105023>.
- Li, L., Liu, J.H., Luo, Y.H., Sun, Y., Zhang, J.M., Wang, T.Z., Zhu, N., Bao, Y.F., Xu, N., Yan, Y.C., 2025. Grazing-induced enhancement of shrub 'multifunctional island' effect is associated with altered soil bacterial β diversity in shrub-encroached grasslands. *J. Appl. Ecol.* 62 (6), 1531–1543. <https://doi.org/10.1111/1365-2664.70025>.
- Li, L.F., Qian, R.Y., Liu, W.J., Wang, W.J., Biederman, J.A., Zhang, B., Kang, X.M., Wen, F.Q., Ran, Q.W., Zheng, Z.Z., Xu, C., Che, R.X., Xu, Z.H., Cui, X.Y., Hao, Y.B., Wang, Y.F., 2022. Drought timing influences the sensitivity of a semiarid grassland to drought. *Geoderma* 412, 115714. <https://doi.org/10.1016/j.geoderma.2022.115714>.
- Lian, X., Piao, S.L., Chen, A.P., Wang, K., Li, X.Y., Buermann, W., Huntingford, C., Peñuelas, J., Xu, H., Myneni, R.B., 2021. Seasonal biological carryover dominates northern vegetation growth. *Nat. Commun.* 12 (1), 983. <https://doi.org/10.1038/s41467-021-21223-2>.
- Liu, R.T., Zhu, F., Steinberger, Y., 2015. Effectiveness of afforested shrub plantation on ground-active arthropod communities and trophic structure in desertified regions. *Catena* 125, 1–9. <https://doi.org/10.1016/j.catena.2014.09.018>.
- Liu, R.T., Pen-Mouratov, S., Steinberger, Y., 2016a. Shrub cover expressed as an 'arthropod island' in xeric environments. *Arthropod-Plant Interact.* 10 (5), 393–402. <https://doi.org/10.1007/s11829-016-9450-z>.
- Liu, R.T., Zhu, F., Steinberger, Y., 2016b. Changes in ground-dwelling arthropod diversity related to the proximity of shrub cover in a desertified system. *J. Arid Environ.* 124, 172–179. <https://doi.org/10.1016/j.jaridenv.2015.08.014>.
- Liu, R.T., Yael, N., Yosef, S., Marcelo, S., 2020. Effects of rainfall manipulations versus a natural aridity gradient on plant litter arthropods in desert and Mediterranean ecosystems. *Appl. Soil Ecol.* 156, 103716. <https://doi.org/10.1016/j.apsoil.2020.103716>.
- Martin-Chave, A., Béral, C., Mazzia, C., Capowiez, Y., 2019. Agroforestry impacts the seasonal and diurnal activity of dominant predatory arthropods in organic vegetable crops. *Agrofor. Syst.* 93 (6), 2067–2083. <https://doi.org/10.1007/s10457-018-0309-4>.
- Martinez Almoyna, C., Calderón Sanou, I., Lionnet, C., Gielly, L., Boyer, F., Dufour, P., Duniach, L., Miqel, C., Ohlmann, M., Poulenard, J., Renaud, J., Saillard, A., Si Moussi, S., Stephan, R., Varoux, M., Münkemüller, T., Thuiller, W., 2024. Vegetation structure and climate shape mountain arthropod distributions across trophic levels. *J. Anim. Ecol.* 93 (10), 1510–1523. <https://doi.org/10.1111/1365-2656.14164>.
- Martins, C.S.C., Delgado-Baquerizo, M., Jayaramaiah, R.H., Tao, D., Wang, J., Sáez-Sandino, T., Liu, H., Maestre, F.T., Reich, P.B., Singh, B.K., 2024. Aboveground and belowground biodiversity have complementary effects on ecosystem functions across global grasslands. *PLoS Biol.* 22 (8), e3002736. <https://doi.org/10.1371/journal.pbio.3002736>.
- Mestre, L., Narimanov, N., Menzel, F., Entling, M.H., 2020. Non-consumptive effects between predators depend on the foraging mode of intraguild prey. *J. Anim. Ecol.* 89 (7), 1690–1700. <https://doi.org/10.1111/1365-2656.13224>.
- Miriti, M.N., 2006. Ontogenetic shift from facilitation to competition in a desert shrub. *J. Ecol.* 94 (5), 973–979. <https://doi.org/10.1111/j.1365-2745.2006.01138.x>.
- Mongil-Manso, J., Navarro-Hevia, J., San Martín, R., 2022. Impact of land use change and afforestation on soil properties in a Mediterranean mountain area of central Spain. *Land* 11 (7), 1043. <https://doi.org/10.3390/land11071043>.
- Mougi, A., 2024. Ecosystem engineering and food web stability. *Sci. Rep.* 14 (1), 19400. <https://doi.org/10.1038/s41598-024-70626-w>.
- Newell, F.L., Ausprey, I.J., Robinson, S.K., 2023. Wet and dry extremes reduce arthropod biomass independently of leaf phenology in the wet tropics. *Glob. Chang. Biol.* 29 (2), 308–323. <https://doi.org/10.1111/gcb.16379>.
- Nielsen, U.N., Ball, B.A., 2015. Impacts of altered precipitation regimes on soil communities and biogeochemistry in arid and semi-arid ecosystems. *Glob. Chang. Biol.* 21 (4), 1407–1421. <https://doi.org/10.1111/gcb.12789>.
- Pichon, B., Gounand, I., Donnet, S., Kéfi, S., 2024. The interplay of facilitation and competition drives the emergence of multistability in dryland plant communities. *Ecology* 105 (8), e4369.
- Prévosto, B., Helluy, M., Gavinet, J., Fernandez, C., Balandier, P., 2020. Microclimate in Mediterranean pine forests: what is the influence of the shrub layer? *Agri. For. Meteorol.* 282–283, 107856. <https://doi.org/10.1016/j.agrformet.2019.107856>.
- Qu, Q., Wang, Z., Xu, H.W., Liu, R.T., Wang, M.G., Xue, S., 2025. Sand dune fixation enhances the contribution of microbial necromass carbon to soil organic carbon: a case study of mu su sandy land in China. *Appl. Soil Ecol.* 209, 106011. <https://doi.org/10.1016/j.apsoil.2025.106011>.
- R Core Team, 2019. R: a Language and Environment for Statistical Computing. R Foundation for Statistical Computing, Vienna, Austria.
- Rudolf, V.H.W., 2019. The role of seasonal timing and phenological shifts for species coexistence. *Ecol. Lett.* 22 (8), 1324–1338. <https://doi.org/10.1111/ele.13277>.
- Sun, J.C., Liu, R.T., Sternberg, M., Zhou, L., Yang, Z.M., 2025. Grazing reduces shrub-facilitated diversity of ground-dwelling arthropods in semiarid ecosystems. *Ecol. Ind.* 170, 113052. <https://doi.org/10.1016/j.ecolind.2024.113052>.
- Svanbäck, R., Quevedo, M., Olsson, J., Eklöv, P., 2015. Individuals in food webs: the relationships between trophic position, omnivory and among-individual diet variation. *Oecologia* 178 (1), 103–114. <https://doi.org/10.1007/s00442-014-3203-4>.
- Tojić, T., Đorđević, T., Đurović-Peješev, R., Ćimović, M., Božić, D., Radivojević, L., Sarić-Krmanović, M., Vrbančanin, S., 2025. Allelopathic potential of *Artemisia absinthium* and *Artemisia vulgaris* from serbia: chemical composition and bioactivity on weeds. *Plants* 14 (11), 1663. <https://doi.org/10.3390/plants14111663>.
- Torode, M.D., Barnett, K.L., Facey, S.L., Nielsen, U.N., Power, S.A., Johnson, S.N., 2016. Altered precipitation impacts on above- and below-ground grassland invertebrates: summer drought leads to outbreaks in spring. *Front. Plant Sci.* 7. <https://doi.org/10.3389/fpls.2016.01468>.
- Varpe, Ø., 2017. Life history adaptations to seasonality. *Integr. Comp. Biol.* 57 (5), 943–960. <https://doi.org/10.1093/icb/ix123>.
- Wang, X., Song, J.L., Xiao, Z.Q., Wang, J., Hu, F.Z., 2022. Desertification in the Mu Us sandy land in China: response to climate change and human activity from 2000 to 2020. *Geogr. Sustain.* 3 (2), 177–189. <https://doi.org/10.1016/j.geosus.2022.06.001>.
- Wang, Y.H., Yu, P.T., Xiong, W., Shen, Z.X., Guo, M.C., Shi, Z.J., Du, A.P., Wang, L.M., 2008. Water-yield reduction after afforestation and related processes in the semiarid Liupan mountains, northwest China. *J. Am. Water Resour. Assoc.* 44 (5), 1086–1097. <https://doi.org/10.1111/j.1752-1688.2008.00238.x>.
- Wilbur, H.M., Rudolf, V.H.W., 2006. Life-history evolution in uncertain environments: bet hedging in time. *Am. Nat.* 168 (3), 398–411. <https://doi.org/10.1086/506258>.
- Xie, L.N., Guo, H.Y., Liu, Z., Gabler, C.A., Chen, W.Z., Gu, S., Ma, C.C., 2017. Shrubs facilitate recruitment of *Caragana stenophylla* pojarik: microhabitat amelioration and protection against herbivory. *Ann. For. Sci.* 74 (4). <https://doi.org/10.1007/s13595-017-0668-4>.
- Xu, J., 2011. China's new forests aren't as green as they seem. *Nature* 477, 371.

- Yela, N.I., Torrén, J., Díaz Casas, A.Y., San Martín, J.A., Aranda-Rickert, A., 2023. Ephedra shrubs facilitate local arthropod communities in the andean puna: implications for conservation and habitat restoration. *Ecología Austral* 33 (3), 938–949. <https://doi.org/10.25260/EA.23.33.3.0.2292>.
- Yin, W.Y., 2000. *The Key to Soil Fauna of China*. Science Press, Beijing.
- Zhai, J.J., Wang, L., Liu, Y., Wang, C.Y., Mao, X.G., 2023. Assessing the effects of China's three-north shelter forest program over 40 years. *Sci. Total Environ.* 857, 159354. <https://doi.org/10.1016/j.scitotenv.2022.159354>.
- Zhang, A.N., Chen, S.Y., Chen, J.W., Cui, H.W., Jiang, X.X., Xiao, S., Wang, J.J., Gao, H. N., An, L.Z., Cardoso, P., 2023. Shrub and precipitation interactions shape functional diversity of nematode communities on the Qinghai-Tibet plateau. *Glob. Chang. Biol.* 29 (10), 2746–2758. <https://doi.org/10.1111/gcb.16638>.
- Zhang, Y.K., Peng, S., Chen, X.L., Chen, H.Y.H., 2022. Plant diversity increases the abundance and diversity of soil fauna: a meta-analysis. *Geoderma* 411, 115694. <https://doi.org/10.1016/j.geoderma.2022.115694>.
- Zhang, C.C., Wang, Y.Q., Jia, X.X., Shao, M.A., An, Z.Z., 2020. Impacts of shrub introduction on soil properties and implications for dryland revegetation. *Sci. Total Environ.* 742, 140498. <https://doi.org/10.1016/j.scitotenv.2020.140498>.
- Zhao, H.L., Liu, R.T., 2013. The “bug island” effect of shrubs and its formation mechanism in Horqin sand land, Inner Mongolia. *Catena* 105, 69–74. <https://doi.org/10.1016/j.catena.2013.01.009>.
- Zheng, L.Y., Gui, H., 1999. *Insect Classification*. Nanjing Normal University Press, Nanjing.