Bottom-up effects of plant quantity and quality on arthropod diversity across multiple trophic levels in a semi-arid grassland

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Abstract
1. Plant quantity and quality can independently affect the diversity of the entire arthropod communities and multiple arthropod taxa in grassland ecosystems. However, it remains unclear how these effects on arthropod taxa at one trophic level propagate through food web to influence the diversity of higher trophic levels.

2. We performed a monoculture experiment with 15 herbaceous species in the Inner Mongolian grassland to investigate how natural variations in plant productivity and host leaf traits affect herbivore taxon richness, which, in turn, affects predator taxon richness.

3. For herbivores, plant productivity indirectly promoted herbivore taxon richness by increasing herbivore biomass, which was attributed to the increases in the richness of dominant sucking herbivores and endophytes with high food requirements. However, the high plant quality indicator (e.g. high leaf protein, phosphorus and water contents, and high leaf protein to carbohydrate ratio) directly increased, whereas the low plant quality indicator (e.g. high leaf lignin content) directly decreased herbivore taxon richness. Taxon richness of chewing and sucking herbivores with specific feeding modes (tearing or sucking mouthparts) showed strong positive responses to increasing plant quality.

4. For predators, herbivore taxon richness, rather than herbivore biomass, mainly mediated the positive effects of plant productivity and the high plant quality indicator, but the negative effect of the low plant quality indicator, on predator taxon richness. At the feeding guild level, the taxon richness of parasitoids, other predators and spiders exhibited positive responses to different herbivores, which was attributed to their different diet preferences. Predator diversity could be promoted by prey partitioning among predator guilds facilitating species coexistence. At the family level, the taxon richness of most predator families was positively correlated with that of more than one herbivore family.
suggested that high predator diversity may be caused by balanced diets owing to high prey diversity.

5. Synthesis. Natural variations in plant quantity and quality can substantially affect the diversity of herbivores and cascade up the food web to affect predators. Specificity and mechanisms of feeding have a large impact on the responses of arthropod guilds at each trophic level.

**KEYWORDS**
arpod biomass, arthropod taxon richness, food web, herbivore, multi-trophic interactions, plant leaf traits, plant productivity, plant-herbivore interactions, predator

### 1 | INTRODUCTION

Arthropods comprise the majority of animal biodiversity in terrestrial ecosystems, and their growth rate and reproductive success depend largely on primary producers (Siemann, 1998; Uchida & Ushimaru, 2014; Wilson, 1987). For example, a previous study showed that increased plant productivity elevated herbivore and predator diversity simultaneously, with predator diversity showing the strongest response (Wimp et al., 2010). Lu et al. (2021) recently reported that changes in plant quantity (e.g. biomass production) and quality (e.g. leaf nutrient content) across different plant species can independently affect the diversity of the entire arthropod communities and different taxonomic groups in grasslands. Both herbivores and predators can be assigned to different guilds based on their feeding habits (Carmona et al., 2011; Pratt et al., 2017). Changes in plant biomass and host plant traits may influence herbivore diversity, which, in turn, affects predator diversity through trophic interactions between feeding guilds (Christenson, 1984; Jacquot et al., 2019; Scherber et al., 2010). However, it remains unclear how effects of plant quantity and quality on arthropod taxa at one trophic level propagate through the food web to influence the diversity of higher trophic levels (Awmack & Leather, 2002; Forbes et al., 2017; Perkins et al., 2004).

**Table 1** Proposed hypotheses regulating the taxon richness of herbivores and predators in grasslands

| No | Hypothesis name | Prediction |
|----|-----------------|------------|
| Plants to Herbivores | H1 | Plant quantity hypothesis | Plant biomass could directly and indirectly promote herbivore richness by increasing herbivore biomass$^1$,$^2$ |
| | H2 | Plant quality hypothesis | Plant nutrient content could directly and indirectly promote herbivore richness by increasing herbivore biomass$^3$,$^4$ |
| Herbivores to Predators | H3 | More individuals hypothesis | Herbivore biomass could promote predator biomass, leading to an abundance-driven accumulation of predator species$^5$,$^6$ |
| | H4 | Resource heterogeneity hypothesis | Herbivore diversity could enhance predator richness by increasing the opportunities of niche specialization for specialist predators and/or by providing more balanced diets for generalist predators$^7$,$^8$,$^9$,$^{10}$ |

Notes: References are given by numbers in table: $^1$Siemann (1998), $^2$Simons et al. (2014), $^3$Awmack and Leather (2002), $^4$Loranger et al. (2012), $^5$Srivastava and Lawton (1998), $^6$Borer et al. (2012), $^7$Hutchinson (1959), $^8$Lewinsohn and Roslin (2008), $^9$Jacquot et al. (2019) and $^{10}$Dassou and Tixier (2016).
quickly access nutrients from leaf or phloem sap for their growth and reproduction (Novotny et al., 2010; Welti et al., 2020; Wilson et al., 2018). However, the diversity of endophytes (e.g. fruit flies and leaf miners) may be less likely to reflect plant leaf quality since they often feed within flowers and fruits and are more sensitive to carbohydrate than protein (Peguero et al., 2017). Alternatively, an increase in plant protein content could increase the fecundity and biomass of arthropods such as flies (Family: Tephritidae) and aphids (Family: Acrididae), which would indirectly increase herbivore richness because of the reduction in resource competition among herbivores (Awmack & Leather, 2002).

Herbivores could mediate the effects of plant quantity and quality on the diversity of higher trophic levels via prey and predator interactions (Jacquot et al., 2019; Siemann, 1998; Welti et al., 2020). Two main hypotheses have been proposed to describe the effects of herbivores on predator diversity. First, the more individuals hypothesis predicts that increases in the biomass of herbivores promote predator biomass and thus increase predator richness (H3; Table 1; Figure 1; Simons et al., 2014; Srivastava & Lawton, 1998). If the increase in plant biomass and host leaf nutrient content promotes biomass of sucking and chewing herbivores, it may increase the number and range of prey available to parasitoids and predators and thus elevate total predator diversity (Hawkins et al., 1997; Petermann et al., 2010; Welti et al., 2020). Second, the resource heterogeneity hypothesis predicts that an increase in herbivore richness promotes predator richness through increased prey niches and diet variety (H4; Table 1; Hutchinson, 1959; Lewinsohn & Roslin, 2008). On one hand, increases in herbivore diversity under high plant resource conditions could increase opportunities of niche specialization for specialist predators, thereby promoting predator richness via the niche partitioning effect (Gamfeldt et al., 2005; Jacquot et al., 2019). For example, increased leaf nutrient content is expected to promote the diversity of sucking herbivores, which may, in turn, promote the diversity of the parasitoids reliant on this specific prey item (Hawkins et al., 1997; Petermann et al., 2010). On the other hand, increases in herbivore richness could enhance predator richness by providing more diverse and balanced prey resources for generalist predators (Dassou & Tixier, 2016; DeMott, 1998). In grasslands, spiders prey not only on sucking herbivores but also on chewing grasshoppers (Uetz, 1992). Hence, arthropod communities with diverse herbivorous feeding guilds may contain a greater variety of nutrient biomolecules essential for spiders, possibly leading to high spider richness (Yip et al., 2008). In fact, positive relationships are commonly observed between herbivore and predator diversity in terrestrial ecosystems (Dassou & Tixier, 2016; Jacquot et al., 2019; Siemann, 1998). It is not yet clear, however, how natural variations in plant biomass and host leaf traits affect the diversity relationships between herbivores and predators in grasslands.

FIGURE 1 Study design and conceptual flow diagrams. (a) The common garden experiment that contains monocultures of 20 plant species in the inner Mongolian grassland, which caused a breadth of natural variations in both plant biomass and host plant leaf traits (leaf carbohydrate, protein, phosphorus, water and lignin contents, and leaf protein:carbohydrate ratio). (b) A simple diagram to explain the direct and indirect effects of plant quantity and quality on taxon richness of herbivores and predators. From plants to herbivores, plant quantity (H1) or plant quality (H2) could directly and indirectly impact herbivore taxon richness by changing herbivore biomass. From herbivores to predators, herbivore biomass (H3) and herbivore taxon richness (H4) could mediate the effects of plant quantity and quality on predator taxon richness.
Although both plant quantity and quality could affect multitudes of arthropods, little is known about their independent roles in grassland ecosystems (Lu et al., 2021; Wimp & Murphy, 2021). First, previous studies manipulated plant communities by watering, fertilization and grazing, largely ignoring the effects of natural variations in plant productivity and host nutrient content on arthropod diversity (Simons et al., 2014; Zhu et al., 2017). Therefore, changes in plant biomass were often tightly linked with concomitant shifts in host leaf traits, confounding investigators’ ability to isolate the effects of plant quantity and quality on the richness of arthropod communities (Wimp & Murphy, 2021). Second, many previous studies examined the effects of plant production and/or host plant traits only on a subset of taxonomic or functional groups (Peeters et al., 2007; Sagers, 1992). Nonetheless, multiple trophic groups of arthropods such as herbivores and predators are mainly regulated by vegetation and are critical for ecosystem function as pollinators and pest control (Joern & Laws, 2013). Third, although a few studies have attempted to elucidate the effects of plant biomass and host leaf traits on the diversity of multiple trophic groups (e.g. herbivores and predators), they did not break each trophic group into different feeding guilds according to their feeding modes and diet preferences (Simons et al., 2014). The specific interactions between plants and herbivorous feeding guilds (Welti et al., 2020) and between herbivorous and predatory guilds could be an important mechanism underlying the effects of plant quality and quantity on the diversity of higher trophic levels (Haddad et al., 2009; Jacquot et al., 2019). Thus, experimental designs that explore the effects of plant quantity and quality on multi-trophic arthropod diversity in realistic communities are needed.

To address these uncertainties, we used replicated monocultures of 15 herbaceous species in the Inner Mongolian grassland, with a wide range of natural variations in plant biomass and host leaf traits under similar environmental contexts. We sampled arthropods in the monoculture plots and determined the taxon richness and biomass of herbivores and predators. We also measured plant productivity and multiple leaf traits related to plant quality in the monoculture plots of different species. We attempted to answer the following questions. First, how do natural variations in plant productivity and plant traits directly and indirectly affect the taxon richness of herbivores across monocultures of different plant species? Second, how do the effects of plant quantity and quality on arthropod taxa at one trophic level propagate through food web to influence the diversity of adjacent trophic levels? To guide our analyses, we tested the following hypotheses: (a) Plant productivity (H1) and host leaf traits (H2) could directly and indirectly impact herbivore taxon richness by changing the biomass of herbivorous feeding guilds, because both plant food quantity and quality are extremely important in every aspect of insect performance, including growth, survival and reproduction, and have strong effects on herbivore biomass and taxon richness (Loranger et al., 2012; Siemann, 1998). (b) Herbivore biomass would mediate the effects of plant resources on predator richness (H3), because the increase in plant resources is likely to promote herbivore and predator biomass, leading to a biomass-driven accumulation of predator species (Lewinsohn & Roslin, 2008; Lind et al., 2017). (c) Herbivore richness mediates the effects of plant resources on predator richness (H4), because higher prey diversity could enhance predator taxon richness either by increasing the opportunities of niche specialization for specialist predators or by providing a more balanced diet for generalist predators (Dassou & Tixier, 2016; Jacquot et al., 2019).

2 | MATERIALS AND METHODS

2.1 | Study site

This study was conducted at the Inner Mongolia Grassland Ecosystem Research Station (IMGERS, 116°42′E, 43°38′N) of the Chinese Academy of Sciences, which is located in the Xilin River Basin of Inner Mongolia, China (Bai et al., 2004). The study area has a semi-arid continental climate and is characterized by a mean annual precipitation of 346.1 mm and a mean annual temperature of 0.3°C. Precipitation mainly occurs in the growing season (June-August), which coincides with high temperatures. The soil is a loamy sand texture (Calcic Chernozem according to the ISSS Working Group RB, 1998).

The monoculture experiment was conducted in June 2014, with a fenced area of 40 × 40 m near the IMGERS (Figure 1a). The soil seed bank was reduced by bulldozing and manually ploughing and harrowing this area to remove the top 10 cm of the soil horizon. Before the seeds were sown, this area was divided into four blocks. We selected 20 native grassland plant species that represented more than 95% of the biomass and plant coverage of the natural community at our study site. These 20 plant species were randomly assigned to each plot (1.2 × 1.2 m) within each block, resulting in a random block design and a total of 80 monoculture plots. In 2013, seeds of all plant species were collected by hand from natural communities and stored at 4°C until use. Seeds were sown in each plot in the middle of June 2014 at a density of 340 seeds per m², according to the density data for the natural communities at the experimental site (Sasaki et al., 2019). After the seeds were sown, the plots were regularly watered until the end of July to encourage germination and plant establishment, and weeds (unwanted plants germinating from the seed bank) were removed manually. Because of high mortality of herbaceous species in 2018, only 15 of the 20 planted species (belonging to four plant families) were investigated in this study (Table S1). All necessary permits were obtained from IMGERS prior to establishing of the monoculture experiment.

2.2 | Plant productivity and leaf trait measurements

For each monoculture plot, the standing biomass of plants was sampled from a 50 cm × 50 cm area in mid-August 2018. Plant material was sampled by cutting all plants in each quadrant at the soil surface
and then was oven-dried at 65°C for 48 h and weighed. Plant biomass was calculated from dry biomass measurements (g m$^{-2}$) of each plot, as the standing above-ground biomass of these steppe communities reached the annual peak at mid-August (Bai et al., 2004).

In August 2018, five undamaged, fully expanded leaves were collected from each of the 15 plant species from each monoculture plot. Plant leaf traits, including leaf non-structural carbohydrate, protein, phosphorus, water and lignin contents were measured. These leaf traits are important determinants of plant nutrient quality for arthropods (Awmack & Leather, 2002; Forbes et al., 2017; Joern et al., 2012). Fresh leaves were weighed and dried for 24 h at 65°C, and leaf water content was expressed as the difference between fresh and dry weight, divided by dry weight. A ball mill was used to grind dry leaf material to a fine powder, and samples of 10 mg were analysed for leaf phosphorus content using an elemental analyzer (VarioEL Element Analyzer; Hanau, Germany). We measured plant protein content with using the Bradford assay and analysed non-structural carbohydrate content using the phenol–sulphuric acid method, following the protocol of Clissold et al. (2006). The leaf protein:carbohydrate ratio was defined as the ratio of leaf protein to leaf non-structural carbohydrate content. Leaf lignin content was measured following sequential extraction analysis of acid detergent lignin (Forbes et al., 2017). We averaged the data of each leaf trait for each plant species and used the mean leaf traits values for data analysis. These 15 plant species encompassed a broad range of leaf trait variation (Figure S1).

2.3 Arthropod sampling and identification

Using the sweep-net sampling, we collected arthropods from the monoculture plots between 10 AM and 4 PM on days with no rainfall in August 2018. The sampling period corresponded with our collection of data on plant biomass and functional traits. Sweep-net sampling facilitates the capture of numerous vegetation-dwelling arthropods by dislodging them from vegetation (Andersen et al., 2019), and the large intake diameter of the sweep net (32.0 cm) also allows the capture of stronger flying insects such as wasps. Although some grasshoppers have different phenology and show seasonal differences in peak abundance (Guo et al., 2009), our sampling period typically coincided with the peak abundance of many arthropod taxa in the study area (Wang et al., 2020). We did not use pitfall trap sampling method to collect the ground-dwelling arthropods, which may have led to the omission of some predators (e.g. carabid beetles) playing key roles in grassland ecosystems (Andersen et al., 2019; Pringle & Fox-Dobbs, 2008). Therefore, arthropod diversity may be underestimated in this study. However, other studies have found that the number of arthropod species obtained from sweep-net sampling is highly obtained with that sampled using vacuum sampling for both vegetation-dwelling and ground-dwelling arthropods (Siemann, 1998). We conducted 50 sweeps by using a muslin net for each monoculture plot. We sampled the arthropods by sweeping at 180° arcs through the vegetation canopy, quickly turning, and reversing the direction at the end of each arc (Doxon et al., 2011). At the end of each arc, a quick but fluid upturn of the sweep net was used to prevent the escape of the captured arthropods. The contents of the sweep net were preserved in bottles containing ethyl acetate.

In the laboratory, all arthropod individuals were identified by optical microscopy at the genus and species levels as far as possible. Some species were treated as reference specimens because they could not be identified to the genus or species level during the initial identification. These reference specimens were placed in vials containing 75% ethanol and sent to taxonomists for accurate identification to morphospecies. Each morphospecies was further placed into one of two trophic categories (Table S2): herbivores and predators (Perner et al., 2005), and then carefully assigned to one of the three feeding guilds based on published accounts for the taxonomic guilds (Carmona et al., 2011; Pratt et al., 2017). Herbivorous feeding guilds consisted of (1) sucking/piercing herbivore (species or genus from Pentatomidae, Rhypharochromidae, Coreidae, Tingidae, Piesmatidae, Mordellidae, Miridae, Curculionidae, Aphididae and Cicadellidae); (2) chewing herbivore (species or genus from Anthicidae, Acrididae and Chrysomelidae) and (3) endophytes (species or genus from Sphedidae, Tephritidae, Tachinidae, Anthomyiidae and Trypetidae; Carmona et al., 2011). Predatory guilds consisted of (1) parasitoids (species or genus from Dryiniidae, Ichneumonidae, Mellinidae, Crabronidae, Bethylidae, Tiphidae and Scollidae); (2) other predators (species or genus from Chrysopidae, Anthocoridae, Asilidae, Syrphidae, Chironomida, Dolichopodidae and Bombyliidae) and (3) spiders (species or genus from Thomisidae; Pratt et al., 2017). We also measured the biomass of each arthropod family collected from the sampled monoculture plots. For herbivores, sucking and endophyte herbivores were the dominant feeding guilds (relative biomass [RB] >10% of total herbivore biomass), and chewing herbivores were the rare feeding guild (RB <10% of total herbivore biomass; Figure S2a). For predators, parasitoids and other predators were the two dominant feeding guilds (RB >10% of total predator biomass), and spiders were the rare predator feeding guild (RB <10% of total predator biomass; Figure S2b). Consequently, we could establish gradients in taxon richness and biomass of the entire community and each herbivore and predator feeding guild across the monoculture plots of different plant species (Tables S3 and S4).

2.4 Data analysis

First, we used the linear mixed-effect model (LMM) to determine the responses of arthropod variables (herbivore richness and biomass as well as predator richness and biomass) to changes in plant quality or quantity. Because plant leaf traits of different species are often correlated, we used principal component analysis to create multivariate indices of plant quality variables for each plant species (Figure 2). The first principal component was treated as the high plant quality indicator for arthropods, which was positively correlated with the leaf protein:carbohydrate ratio and leaf protein, phosphorus and water.
contents, explaining 36.3% of the total variance. The second principal component was treated as the low plant quality indicator for arthropods, which was positively correlated with leaf lignin content, accounting for 20.1% of the total variance (Figure 2). In the LMMs, plant biomass or plant quality indicators were treated as fixed factors, and block was treated as a random factor, using R package lme4. Because of the potential linear and nonlinear relationships between plants and arthropods (Boersma & Elser, 2006), we compared the fit of the first- and second-order polynomials. To evaluate the goodness of model fit, we used R package MuMln to calculate the marginal and conditional $R^2$, which quantified the proportion of model variation explained by fixed effects and the combination of fixed and random effects, respectively (Nakagawa & Schielzeth, 2013).

Next, we used the structural equation modelling (SEM) to analyse hypothetical pathways that may explain how changes in plant quantity and quality across the monocultures of different plant species directly and indirectly affect the taxon richness of herbivores and predators. Based on the hypothesized mechanisms, first, we developed an a priori conceptual model depicting the causal relationships among these variables in a path diagram (Figure 1b). From plants to herbivores, the conceptual SEM contained the direct and indirect pathways for the effects of plant quantity (plant quantity hypothesis H1) or plant quality (plant quality hypothesis H2) on herbivore biomass and taxon richness. From herbivores to predators, the conceptual SEM contained the direct and indirect pathways for the effects of plant quantity and quality via the changes in herbivore biomass (more individuals hypothesis H3) or herbivore taxon richness (resource heterogeneity hypothesis H4) on predator taxon richness. We considered all explanatory variables because we assumed no multicollinearity between the explanatory variables (all variance inflation factors were <10). The SEMs were implemented using the lavaan package. All variables were transformed to natural logarithms before SEM to mitigate departure from normality and linearity. Because of the potential nonlinear relationships between plants and arthropods, we used the nonparametric Bollen–Stine bootstrapping estimations to increase the robustness of our SEM (Bollen & Stine, 1992). A good model fit was indicated by a Bollen–Stine bootstrap $p > 0.10$.

Finally, the relationships between herbivore richness and predator richness were further examined using linear regression at the feeding guild level and at the family level.

3 | RESULTS

3.1 | Responses of richness and biomass of herbivores to plant quantity and quality

Herbivore richness and biomass increased quadratically with increase in plant biomass (Figure 3a,d; Table S5). This was associated with significant increases in the richness and biomass of endophyte and sucking herbivores (Figure S3a,d; Tables S6 and S7). Herbivore richness increased linearly with increase in the high plant quality indicator (Figure 3b; Table S5), but herbivore biomass did not (Figure 3e). The richness of chewing and sucking herbivores increased linearly with increasing the high plant quality indicator (Figure S3b; Table S6). In contrast, herbivore richness and herbivore biomass decreased linearly with increase in the low plant quality indicator (Figure 3c,f; Table S5). The richness of chewing, endophyte, and sucking herbivores and the biomass of endophyte and sucking herbivores decreased linearly with increase in the low plant quality indicator (Figure S3c,f; Table S6 and S7).

FIGURE 2. Results of principal component analysis of plant leaf traits. Plant traits include leaf carbohydrate, protein, phosphorus, water and lignin contents, and leaf protein:carbohydrate ratio. Light blue dots represent different plant species growing in monoculture plots. For each component, the percentage of explained variance is indicated.
FIGURE 3 Effects of plant biomass and plant quality indicators on herbivore richness (e.g. species or genera richness per m$^2$) (a–c), herbivore biomass (e.g. g per m$^2$) (d–f), predator richness (g–i) and predator biomass (j–l) across monocultures of different plant species. The high plant quality indicator indicates plants with high nutrient content (e.g. high leaf protein:carbohydrate ratio, high protein, phosphorus and water contents) for arthropods, and the low plant quality indicator indicates plants with low nutrient content (e.g. high leaf lignin content). Solid lines indicate fits of bivariate linear and non-linear mixed effects models with block as a random effect. The shaded grey areas indicate 95% confidence intervals for the regressions. Marginal $R^2_m$ (variance explained by fixed effects) and $p$ values are also shown.
3.2 | Responses of the richness and biomass of predators to plant quantity and quality

Predator richness and biomass showed linear relationships with plant biomass (Figure 3g; Table S5). For different feeding guilds, taxon richness of other predators and parasitoids (Figure S3g; Table S6), and biomass of parasitoids increased with increasing plant biomass (Figure S3; Table S7). Predator richness increased quadratically and predator biomass increased linearly with increasing the high plant quality indicator (Figure 3h,k; Table S5). In particular, the taxon richness of other predators and the biomass of parasitoids increased linearly with increase in the high plant quality indicator (Figure S3h,k). Conversely, predator richness and biomass decreased quadratically with increase in the low plant quality indicator (Figure 3i,l). The taxon richness and biomass of other predators and parasitoids decreased quadratically with increase in the low plant quality indicator (Figure S3i,l).

3.3 | Pathways determining arthropod richness across trophic levels

Our SEM analysis showed that plant biomass increased herbivore biomass (standardized regression weight = 0.68), which, in turn, increased herbivore taxon richness (0.45; Figure 4). The altered herbivore richness, in turn, increased predator richness (0.28). Therefore, plant biomass had total positive effects (0.31) on herbivore richness and predator richness (0.09). The high plant quality indicator increased herbivore richness (0.23), which, in turn, increased predator richness, resulting in total positive effect on predator richness. However, the low plant quality indicator decreased herbivore richness (~0.54), which, in turn, increased predator richness, resulting in total negative effect on predator richness (~0.15). Predator biomass also increased predator richness (0.63; Figure 4).

3.4 | Relationship between herbivore richness and predator richness

At the feeding guild level, sucking herbivore richness was positively related to the taxon richness of parasitoids and total predators (Figure 5a); endophyte richness was positively related to the taxon richness of parasitoids, other predators and total predator (Figure 5b), and chewing herbivore richness was positively related to the taxon richness of spiders (Figure 5c). The biomass of sucking herbivores and endophytes were positively related to the taxon richness of both overall and each herbivore feeding guild (Figure S4a,b). The biomass of spiders, parasitoids and other predators were positively related to the taxon richness of overall and with each predator feeding guild (Figure S5a–c).

At the family level, the taxon richness of Ichneumonoidea, Crabronidae, Tephridae, Chrysopidae, Anthocoridae, Asilidae, Chironomida and Thomisidae (accounting for 53.3% of total predator families) were positively related to the taxon richness of more than one herbivore family (Figure 6a,b; Figure S6), indicating that these predators could be the generalist predators with more than one kind of edible prey. The taxon richness of Dryinidae and Meliinidae (accounting for 13.3% of total predator families) was positively related to the taxon richness of one herbivore family (Figure 6a;b; Figure S6), indicating that these predators could be the specialist predators with only one prey. However, the taxon richness of Scoiliidae, Syrphidae, Dolichopodidae and Bombyliidae (accounting for 33.3% of total predator families) was not related to the taxon richness of any herbivore family, indicating the absence of edible prey for these predators (Figure 6a,b; Figure S6).

4 | DISCUSSION

4.1 | Effects of plant quantity and quality on herbivore richness

Plant biomass production and leaf nutrient content each have been shown to independently influence the diversity of the entire arthropod communities and multiple arthropod orders (Lu et al., 2021). Therefore, changes in plant quantity and quality may directly and/or indirectly affect the diversity of adjacent trophic levels, with effects cascading up to higher trophic levels (Barnes et al., 2020; Dyer & Letourneau, 2003; Scherber et al., 2010). We found that plant biomass was positively associated with herbivore taxon richness, which is consistent with our first hypothesis. However, previous studies, which focused on plant–herbivores interactions, have shown that the relationship between plant productivity and trophic diversity can be positive (Siemann, 1998), negative (Jepsen & Winemiller, 1998) or neutral (Post, 2002). These studies often manipulated plant community productivity with simultaneous changes in plant composition, confounding the effects of plant production on herbivore diversity. After the effects of host plant traits were controlled, SEM showed that plant productivity could indirectly promote herbivore taxon richness by promoting herbivore biomass. Our finding is consistent with that of a previous study, which found that increases in plant production without changes in community composition increase herbivore richness (Wimp et al., 2010). With respect to different feeding guilds, we found that plant biomass promoted the biomass of dominant sucking herbivores and endophytes, which, in turn, increased their taxon richness and thus total herbivore richness. Plant production, in contrast, has been shown to promote herbivore richness by allowing more rare species to persist (Siemann, 1998). In our study, the strong positive responses of dominant herbivore feeding guilds to increase in plant biomass may be explained by their higher food requirements than those of the rare feeding guilds (Lu et al., 2021; Rich et al., 2013; Welti et al., 2020). For example, common sucking herbivores such as aphids often require larger amounts of food to maintain their growth rate (Lu et al., 2021; Perner et al., 2005). Consequently, the populations of dominant herbivores with high biomass and abundance would be less prone to extinction.
due to environmental disturbance, resulting in high arthropod richness. In addition, increased primary production could provide more habitat volume and energy for sucking herbivores such as leafhoppers (Prather & Kaspari, 2019), which may potentially contribute to their survival, growth and reproduction (Kansman et al., 2021). Furthermore, increased plant biomass may promote herbivore diversity via indirect effects like microclimates (Prather & Kaspari, 2019). For example, herbivores, such as Hemiptera, often choose plant vegetation with high plant biomass as oviposition sites due to the low temperature and high humidity environment (Clissold et al., 2013; Grevstad & Klepetka, 1992; Obermaier et al., 2008).

We found a direct positive effect of a high plant quality indicator (e.g. high leaf protein:carbohydrate ratio, high leaf protein, phosphorus and water contents) on herbivore taxon richness. These results are consistent with our second hypothesis that high plant quality enhances herbivore richness (Awmack & Leather, 2002; Joern et al., 2012). Contrary to our findings, other studies have shown that plant food with a high phosphorus to carbon ratio can inhibit the growth of several herbivorous groups (e.g. chironomids) and thus decrease arthropod diversity (Boersma & Elser, 2006; Forbes et al., 2017). Possible mechanisms for these patterns include herbivores experiencing costs associated with the storage and excretion of excess macronutrients from their body, which could impair their development and growth (Boersma & Elser, 2006). Additionally, other herbivorous groups (e.g. female locusts) have been shown to be sensitive to plant food with high protein:carbon ratios (Boersma & Elser, 2006; Le Gall et al., 2020). However, in the present study, we found that the high plant quality indicator significantly increased, while the low plant quality indicator significantly decreased taxon richness of chewing and sucking herbivores, suggesting a bottom-up nutrient limitation for herbivores. In grassland ecosystems, chewing and sucking herbivores are two important functional groups with specific feeding modes for effectively accessing plant nutrients, and their diversity and abundance may depend largely on leaf quality (Welti et al., 2020; Wilson et al., 2018). For example, chewing herbivores (Family: Acrididae) often use their tearing mouthparts to quickly consume leaf tissue, which provides them with essential proteins and thus their high growth and reproduction may be likely to reflect plant quality (Prather et al., 2021). Unlike chewers, sucking insects such as aphids and whiteflies are

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**Figure 4** The structural equation model showed how plant quantity and plant quality affected herbivore taxon richness, which, in turn, affected predator taxon richness. Because plant leaf traits of different species are correlated, we used principal component analysis to create multivariate indices of plant quality variables for each plant species. The high plant quality indicator indicates plants with high nutrient content (e.g. high leaf protein:carbohydrate ratio, high protein, phosphorus and water contents) for arthropods, and the low plant quality indicator indicates plants with low nutrient content (e.g. high leaf lignin content). Solid lines represent significant paths (p < 0.05), and dashed lines were non-significant paths. Numbers near the lines show standardized regression weights. Red (blue) arrows indicate positive (negative) effects. Model fit metrics ($\chi^2$ and Bollen–Stein bootstrap $p$ value) are shown. $R^2$ values for component models are given below the boxes of endogenous variables.
equipped with piercing and sucking mouthparts; this could facilitate their feeding on nutrient-rich leaf phloem (Petermann et al., 2010). As a result, the density and diversity of sucking herbivores may be strongly influenced by the phloem sap quality of different plant species. Notably, we found that the taxon richness of endophytes did not change significantly with increased plant quality. This outcome is likely attributable to the fact that the host plant organs preferred by many endophytes (e.g. fruit flies) are flowers, fruits and seeds (Peguero et al., 2017), which would weaken the responses of endophytes to changes in plant leaf traits. Overall, our results suggest
that the responses of herbivore taxon richness to variation in plant leaf quality are guild specific in grasslands, and the increase in total herbivore diversity was mainly driven by the increases in taxon richness of chewing and sucking herbivores under high plant nutrient conditions.

4.2 | Herbivore richness mediated the effects of plant quantity and quality on predator richness

In our study, herbivore biomass did not mediate the effects of plant nutrient quality indicators on predator taxon richness, which does not agree with the core predictions of our third hypothesis. This conclusion contradicts the findings of many previous experimental and observational studies in grasslands showing positive relationships between herbivore and predator biomass (Haddad et al., 2009; Welti et al., 2020). This unexpected result may be explained in several ways: First, previous studies that showed significant positive impacts of herbivore biomass on predator biomass were often conducted in fertilization and irrigation experiments, and the increased plant nutrient content could remarkably promote herbivore biomass and thus lead to biomass-driven accumulation of predator species (Simons et al., 2014; Zhu et al., 2019). However, under natural conditions, plants need to invest considerable carbon in physical and chemical defences against herbivores (Carmona et al., 2011); this could decrease plant nutrient content and thus nitrogen-rich herbivore tissues, which would weaken the positive correlation between herbivore and predator biomass (Awmack & Leather, 2002). Second, the lack of significant positive relationships may be attributed to the fact that the biomass of predators is constrained by the presence of their own predators (Cronin et al., 2004). For example, many parasitoids and spiders are consumed by birds in grasslands (Tscharntke, 1992). Third, some spiders have relatively low metabolic rates, which allows them to burn less energy and thus to maintain relatively high biomass with limited available prey biomass (Welti et al., 2020). Finally, the increased plant biomass could provide additional habitat volume for spiders to hang their webs, and more flowers and pollen to feed parasitoid wasps, leading to high predator and parasitoid biomass and abundance (Prather et al., 2021). Therefore, herbivore biomass could be constrained by high predation rates, which would damp the relationship between herbivore and predator biomass (Barnes et al., 2020). Surprisingly, we found that taxon richness of predators increased significantly with predator biomass, both overall and within each feeding guild (parasitoids, other predators, and spiders). This is easily explained by the increases in biomass of all feeding guilds, which can enhance the total number of predator individuals, and thus allow both common and rare species to persist locally (Siemann, 1998). However, we did not use pitfall trap method to sample the ground-dwelling arthropods, which may limit our ability to completely characterize the responses of predator richness to changes in plant resources (Hertzog et al., 2017). For instance, some ground-dwelling predators (e.g. carabid beetles) have been shown to prey at significant rates upon herbivores feeding on both C₃ and C₄ plants (Beckerman et al., 1997; Hawlena et al., 2012; Pringle & Fox-Dobbs, 2008). Future studies should determine the effects of plants on arthropod diversity using both pitfall trap and sweep-net sampling methods in grassland ecosystems.

Although many studies have shown positive effects of plant production and host plant traits on predator richness, they did not distinguish between direct and indirect effects (Dassou & Tixier, 2016; Haddad et al., 2009; Siemann, 1998). Based on the monoculture experiment, our SEM revealed that herbivore taxon richness mainly mediated the effects of plant productivity and host leaf traits on predator richness, supporting the fourth hypothesis. This is in contrast with the findings of previous studies showing that there was no effect of herbivore diversity on predator diversity (Fox, 2004; Jacquot et al., 2019). The absence of bottom-up diversity effects in those studies is partly explained by the lack of differentiation in predation for herbivores among predator feeding guilds (Gamfeldt et al., 2005). However, we documented a wide range of positive relationships between the taxon richness of herbivorous and predatory feeding guilds. The possible mechanism for these patterns lies in different feeding modes of predator guilds for consuming different herbivores (Hawkins et al., 1997). Specifically, we found that plant biomass and host traits significantly promoted taxon richness of sucking herbivores and endophytes, which, in turn, were positively correlated with the taxon richness of parasitoids. Parasitoid wasps often attack sucking herbivores (e.g. aphids) and endophytes (e.g. leaf miners) by laying a single egg into the body of their host, and utilizing up most of the host's nutrients for development and growth of the parasitoid larva until it eventually pupates (Hawkins, 1992; Petermann et al., 2010). Therefore, it is possible that increasing plant quantity and quality could increase the number of specifically associated aphids and leaf miners, leading to an increase in the number of specifically associated parasitoid species. Additionally, we found that the taxon richness of endophytes was positively related to that of other predators. Although endophytes (e.g. leaf miners) feeding within plant tissues could be protected from general predation to a certain extent (Hawkins et al., 1997; Peguero et al., 2017), they can suffer high predation pressure from other types of enemies such as robber flies (Family: Asilidae), which have high mobility and actively search for food (Dennis & Lavigne, 2007). Moreover, we found that the taxon richness of chewing herbivores was positively related to that of spiders. Chewers such as grasshoppers usually have a larger body size and struggle longer than do other herbivores when they interact with spiders (Nentwig, 1985). Communal or cooperative attacks on grasshoppers have been observed in many social spider species, which is a major driving factor maintaining sociality and diversity of spider communities (Yip et al., 2008). Our results suggest that herbivores governing predator richness differed among different predator guilds with feeding specificity, which could promote predator diversity through finely prey resource partitioning (Muller et al., 1999; Peguero et al., 2017). At the family level, we further found that taxon richness of most predators such as Ichneumonidae, Crabronidae,
Tiphilidae, Chrysopidae, Anthocoridae, Asilidae, Chironomia and Thomisidae were positively associated with taxon richness of more than one herbivore family. We may speculate that the food web in our study is characterized by a high proportion of generalist predators (Jacquot et al., 2019). Hence, the positive effects of herbivore richness on predator richness may be attributed to a more balanced diet (Dassou & Tixier, 2016) since predator richness benefits from a mixed prey pool under high plant resource conditions (DeMott, 1998). We acknowledge that our conclusion here is based on correlation analyses; thus, more arthropod diversity experiments should be conducted in laboratory and/or in natural conditions to describe the trophic relationships between herbivores and predators.

5 | CONCLUSIONS

Our previous study from the same experiment demonstrates that plant quantity and quality can independently influence the diversity of arthropod communities, and with different patterns in each taxonomic group (Lu et al., 2021). Our findings in the present study provide new insights into the mechanisms underlying the bottom-up effects of plant quantity and quality on the taxon richness of multiple trophic levels of arthropods in grasslands. For herbivores, the increase in herbivore taxon richness was directly driven by the increase in plant nutrients and indirectly driven by higher herbivore biomass in plots where plant biomass was also greater. For predators, herbivore taxon richness, rather than herbivore biomass, mainly mediated the effects of plant quantity and quality on predator taxon richness. At the feeding guild level, taxon richness of parasitoids, other predators and spiders showed positive responses to different herbivores, which is probably attributed to their different diet preferences. At the family level, the taxon richness of most predator families was positively correlated with that of more than one herbivore family, suggesting that high predator diversity may be attributed to more balanced diets owing to the high prey diversity. Because the taxon richness of herbivores and predators depends largely on plants in natural communities, changes in plant quantity and quality may trigger cascading effects on the multiple services (e.g. pollination and pest control) that arthropods provide to humanity (Haddad et al., 2009; Levinsohn & Roslin, 2008). Given the important role that plant diversity plays in sustaining arthropod diversity across trophic levels (Dyer & Letourneau, 2003; Haddad et al., 2009; Scherber et al., 2010), future experiments should aim to determine the effects of plant quantity, plant quality and plant diversity on the multi-trophic diversity of arthropods and their linkages to the functioning of grassland ecosystems.

AUTHOR CONTRIBUTIONS

Yongfei Bai designed the research. Xiaoming Lu, Xuezhen Zhao, Taiki Tachibana, Kei Uchida and Takehiro Sasaki performed the experiments and collected the data. Xiaoming Lu, Xuezhen Zhao and Yongfei Bai conducted the data analysis and wrote the manuscript. All authors contributed substantially to the revision of the manuscript.

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CONFLICT OF INTEREST

The authors declare no conflict of interest.

DATA AVAILABILITY STATEMENT

Data are available from the Dryad Digital Repository https://doi.org/10.5061/dryad.jq2bqv8c7 (Lu et al., 2022).

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