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Priority effects of forbs arriving early: the role of root interaction and asymmetric competition

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Abstract

Background The priority effect of plant arrival is a key driver of community assembly and ecosystem succession during the restoration of degraded plant communities. However, the significance of the arrival order of different plant functional groups and their interactions with community assemblies remains unclear. Using a phytotron experiment with three fully crossed factors, we investigated the underlying mechanisms of priority effects and their relationships with the biomass and biodiversity effects in mixed plant communities by manipulating the order of arrival of species, isolation of roots, and removal of specific plants.

Results The results showed that the strength and direction of priority effects were influenced by arrival order, root interactions, asymmetric competition among species, and their interactions. The identities of early and late-sown species also determined the magnitude of priority effects. The priority effects were stronger in grass-first (24.76%) and legume-first communities (24.48%) than in forb-first communities. The pot biomass of the different priority treatments was highest in grass-first (5.85 g), followed by legume-first (3.94 g) and forb-first (2.48 g). The order of arrival in the mixture significantly affected the net biodiversity effects ($P < 0.001$), which were driven by dominance effects. The community had lower overall biomass when forbs were sown first, whereas the species grown later had fewer costs with an increased overall net benefit for the resulting community.

Conclusions Our results emphasize that root interactions and asymmetric competition are vital determinants of order-specific priority effects in community assemblies. In addition, the importance of the priority effect of forbs sown first is related to community assembly, which may be a key determinant in successfully establishing a highly diverse community in the early stages of restoration. Species with weak competition should be considered in the early stage of community assembly. The rational use of the priority effect is conducive to improving the quality and efficiency of ecological restoration efforts.

Keywords Community assembly, Order of arrival, Overyielding, Plant functional group, Root isolation

Background

In the restoration of degraded grassland ecosystem, the priority effect of plant assembly order has been paid more and more attention by ecologists (Weidlich et al. 2021; Werner et al. 2016), and is increasingly being considered an important driver of ecosystem restoration (Hess et al. 2019; Stuble and Young 2020; Tanentzap et al. 2015). In the assembly of a plant community, the species sown first can affect the establishment, growth, and reproduction of species that arrive later; this is known as the priority effect (Fukami 2015; Hess et al. 2019; Quinn and Robinson 1987). Some studies have shown that priority effects can alter the species composition, diversity, productivity, and diversity–productivity relationships of ecological communities (Delory et al. 2019b; Plückers et al. 2013; Reijenga et al. 2021; Sarneel et al. 2016; Uricchio et al. 2019). In addition, priority effects can lead to diverse alternate states of community development (Martin and

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Wilsey 2012; Werner et al. 2016). However, there is still a lack of relevant data related to taking advantage of the priority effects on community assembly to promote the successful establishment of plant species and improve ecosystem function in the early establishment stages of deteriorated grasslands. Moreover, it is significant to study the priority effect of species assembly in order to improve ecological restoration theory.

Previous studies have found that the priority effect is significantly influenced by early sown plant species or functional groups (Delory et al. 2019a, b; von Gillhaussen et al. 2014). Plant functional groups are species with similar morphology and phenology (Hooper and Dukes 2004). Weidlich et al. (2017) found that sowing legumes first can increase productivity while maintaining the diversity of Central European grasslands. In contrast, Burkle and Belote (2015) found that sowing forb species first can slightly influence the recruitment and establishment of the later colonizing species. Hence, the priority effects of sowing different plant functional groups on the development of the resulting plant communities are generally inconsistent across different experiments. The difference in sowing order may lead to differences in the growth or resource competition of different functional groups in a community (Weidlich et al. 2021). How assembly order of different plant functional groups regulates subsequent community construction and succession have not been adequately explored in previous research. Therefore, studies manipulating the plant functional groups sowing order are needed to investigate subsequent community development, especially in the context of restoration.

In biodiversity experiments, plant productivity is affected by species richness, and unimodal, positive, and negative relationships exist between them (Chen et al. 2018; de Aguiar et al. 2013; Tilman et al. 2001; Waide et al. 1999; Yang and Liu 2019), which can be explained by complementarity and selection effects (Fox 2005; Loreau and Hector 2001). Delory et al. (2019b) found that the magnitude and direction of biodiversity effects were limited by the priority effects of the order of arrival of plant species. Although studies have assessed how the priority effects affect the relationship between productivity and diversity (overyielding), its mechanisms of action remain poorly understood. Overyielding is a phenomenon in which plant production in mixed cultures exceeds the expectations based on monoculture yields (Hooper et al. 2005; Tilman et al. 2014).

Niche preemption and modification are widely recognized as the two main mechanisms of priority effects (Fukami 2015; Helsen et al. 2016; Vannette and Fukami 2014; Weidlich et al. 2021). In the assembly of a plant community, species that arrive earlier have a competitive advantage in obtaining light resources, soil nutrients, and niche space needed for plant growth (Abraham et al. 2009; Grman and Suding 2010; Kardol et al. 2013), thus limiting the growth of species arriving later. Alternatively, early arriving species can promote or inhibit the growth of late-arriving species by changing the soil environment (e.g., allelochemicals and soil mutualists) (Aschehoug et al. 2016; Boyle et al. 2021; Burkle and Belote 2015; Murrell et al. 2011). Although ecologists have explained the mechanism of priority effects from different perspectives, we lack a generalized understanding of how different plant functional groups (e.g., grasses, legumes, and forbs) interact to drive priority effects in community assembly.

In the present study, we tested priority effects in combination with plant species diversity using three fully crossed factors (i.e., manipulation of plant sowing order, root isolation, and species removal) in a phytotron to investigate the mechanism of priority effects driven by different plant functional groups in the early stage of community construction. This study aimed to evaluate (1) how priority effects created by different plant functional groups affect the overyielding of the resulting plant community, (2) how competition and root interactions influence the strength and direction of priority effects, and (3) which first-arriving plants are more conducive to the successful establishment of the community (restoration context). Therefore, this study contributes to a further understanding of the role of priority effects in community assembly, provides theoretical support for what species should be selected in restoration practices, and provides insights for degraded grassland management.

Methods

Experimental conditions and materials

This experiment was conducted in a phytotron at the Chinese Academy of Agricultural Sciences' Shaerqin Research Station at Hohhot, Inner Mongolia of China (photoperiod of 14 h/10 h (light/dark), a temperature of 25 °C in the light and 15 °C in the dark, and light intensity of 500 μmol m^{-2} s^{-1}). Three species of different functional types commonly found in temperate grasslands in Northern China (Inner Mongolian Steppe) were selected for analysis: *Leymus chinensis* (grass), *Medicago ruthenica* (legume), and *Allium ramosum* (forb). These three plants are the dominant species in these regions and, thus, have strong stress resistance (for example, cold, drought, and barren tolerances.) and adaptability (Li et al. 2022; Meng et al. 2019; Shi et al. 2021; Wang et al. 2021; Yi et al. 2019; Zhao et al. 2016). They are important plant materials for applications in restoration practices (Li et al. 2022; Yi et al. 2019; Zhu et al. 2022). Their

seeds were collected from a garden at Shaerqin Research Station. Seeds used in the test were full and disinfected with 2% sodium hypochlorite (Li et al. 2021). *Medicago ruthenica* seeds were broken dormancy to promote germination by using sandpaper (Ahmed et al. 2019). The base soil in the test pots was 0–10 cm topsoil collected from Shaerqin Research Station. The soil was sieved to remove roots, stones, and macroinvertebrates (sieve mesh size, 5 mm).

Experimental design and treatments

In this study, the priority effect on biomass production and diversity-dependent overyielding of the resulting communities, as well as the underlying mechanisms, were assessed by manipulating the sowing order (Weidlich et al. 2021), root isolation (Kong et al. 2018; Yu et al. 2020), and plant removal (Flory and Clay 2009). First, the sowing order was investigated at five different levels: either grasses, legumes, or forbs were sown first, or all species were simultaneously sown early or late. Seeds were sown in two batches when different species were mixed (at first, only one species was sown, and the remaining two species were sown at a later time). The interval between the first and second sowings was four weeks. For example, legumes and forbs were included in the second sowing when grasses were sown first (Fig. 1). Root isolation was investigated under three treatments: no isolation, incomplete isolation using a nylon mesh (mesh size 30 μm), and total isolation using a plastic film barrier (Kong et al. 2018; Yu et al. 2020). Incomplete and total isolation were designed to prevent root intermingling and/or soil nutrient exchange of early sown and late-sown species. Incomplete isolation was designed to segregate the roots of early and late-sown species, allowing for communication among soil nutrients (Yu et al. 2020). Third, two levels of plant removal were investigated: early sown species were either removed or not. Both root isolation and plant removal were manipulated to test the mechanisms of priority effects (niche preemption and niche modification). Root isolation focused on underground interactions (e.g., root space occupation and nutrient exchange), whereas plant removal focused

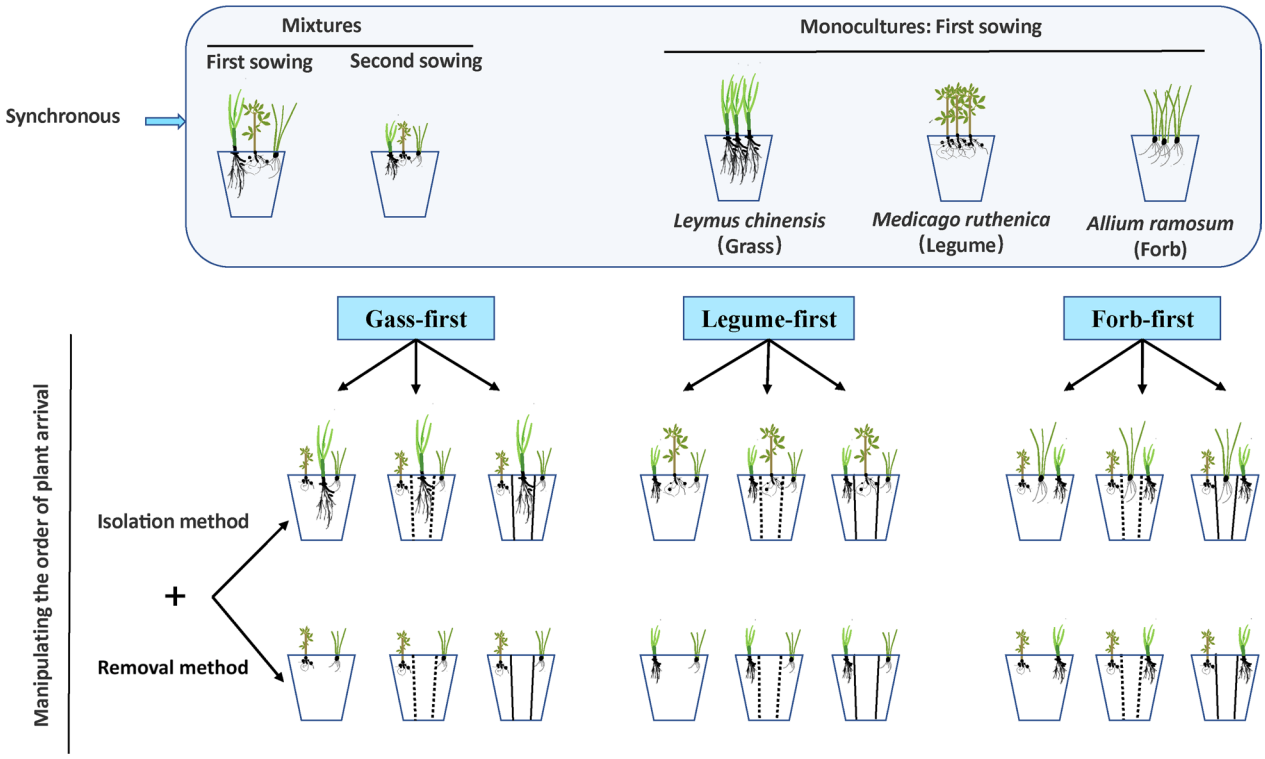

Fig. 1 Assembly method of different functional species in the phytotron experiment. Priority effects were created by manipulating plant order of arrival in the experiment: one plant species was sown four weeks before the two others and all plant species sown together at the same time (synchronous). The seeds of different species were spaced and sown symmetrically along the vertex of a hexagon, with each species sown in two sites. Different sizes of the same plants represent different sowing times: the larger plants represent the first sowing and the smaller plants represent the second sowing. Grass-first, grass was sown first in a mixed community; Legume-first, legume was sown first in mixed community; Forb-first, forb was sown first in mixed community. Dotted lines in pots represent nylon mesh isolation (mesh size 30 μm), incomplete isolation; Solid lines in pots represent plastic film isolation, total isolation. The first sowing plants were planted in the middle of the pot, and were removed in the corresponding treatment at the second sowing

on aboveground interactions or size-asymmetric competition (e.g., aboveground space occupation and light resource competition) between early and late-sown species. The design of the interaction between the two can reflect niche preemption and modifications. Treatments with three fully crossed factors were performed for the three early sown treatments (grasses, legumes, and forbs sown first) (Fig. 1). In addition, three monoculture treatments were used to understand the relationship between the priority effect and diversity-dependent overyielding (Fig. 1). Each treatment had four replicates, totaling 92 pots. The soil was packed in equal quantities (3 kg) in pots (16 cm diameter × 17 cm depth).

Plants and harvests

Based on the experimental design, the seeds of different species were sown in pots along a hexagonal pattern to ensure balanced competitive interactions. Three species were sown symmetrically along the vertex of the hexagon, and one species was sown at two sites. In the first sowing, the plants were planted in the middle of the pot and removed in the second sowing for the plant removal treatments (Fig. 1). The number of seeds planted was scaled according to the germination rate (the proportion of germinated seeds in the total number of seeds tested) (Yi et al. 2019) to achieve the target of three germinated individuals of each species at each site in a pot. The pots were adequately watered after each sowing period, followed by watering twice a week. All plants were clipped at the beginning of July 2021 (60 days after the first sowing), and the aboveground and belowground biomass for each species was harvested individually. The number of each species was counted immediately before harvest. All biomass was dried in an oven at 65 °C for 48 h before weighing.

Statistical analyses

The difference in pot biomass (the overall biomass of all species) between different treatments, excluding the root isolation and plant removal treatments, was analyzed to determine the impact of priority effects on the biomass of mixed-sowing communities. The pot biomass was determined by adding the average biomass, including the aboveground, belowground, and total biomass, of each species in the combined community. The biomass of each species was six times (the species density was designed) the average biomass of an individual plant to minimize deficiencies in the planting process.

The diversity effect indices (net biodiversity, complementary, and selection effects) were calculated using the additive partitioning method described by Fox (2005) based on the average biomass of each species in the mixed culture and monoculture treatments, which is a widely recognized method used by ecologists to study the relationship between diversity and productivity (Chacon-Labella et al. 2019; Delory et al. 2019b; Loreau and Hector 2001). The relative interaction index for each species was calculated, as described by Armas et al. (2004) (Additional file 1: Table S1). The complementary effect indicates resource partitioning or interaction relationships among species in total resource use. The selection effect indicates that the dominance of species with particular traits affects ecosystem processes. The net biodiversity effect is the sum of the selection and complementarity effects and reflects the net benefit of mixed cultures compared with the average yield from monocultures. These indices were used to further evaluate the relationship between priority effects and diversity-dependent overyielding and the magnitude of each species' competitiveness in the community assembly. Fox (2005) divided the selection effect into dominance and trait-dependent complementarity effects, which allows for a better understanding of the relationship between species competition and productivity. The net biodiversity effect (NE), trait-independent complementarity effect (TICE), dominance effect (DE), and trait-dependent complementarity effect (TDCE) were calculated using the tripartite additive partitioning method described by Fox (2005) (Additional file 1: Table S1). A negative or positive NE value indicates that the observed yield in the mixture was higher or lower than the weighted average of the monoculture yields. Positive TICE values indicate that species occupy different niches or facilitate each other, whereas negative values indicate interspecific competition or other processes with the same effect. Positive (negative) DE values indicated that species with higher (lower) than the average monoculture yields dominated at the expense of species with low (high) monoculture yields. Large values were expected when species occupied similar niches. However, positive (negative) TDEC values indicated that species with higher-than-average (lower-than-average) monoculture yields dominated, but not at the expense of species with low (high) monoculture yields. Large values suggest that this species has a nested niche.

In addition, the priority effect index, the early sown benefit, and the late-sown cost for the different functional species were calculated to quantitatively evaluate the strength of the priority effect and the assembly mode more conducive to the successful establishment of a community based on the average biomass of each species in priority treatments. The priority effect indices directly reflected the impact of early sown species on late-sown species in mixed-sowing communities. The absolute values of the priority effect indices indicate the strength of order-specific priority effects, and positive or negative values indicate the direction (facilitation or inhibition

effects of species sown early on species sown late). The greater the absolute value, the stronger the effect. The species sown early did not affect the growth of the species sown late when the absolute value of the priority effect indices was 0. However, priority effect indices do not reflect the impact of species sown early on a specific species sown late in a mixed-sown plant community. In addition, priority effect indices cannot be used to evaluate the differences between early sown and late-sown species in the priority treatment and the corresponding species of the same age in the control treatment (simultaneously sown early or late). In this study, the benefits (*B*) of species sown early and the costs (*C*) of species sown late were calculated using the biomass of species of the same age to evaluate the species that are more conducive to the overall development of the plant community by sowing early and to enhance the understanding of the mechanism of priority effects (Delory et al. 2019a). The *B* values were calculated based on the biomass of the species sown early in the priority treatments and the corresponding species in the simultaneously sown early treatments. The *C* values were calculated based on the biomass of the species sown late in the priority treatments and simultaneously sown late. Positive or negative *B* or *C* values for a species indicate the facilitation or inhibition effects of other species in mixed cultures. The larger the *B* or *C* values, the larger the benefit and the smaller the loss of this species. The formulae used to calculate these indices are listed in Table S1. These indices share the same mathematical properties (e.g., standardized, symmetric, and bounded) as the neighbor-effect indices developed by Díaz-Sierra et al. (2017). The underlying mechanisms of the priority effects of different functional species in combination with root isolation and species removal treatments were also assessed.

The software package IBM SPSS Statistics (version 21.0) was used for all the statistical analyses. Differences among the treatments were determined using a general linear model (ANOVA). Graphs were generated using the Origin 2021 software. The relationships between the different indicators were determined using Pearson's correlation coefficient analysis. A correlation was considered significant at $P<0.05$.

Results

The impact of priority effects of different plant species on pot biomass

The sowing order of the different species significantly affected the pot biomass of the mixed-sowing community, including the aboveground, belowground, and total biomasses ($P<0.001$; Fig. 2). The pot biomass of *Leymus chinensis* when sown first did not differ from that of the simultaneously sown early treatments ($P>0.05$; Fig. 2).

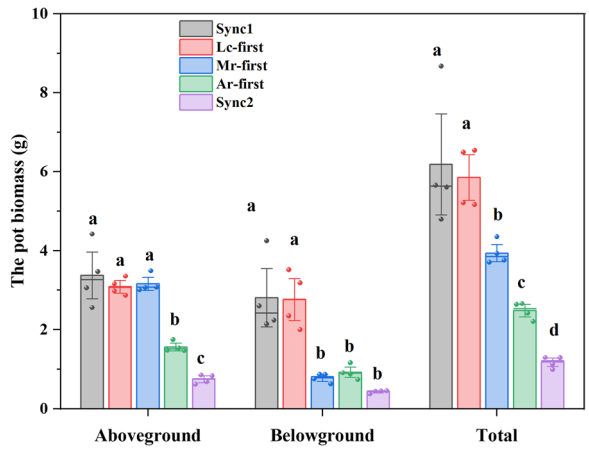

Fig. 2 Effects of priority effects of different species on overall pot biomass. The relevant data in the figure do not include root isolation and plant removal treatments. Sync1, all species were simultaneously sown early; Sync2, all species were simultaneously sown late; Lc-first, *Leymus chinensis* was sown first in mixed community; Mr-first, *Medicago ruthenica* was sown first in mixed community; Ar-first, *Allium ramosum* was sown first in mixed community. Different small letters represent significance levels ($P<0.05$)

Belowground and total pot biomass were significantly lower in the treatment where *Medicago ruthenica* was sown first than in the *Leymus chinensis*-first and simultaneously sown early treatments ($P<0.05$; Fig. 2). However, pot biomass was significantly lower in the treatments where *Allium ramosum* was sown first than in the other priority treatments ($P<0.05$; Fig. 2). However, the overall pot biomass of each priority treatment was higher than that of the simultaneously sown late treatments ($P<0.05$; Fig. 2). The biomass of the mixed species in the pots varied significantly depending on whether the species was sown early or late. The overall pot biomass of the different priority treatments was highest in *Leymus chinensis*-first (5.85 g), followed by *Medicago ruthenica*-first (3.94 g) and *Allium ramosum*-first (2.48 g) (Fig. 2).

Response of diversity-dependent overyielding to the order of plant arrival

The biodiversity effects based on the aboveground biomass of each species varied significantly among the different priority treatments ($P<0.05$; Additional file 1: Fig. S1 and Table S2). Compared with the simultaneously sown early treatment (control), the net biodiversity effects of the priority effect treatments were significantly lower ($P<0.001$; Additional file 1: Fig. S1a and Table S2). The net biodiversity effects were consistent with the dominant effects of different treatments (Fig. S1a–d). Dominance effects simultaneously drove diversity-dependent overyielding in the priority effect treatments. In addition, the values of trait-independent complementarity effects

were negative in each priority treatment and markedly lower in *Leymus chinensis*-first and *Allium ramosum*-first pots than in the control ($P=0.003$, $P<0.001$; Additional file 1: Fig. S1b). Moreover, the values of the dominance effects were positive and higher in *Leymus chinensis*-first pots ($P=0.048$; Additional file 1: Fig. S1c) compared with the control. No significant difference was observed ($P=0.153$; Additional file 1: Fig. S1c) between the values of the dominance effects in *Medicago ruthenica*-first pots and control. In contrast, the values of dominance effects were negative for *Allium ramosum*-first pots and lower ($P<0.001$; Additional file 1: Fig. S1c). Pearson's correlation analysis showed that priority effects were significantly and negatively correlated with the relative interaction index of the species sown first ($P<0.001$; Additional file 1: Fig. S2). Furthermore, the net biodiversity effect was significantly and positively correlated with the relative interaction index of the species sown first ($P<0.001$; Additional file 1: Fig. S2).

Responses of priority effects to sowing order, root isolation, and plant removal

The values for the priority effect indices were negative, and the magnitude was significantly affected by the order of arrival of different functional species during community assembly ($P<0.001$; Table 1 and Additional file 1: Table S3). The priority effects (based on total biomass) were stronger in *Leymus chinensis*-first (24.76%) and *Medicago ruthenica*-first communities (24.48%) than in *Allium ramosum*-first communities ($P<0.001$; Additional file 1: Table S3) because the absolute values of priority effect indices were larger in these communities, excluding root isolation and plant removal treatments. The strength of the priority effects depended on the species sown first. Root isolation and plant removal also significantly affected priority effects (Table 1 and Additional file 1: Table S3). The absolute values of the priority effect indices of the communities significantly decreased when the first arriving species were removed or isolated from other species if *Leymus chinensis* or *Medicago ruthenica* were sown first but increased if *Allium ramosum* was sown first (Additional file 1: Table S3). In the simultaneously sown early treatment, the average value of relative interaction index of each species (based on total biomass) was as follows: *Leymus chinensis* (0.1952) > *Medicago ruthenica* (0.0138) > *Allium ramosum* (− 0.2571). Compared with the other two plants, *Allium ramosum* was less competitive in the mixed-sowing communities. These results, combined with the overall pot biomass results, showed that root isolation significantly altered the correlation between priority effect indices and the pot biomass of the resulting plant community (Fig. 3). The magnitude of the priority effects of different functional species was significantly influenced by the interactions among sowing order, root isolation, and plant removal ($P<0.001$; Table 1).

Table 1 ANOVA analysis of priority effects indices

Source of variation		*df*	*F*	*P*
SO	Aboveground biomass	2	44.25	< 0.001
	Belowground biomass	2	58.04	< 0.001
	Total biomass	2	33.00	< 0.001
IM	Aboveground biomass	2	9.95	< 0.001
	Belowground biomass	2	28.10	< 0.001
	Total biomass	2	31.07	< 0.001
RM	Aboveground biomass	1	3.64	0.062
	Belowground biomass	1	55.89	< 0.001
	Total biomass	1	14.73	< 0.001
SO × IM	Aboveground biomass	4	34.45	< 0.001
	Belowground biomass	4	26.52	< 0.001
	Total biomass	4	60.21	< 0.001
SO × RM	Aboveground biomass	2	35.27	< 0.001
	Belowground biomass	2	49.54	< 0.001
	Total biomass	2	25.79	< 0.001
IM × RM	Aboveground biomass	2	5.92	0.005
	Belowground biomass	2	15.05	< 0.001
	Total biomass	2	0.66	0.520
SO × IM × RM	Aboveground biomass	4	57.07	< 0.001
	Belowground biomass	4	25.04	< 0.001
	Total biomass	4	84.04	< 0.001

SO sowing order of species in community assembly, *IM* underground isolation method, *RM* plant removal method, *df* degrees of freedom, *F* variance, *P* error probability

In addition, the relative interaction indices of the three species varied significantly with the priority treatments (Additional file 1: Tables S4 and S5). The relative interaction indices for *Leymus chinensis* and *Medicago ruthenica* sown early were positive (Additional file 1: Table S4). However, root isolation reduced the relative interaction indices of *Leymus chinensis* and *Medicago ruthenica* sown early and increased those of the species sown late (Additional file 1: Table S4). The opposite result was observed when *Allium ramosum* was sown first (Additional file 1: Table S4). The aboveground and belowground interactions among the species significantly affected the competitiveness of each species in priority treatments. Furthermore, there was a significant interaction between the order of arrival of species, isolation methods, and removal methods within the community assembly ($P<0.001$; Additional file 1: Table S5).

Benefit indices were tested based on the biomass of species sown early in priority treatments and simultaneously sown early. Each species benefited from arriving early in the community, particularly *Medicago ruthenica*, followed by *Leymus chinensis* and *Allium ramosum*

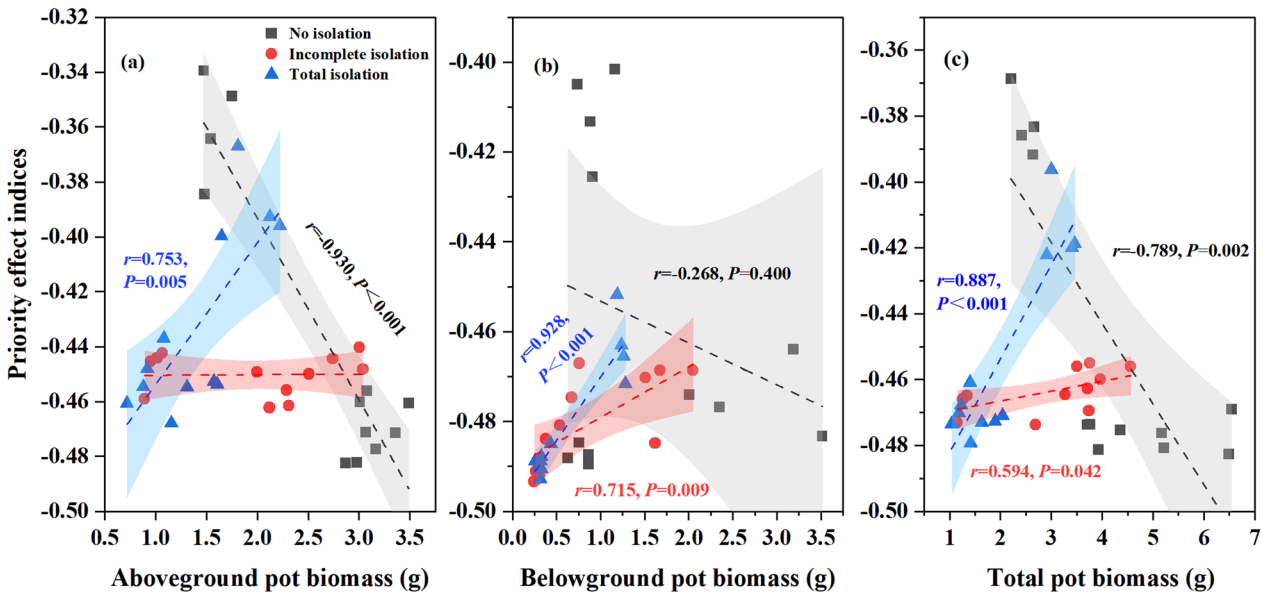

Fig. 3 Root isolation changes the correlation between priority effect index and pot biomass. This figure only includes the no plant removal treatments. Priority effects indices values based on aboveground (**a**), belowground (**b**), and total biomass (**c**) of each species in mixed plant community. The absolute values indicate the strength of order-specific priority effects. The greater the absolute value, the greater the impact of early sown on late-sown species. The positive or negative values indicate the direction (the facilitation or inhibition effects of early sown species on late-sown species). Each dotted line represents the effect of a linear model fit, while the shaded area shows the 95% confidence intervals around the fit. *r*, Pearson correlation coefficient; *P*, error probability

($P<0.001$; Additional file 1: Fig. S3, gray). Interestingly, the underground isolation treatments considerably affected the benefit of arriving early (Additional file 1: Fig. S3). Compared with no-isolation treatments, the benefit values of *Leymus chinensis* and *Medicago ruthenica* were lower in the incomplete isolation and total isolation treatments owing to their early arrival in community assembly (Additional file 1: Fig. S3). In contrast, the benefit values of *Allium ramosum* sown first were higher in the incomplete and total isolation treatments than in the no-isolation treatments (Additional file 1: Fig. S3a, c). Underground root isolation treatments markedly inhibited the growth of *Leymus chinensis* and *Medicago ruthenica* sown first ($P<0.05$; Additional file 1: Fig. S3, pink and blue) but improved the growth of *Allium ramosum* sown first. Isolation treatment and order of arrival had significant interaction effects on the benefits of the species sown first ($P<0.001$; Table 2).

Table 2 ANOVA analysis on benefits of different species arriving early

Source of variation		*df*	*F*	*P*
SO	Aboveground biomass	2	38.14	< 0.001
	Belowground biomass	2	41.87	< 0.001
	Total biomass	2	55.01	< 0.001
IM	Aboveground biomass	2	233.04	< 0.001
	Belowground biomass	2	2.65	0.089
	Total biomass	2	40.18	< 0.001
SO × IM	Aboveground biomass	4	34.97	< 0.001
	Belowground biomass	4	6.66	0.001
	Total biomass	4	25.46	< 0.001

SO sowing order of species in community assembly, *IM* underground isolation method, *df* degrees of freedom, *F* variance ratio, *P* error probability

Cost of arriving late for different functional species in the community assembly

Similar to the benefit indices of early sown species, excluding the plant removal treatments, the cost indices of late-sown species were evaluated based on the biomass of species sown late in the priority treatments and controls (simultaneously sown late). The cost of species sown late varied significantly depending on the species sown early, especially *Medicago ruthenica* and *Leymus chinensis* (Additional file 1: Fig. S4 and Table 3). The cost of sowing *Leymus chinensis* in the no isolation priority treatments was higher after *Medicago ruthenica* sown than after *Allium ramosum* sown (Additional file 1: Fig. S4). Moreover, the cost of sowing *Medicago ruthenica* in the no-isolation priority treatments was higher after *Leymus chinensis* sown than after *Allium ramosum* sown (Additional file 1: Fig. S4). Furthermore, the cost of sowing *Allium ramosum* was higher after *Leymus chinensis*

Table 3 ANOVA analysis of the cost of species sown late

Source of variation		*df*	*Leymus chinensis*		*Medicago ruthenica*		*Allium ramosum*	
			F	*P*	*F*	*P*	*F*	*P*
SO	AM	2	111.15	< 0.001	3.16	0.093	2.72	0.117
	BM	2	24.48	< 0.001	451.37	0.000	1.38	0.255
	TM	2	99.30	< 0.001	162.46	0.000	2.13	0.162
IM	AM	2	4.53	0.025	99.10	0.000	42.26	< 0.001
	BM	2	28.39	< 0.001	11.28	0.001	7.17	0.005
	TM	2	12.39	< 0.001	97.48	0.000	17.36	< 0.001
SO × IM	AM	4	8.57	0.002	44.63	0.000	8.29	0.003
	BM	4	134.18	< 0.001	11.63	0.001	4.57	0.025
	TM	4	38.91	< 0.001	73.55	0.000	4.22	0.031

SO sowing order of species in community assembly, *IM* underground isolation method, *AM* the cost index of species sown late was calculated by aboveground biomass of it, *BM* the cost index of species sown late was calculated by belowground biomass of it, *TM* the cost index of species sown late was calculated by total biomass of it. *df* degrees of freedom, *F* variance ratio, *P* error probability

sown than after *Medicago ruthenica* sown. In addition, *Allium ramosum* sown early was beneficial for the species sown late. The average biomasses of late-sown *Leymus chinensis* and *Medicago ruthenica* were two- and fivefold higher than that of the control, respectively, in the pots where *Allium ramosum* was sown first. The higher the cost, the lower the loss of late-sown species. However, root isolation treatments decreased the cost of the species being sown later (Additional file 1: Fig. S4). Similarly, the interaction between sowing order and root isolation significantly affected the growth of plants sown later ($P < 0.05$; Additional file 1: Fig. S4 and Table 3).

Early sown species were removal in the plant removal treatments, so there were no the benefits of early sown species. The cost indices were then analyzed using the relevant dates from the sowing order and root isolation treatments to quantitatively evaluate the impact of priority effect on the overall net benefits of the mixed-planting community. The overall net benefits were calculated by adding the benefits of early sown species to the costs of late-sown species in a community. The results showed that the overall net benefits of *Allium ramosum* sown early were significantly higher than those of *Leymus chinensis* and *Medicago ruthenica* sown early ($P < 0.001$; Fig. 4 and Additional file 1: Table S6). However, sowing order, root isolation, and their interactions strongly influenced the benefits of the mixed communities ($P < 0.05$; Additional file 1: Table S6).

Discussion

In this study, the priority effects of the order of arrival of different species strongly governed the overall biomass- and diversity-dependent overyielding effects of the resulting communities. In addition, the priority effects of the order of arrival of different species affected the benefits and costs of early or late-arriving species, and all species benefited from being sown first. Sowing order, root interactions, and competition among species are important drivers of the priority effect during community assembly. The results indicated that the interactions among sowing order, root isolation, and plant removal influenced the strength and direction of priority effects. The community had lower overall pot biomass when the forb species were planted first, whereas the species sown later had lower costs of being planted later, and the overall net benefit to the resulting community was higher.

The priority effect of an appropriate sowing order may determine the biomass production or diversity of a mixed-sowing community

In this study, the priority effects of the sowing order of different species had a strong impact on community biomass production, which is consistent with the findings of previous studies (Körner et al. 2008; von Gillhaussen et al. 2014; Weidlich et al. 2017; Wilsey et al. 2015). However, the overall pot biomass was lower when the forbs were sown first than when the other plants were sown first. As a first-sown plant, *Allium ramosum* is smaller than the other plants, enabling better colonization of plants later due to their less competition (Grman and Suding 2010; Weiner 1985). In other words, other species in the mixed community were least inhibited by forb (*Allium ramosum*) when it was sown first, because the relative interaction index of species sown first and the priority effect index were larger (Additional file 1: Tables S3 and S4). Although the other plants were larger at the time of the second sowing, the overall pot biomass decreased at the end. In addition, pot biomass, particularly belowground biomass, was lower in legumes sown first than in other first-sown plants. Fixed nitrogen returns to the soil when

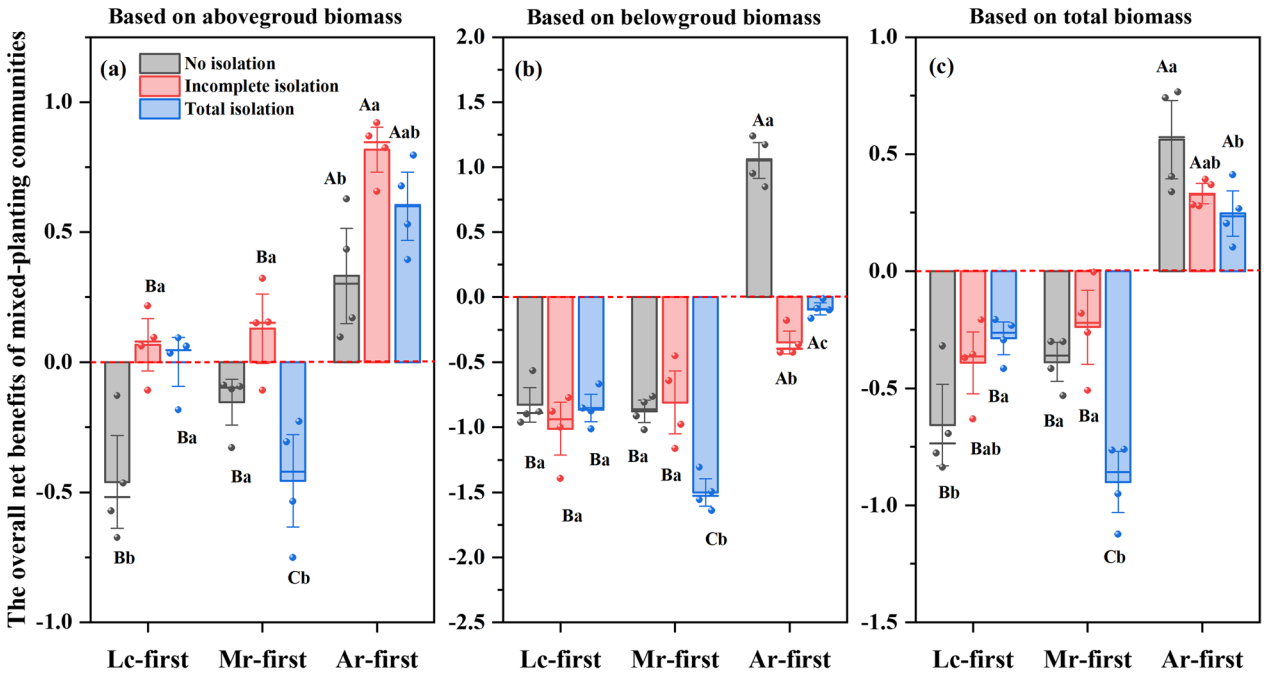

Fig. 4 Overall net benefits or costs of mixed community in different priority treatments. The overall net benefit value of mixed community was defined as the sum of the benefits of species sown early and the costs of species sown late. The higher the overall net benefit value, the better the sowing order for the construction of mixed community. Lc-first, *Leymus chinensis* was sown first in mixed community; Mr-first, *Medicago ruthenica* was sown first in mixed community; Ar-first, *Allium ramosum* was sown first in mixed community. Different capital letters represent significance levels ($P < 0.05$) between sowing order treatments; different lowercase letters represent significance levels ($P < 0.05$) between isolation methods

the lifecycle of the legume *Medicago ruthenica* is complete, potentially facilitating the growth of future species (Fox et al. 2020). These effects can be captured over longer timescales. This also indicates that priority effects affect aboveground and belowground biomass allocation, possibly because of the identity of early and late-sowed species (Burkle and Belote 2015; Weidlich et al. 2018a). Priority treatment changes the competitive relationships among species (Young et al. 2017). These results also indicate that the priority effects of a particular sowing order may benefit species coexistence but not necessarily biomass productivity at an early stage. Unlike previous findings (Chacon-Labella et al. 2019; Hooper et al. 2005) (productivity increases with diversity), the work shows that the priority effect is important in maintaining the relationship between productivity and diversity. Nevertheless, long-term experiments are required to verify the influence of priority effect on community development. Interestingly, the impact of priority effect on community biomass could change via root isolation treatments because isolation treatments change the pattern of interaction among species, and the growth of plants is limited owing to allelopathic interactions (Aschehoug et al. 2016) and root development (Weidlich et al. 2018b). These results indicate that niche preemption and modification among species are altered in the community. The sowing order of species in a community should be appropriately manipulated according to the restoration objective to create the desired priority effects. Accordingly, species with weak competition should be paid attention to in the early stage of community assembly. Noncompetitive plants should be planted first if the goal is to increase plant diversity; otherwise, a different strategy should be used if the goal is to increase productivity.

Priority effect can impact the diversity-dependent overyielding of a community by varying species competitiveness

In this study, the sowing order significantly affected net biodiversity effects in different priority treatments. Similarly, a previous study indicated that order-specific priority effects could alter the relationship between productivity and diversity (Delory et al. 2019b). Specifically, the net biodiversity effects were consistent with the dominance effects in the different priority treatments, revealing that the net biodiversity effects among priority treatments were largely driven by dominance effects in the mixtures. Positive dominance effects indicated that species with high monoculture biomass dominated the biomass of the mixture at the expense of species with low

monoculture biomass. In contrast, negative values indicate the dominance of species with low monoculture biomass at the expense of others. Dominance effects were significantly higher in the grass-first treatments than in the simultaneously early sown treatment (control), and the values were positive. The dominance effects were significantly lower in the forb-first treatments than in the control, and the values were negative. However, the monoculture biomass of grass (*Leymus chinensis*) was the highest, and one of forb (*Allium ramosum*) was the least in this study. These findings indicate that the magnitude and direction of the net biodiversity effects (overyielding) depend on the species sown first and their competitiveness. This differs from the findings of Delory et al. (2019b), who suggest that the increase of overyielding influenced by priority effects is mainly due to the increase of complementary effects. The possible reason is that the materials used in the two tests are different, and our study focuses on the influence of priority effects on early community construction. From the above results, it can be inferred that the influence of priority effect on overyielding may change over time. In addition, the sowing order of different species alters the direction of trait-independent complementarity effects from positive to negative in this study, which indicates that priority treatment makes competition stronger than complementarity among mixed species and reflects changes in resource partitioning or interactions among species in mixed-planting communities (Fox 2005). This further suggests that priority treatments change the competitiveness of species in mixed-planting communities (Young et al. 2017) because of the differences in the relative interaction index of species sown with different priorities (Additional file 1: Table S4). Hence, the impact of the priority effect on overyielding could be due to variations in species-specific competitive advantages or resource partitioning in mixed-planting communities (Delory et al. 2019b).

The mechanism of priority effect was jointly influenced by sowing order, aboveground, and belowground interaction among species

Sowing order, root isolation, and plant removal treatments had significant interaction effects on the magnitude and direction of the priority effect, revealing that the identity of species sown early, root interactions, and aboveground interactions or size-asymmetric competition among species influenced the priority effect during community assembly. The growth inhibition of late-sown species in complete isolation treatments increased (the absolute priority effect index was larger) when early sown *Leymus chinensis* was removed. However, this inhibition was reversed when early sown *Medicago ruthenica* and *Allium ramosum* were eliminated. These results indicate that competition for aboveground resources among plants affects the growth of different functional late-sown species (Ding et al. 2016; Jing et al. 2015), suggesting that the strength of priority effects also depends on the characteristics of the late-sown species. This may also be due to changes in resource allocation resulting from root isolation and plant removal treatments, such as previously described with competition for light (Fukami 2015; Wilsey et al. 2015), root niches (Körner et al. 2008; Weidlich et al. 2018a), and allelopathy (Aschehoug et al. 2016; Boyle et al. 2021; Grman and Suding 2010; Murrell et al. 2011). Therefore, the species sown first during community assembly is important (Cleland et al. 2015). Furthermore, root isolation in the plant removal treatments significantly changed the strength of specific-order priority effects, suggesting that differences in space occupancy (niche preemption) and nutrient exchange (niche modification) of underground plant roots promoted priority effects. Therefore, different species or functional groups drive diverse priority effects due to differences in root development, secretion, nutrient conversion ability, and other plant characteristics. Before this study, no research has been observed on this aspect, and which of these factors is the crucial driver of priority effect needs further research. Early sown grasses have difficulty creating a positive priority effect because of their developed root systems and strong competitiveness (Burkle and Belote 2015), whereas early sown legumes or forbs have greater potential. A past study (Weidlich et al. 2017) showed that early sown legumes can create a positive priority effect. Therefore, the priority effect in early community assembly should consider assembly order and species characteristics.

The priority effect of different functional species could regulate the overall net benefit of the community

In this study, three species benefited from sowing first, with forbs sown first having the weakest inhibitory effect on species sown later, suggesting that sowing forbs first can benefit the colonization and growth of other species in the community. This supports the view of Burkle and Belote (2015). However, we found that the pot biomass of forbs sown first was lower than that of the other species, the overall net benefit to the resulting community was higher. Combined with the above analysis, this result implies that the early sowing of species with weak competition improves species coexistence and positive development in community assembly. Meanwhile, root isolation treatments decreased the cost of late-sown species, revealing that underground interactions among different species (niche preemption and niche modification) are crucial for the development of plant communities. Furthermore, forbs sown first can support the assembly

of divergent communities (Burkle and Belote 2015), and the priority effect created by the order of species arrival can have long-lasting effects on community development (Vaughn and Young 2015; Werner et al. 2016). Therefore, suitable forbs could be selected as early sown species for ecological restoration to enhance the diversity of reconstructed communities.

Conclusions

The results of this study showed that priority effects could strongly alter the overall biomass and diversity-dependent overyielding effects in mixed-species communities by changing the competitiveness of species and resource partitioning. Plant sowing order, root interactions, and competition among species drive this effect. This effect was also closely related to the species selected in the mixed-sowing communities. Furthermore, early sown species with weak competition have potential advantages during community assembly, especially because of the decreasing costs incurred by delayed sowing. Therefore, suitable forbs should be selected for early sowing to successfully construct and develop community restoration. Especially, species with weak competition should be paid attention to in the early stage of community assembly. The study highlighted that the rational use of the priority effect of species assembly order is conducive to improving the quality and efficiency in ecological restoration efforts.

Abbreviations

NE	Net biodiversity effect
TICE	Trait-independent complementarity effect
DE	Dominance effect
TDCE	Trait-dependent complementarity effect

Supplementary Information

The online version contains supplementary material available at https://doi.org/10.1186/s13717-024-00483-y.

Additional file 1: Fig. S1. Impact of priority effects on biodiversity effects. This figure only includes the no root isolation and no removal priority treatments. Negative or positive values of net biodiversity effect indicate that the observed yield in mixture is higher or lower than the weighted average of the monoculture yields. Positive values of trait-independent complementarity effect indicate that species occupy different niches or facilitate one another, while negative values indicate interspecific competition or other processes with the same effect. Positive (negative) dominance effect values indicate that species with higher (lower)-than-average monoculture yields dominate at the expense of species with low (high) monoculture yields. Large values are expected when species occupy similar niches. However, positive (negative) trait-dependent complementarity effect values indicate that species with higher (lower)-than-average monoculture yields dominate, but not at the expense of species with low (high) monoculture yields. Large values suggest that species have nested niches. Sync, all species were simultaneously sown early; Lc-first, *Leymus chinensis* was sown first in mixed community; Mr-first, *Medicago ruthenica* was sown first in mixed community; Ar-first, *Allium ramosum* was sown first in mixed community. Different lowercase letters represent significance levels between priority effect treatments ($P \leq 0.05$). **Fig. S2.** Correlation between biodiversity effects and priority effects. NE, net biodiversity effect; TICE, trait-independent complementarity effect; DE, dominance effect; TDCE, trait-independent complementarity effect; PEI, priority effects index; RII, relative interaction index of species sown first. Blue and red represent correlation, red represents positive correlation, blue represents negative correlation, circle size represents the degree of correlation, the numbers are Pearson correlation coefficients; the asterisk represents the level of significance, "*" represents $P \leq 0.05$; "**" represents $0.05 < P \leq 0.01$; "***" represents $0.01 < P \leq 0.001$. **Fig. S3.** Benefits of species sown early in community assembly. The benefits of species sown early was calculated using the biomass of species sown early in the priority treatments and simultaneously sown early, including aboveground biomass (a), belowground biomass (b), and total biomass (c). Since early sowing species has been removed in plant removal treatments, the benefits of species sown early were excluded plant removal treatments. NI, no isolation; II, incomplete isolation; TI, total isolation. Lc-first, *Leymus chinensis* was sown first in community assembly; Mr-first, *Medicago ruthenica* was sown first in community assembly; Ar-first, *Allium ramosum* was sown first in community assembly. Different capital letters represent significance levels ($P < 0.05$) between sowing order treatments; different lowercase letters represent significance levels ($P < 0.05$) between isolation methods. **Fig. S4.** Costs of species sown late in community assembly. Similar to the benefit indices of early sown species, excluding plant removal treatments, the cost indices of late sowing species were also evaluated based on the biomass of species sown late in priority treatments and controls (simultaneously sown late). The positive or negative cost value for a species indicates the facilitation or inhibition effects of other species on it in mixed cultures, and the larger the value, the smaller loss of this species due to sowing late. Lc, *Leymus chinensis*; Mr, *Medicago ruthenica*; Ar, *Allium ramosum*. NI, no isolation; II, incomplete isolation; TI, total isolation. Lc-first, *Leymus chinensis* was sown first in community assembly; Mr-first, *Medicago ruthenica* was sown first in community assembly; Ar-first, *Allium ramosum* was sown first in community assembly. Different capital letters represent significance levels ($P < 0.05$) between sowing order treatments; different small letters represent significance levels ($P < 0.05$) between isolation methods. **Table S1.** Formulas of relevant indices in this study. **Table S2.** ANOVA analysis of the biodiversity effects based on aboveground biomass in priority treatments. **Table S3.** Priority effect indices in different treatments. **Table S4.** Relative interaction indices in different priority treatments. **Table S5.** ANOVA analysis of relative interaction indices. **Table S6.** ANOVA analysis of the overall net benefit of mixed community controlled by priority effects.

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Author contributions

XY, XL, and KJ conceived the ideas and wrote the manuscript. XY analyzed the data. XY, XL, and KJ led the writing of the manuscript. All authors read and approved the final manuscript.

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Availability of data and materials

Data are available from the corresponding author on reasonable request.

Declarations

Ethics approval and consent to participate

Not applicable.

Consent for publication
All authors approved the manuscript for publication in ecological processes.

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