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Species patch size at seeding affects the productivity of mixed legume-grass communities

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ABSTRACT

The impact of inter- and intraspecific neighboring plants on mixed legume-grass communities has rarely been explored in relation to seeded species patch size. In this study, two native perennial species, the legume alfalfa (*Medicago sativa* L.) and the grass tall fescue (*Festuca arundinacea* L.), were investigated as monocultures and in mixture. A three-year growth experiment was conducted to investigate the effects of plant-plant competitive interactions on fine-scale seeding patterns: monoculture, three different conspecific patch sizes (1.0, 0.5, and 0.25 m side length of squares) and a control in which the seeds were mixed and scattered (i.e., patches were not formed) as in conventional seeding. The results demonstrated significant differences in the mutual effect intensity in all conspecific patch sizes, indicating the presence of grass-legume interactions on mixed plant communities. Smaller patch sizes resulted in better facilitation by higher neighbor effect intensity when compared with a larger patch size and the conventional mixture. Seedlings in the smallest patch size of 0.25 m × 0.25 m showed intra- and interspecific competition and significantly improved aboveground productivity compared with the other patch sizes. We directly quantified the variation of species neighbor effect intensity between grass and legume mixtures among different species patch sizes at seeding. Integrating this knowledge into species interaction models in plant community ecology could greatly enhance our understanding of species coexistence in grasslands as well as provide opportunities for manipulating competition to achieve specific agronomic aims.

1. Introduction

Locations with higher species diversity can have higher productivity than monocultures (Loreau and Hector., 2001; Tilman et al., 2001; Richards et al., 2010). An important underlying mechanism of these highly productive systems is the complementarity in resource uptake. The interaction of different mixes of plant species is assumed to increase the strength of the complementarity effects through more effective resource utilization related to spatial and temporal differences in the aboveground and belowground resources used by a species (Zhang et al., 2007; Seneviratne et al., 2010). Complementarity can either occur when the intensity of facilitative plant-plant interactions increase or when competitive plant-plant interactions decrease (Loreau and Hector.,

2001; Roscher et al., 2016; Slade et al., 2017). In mixtures, the strongest interactions between neighboring allo-specific plants occur by individual species capturing light, water and nutrients (Zhang and Li, 2003; Brooker et al., 2016; Letten et al., 2017). Neighbor-effect intensity based on aboveground biomass is a common indicator of the intensity of plant-plant interactions, whereas positive or negative values indicate a facilitative or competitive plant-plant interaction, respectively (Diaz-Sierra et al., 2017; Schob et al., 2018). From the perspective of ecosystem management, these effects are important because a maximal, positive neighbor-effect intensity is often expected to increase community productivity or to facilitate the restoration of degraded lands.

Seeding distance among species is strongly related to neighbor-effect intensity. In a given plant species pool, the distance between plant

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individuals is the dominant factor determining the intensity of plant-plant interactions. Neighboring species show a strong interaction when individuals are more densely packed (Kennedy et al., 2002; Rayburn and Schupp., 2013). In mixed cropping systems, intercropping primarily utilizes the advantages of species interactions by adjusting the planting distances between species (Ma et al., 2007; Wang et al., 2020). Because species interactions can be controlled by the sizes of conspecific patches at seeding, it is possible to test the association of neighbor-effect intensity with the scale of facilitation or competition in plant communities and further quantify the intensity of negative and positive plant interactions. The aggregation of manipulated species allows for the measurement of inter- and intraspecific interactions in cultivated agricultural grasslands (Yurkonis et al., 2012; Liao et al., 2014; Seahra et al., 2016). Seahra et al. (2016) and Houseman (2014) have shown that the discontinuous pattern of mixtures of over 15 species increase plant biomass and maintain community stability.

The patch size of different species at seeding as a result of the edge/area ratio in a mixture may cause changes in soil properties and lead to differences in the initial growth of a species. The early stage of soil nutrient and plant establishment is important in shaping the competitive dynamics of different species (Andersen et al., 2007) and is strongly affected by the size of seeding (Schwinning and Fox, 1995). Size related traits likely result in an early growth advantage among species in a mixture because different plant species will compete for different resources accompanied by size inequality and further induce facilitation or competition (Facelli et al., 1999; Chesson, 2000). Species that have complementary effects on one another may be dependent on suitable competition intensity between intraspecific and interspecific interactions (Turkington, 1996; Turkington and Jolliffe., 1996; Chesson, 2018). In smaller patches with a higher edge/area ratio, the likelihood of a close neighbor being conspecific is reduced, and conspecifics are assumed to exert greater competition on each other than heterospecifics, which would lead to greater mixture effects.

Leguminous plants strongly influence aboveground competition (Marquard et al., 2013; Orwin et al., 2014) and mixes of legume and grass species are often applied in cultivated agricultural grasslands. These interspecific interactions, while promoting increases in nitrogen fixation rates by legumes, result in the uptake of nitrogen by grasses (Xi et al., 2017). Legume neighbors, known to have strong effects on plant-plant interactions, can affect neighbor-effect intensity as benefactors or beneficiaries, which requires further testing by comparing neighbor-effect intensity values (Schob et al., 2018). With higher productivity in legume-grass mixtures than in monocultures (Hector et al., 1999; Tilman et al., 2001), we expect a higher neighbor-effect intensity value and increased facilitation in smaller species patch sizes at seeding due to the facilitation of competitive exclusion when the time effect on plots gradually occurs.

Here, we conducted a three-year study by manipulating the interaction of individuals in cultivated legume-grass grasslands. We grew monocultures and mixtures of the legume alfalfa and the grass tall fescue in five replicates at varied species patch sizes at seeding and in a mixed-seeded control. These treatments were used to quantify the intensity of negative and positive plant interactions. We hypothesized the following: first, smaller conspecific patches have stronger positive neighbor-effect intensity compared with conventional uniform mixtures, and this effect continues to enhance with the study duration, because facilitative interactions and interspecific niche differentiation with patchy pattern lag behind in the upcoming year; Second, legume species impose stronger impacts on grass through inter-specific plant interactions. Finally, we explore the species patch size that provided a competitive balance between interspecific competition and intraspecific competition, which allows for the manipulation of the seeding mixture for long-term plant productivity. In this study, we expect that reduced competition or enhanced facilitation with reduced neighbor-effect intensity would be stronger as species patch size at seeding decreases. The findings from our study will be applicable to arable and grassland agroecosystems as the

target species are perennial forage species that can contribute, in the long-term, to grassland and forage production. Also, in the short-term, both of the species can be used as a cover crop and green manures where they can improve soil properties in organic systems or in soil revegetation.

2. Material and methods

2.1. Experimental design

A randomized complete block design was conducted in this study. We selected two perennial species for this mixture experiment, the legume *Medicago sativa* and the grass *Festuca arundinacea*. Both species are highly productive in the study region. The proportion of *M. sativa* to *F. arundinacea* was 1:1 in current study, differing from local traditional cultivation proportion 2:1. Seeds of these two species were obtained from White-Horse Farm, Nanjing, Jiangsu, China. The study was conducted at Nanjing Agriculture University, Nanjing, Jiangsu Province, China (32° 32' 56" N, 118° 12' 39" E). The study area has a mean annual precipitation (MAP) of 1037 mm and a mean annual temperature (MAT) of 15.5 °C. MAP and MAT in 2016–2018 year were investigated and had no significant difference among years (Table S1). There has been no grazing at the experimental site for a decade. The major soil types include Haplic Luvisol soil. The soil physical and chemical properties in 2016–2018 were measured (Table S1). Because of storm runoff, soil nutrients levels were low.

In the beginning of April 2016, 2 × 2 m plots were seeded with four different patch size treatments: 1.0, 0.5, 0.25 m long on a side and a mixed-seeded control in which the seeds were simply mixed and scattered (i.e., patches were not formed) as in conventional seeding (Fig. 1, Fig. S1). Each plot had 0, 4, 16, or 64 patch treatments and were seeded equally at a rate of 1000 viable seeds / m² (i.e., the recommended agronomic planting density in the study region), with 10 replicates of each treatment. The number of sown seeds was adjusted for germination rates obtained from laboratory tests prior to seeding and only one species was seeded in each patch. For a comparison, a monoculture of each species was seeded with broadcasting as in the case of the control mixture, with 12 replicates for a total of 64 plots. Seeds were intermixed and scattered evenly on the soil surface in all plots. After seeding, all plots were watered regularly maintaining 65 % soil moisture content (using COMBI6000 meter). After four months of growth (the growing degree days of each target species was estimated), plant aboveground biomass in the study area was harvested to 3 cm above the soil surface in each experimental year (2016–2018). In the study area, the rainy season began in August; therefore, the aboveground biomass was harvested at the end of July to avoid loss due to flooding. In the coming fall of each year, the study field was slightly ploughed for soil preparation, weeded regularly and enclosed for use. Biomass is presented based on dry weight.

2.2. Calculations of the neighbor effect index (NEI) and the neighbor effect intensity index with commutative symmetry (NIIntC)

The assessment of plant-plant interactions was estimated using a cumulative neighbor effect index (NEI) calculated using the following equations (Manea and Leishman., 2011; Diaz-Sierra et al., 2017):

$$NEI_{i/j} = (B_{i/j} - B_i) / (B_{i/j} + B_i); NEI_{j/i} = (B_{j/i} - B_j) / (B_{j/i} + B_j) \quad (1)$$

Where $NEI_{i/j}$ and $NEI_{j/i}$ indicate inter-specific plant interactions for species *i* and *j*, respectively; B_i and B_j are the biomass of species *i* and *j* in monoculture, respectively; and $B_{i/j}$ and $B_{j/i}$ are the biomass of *i* and *j* with interspecific interactions in their mixtures, respectively. NEI is a measure of simple relative effect size with values ranging from -1 to 1. A positive NEI value indicates that a plant positively benefits from its neighbor.

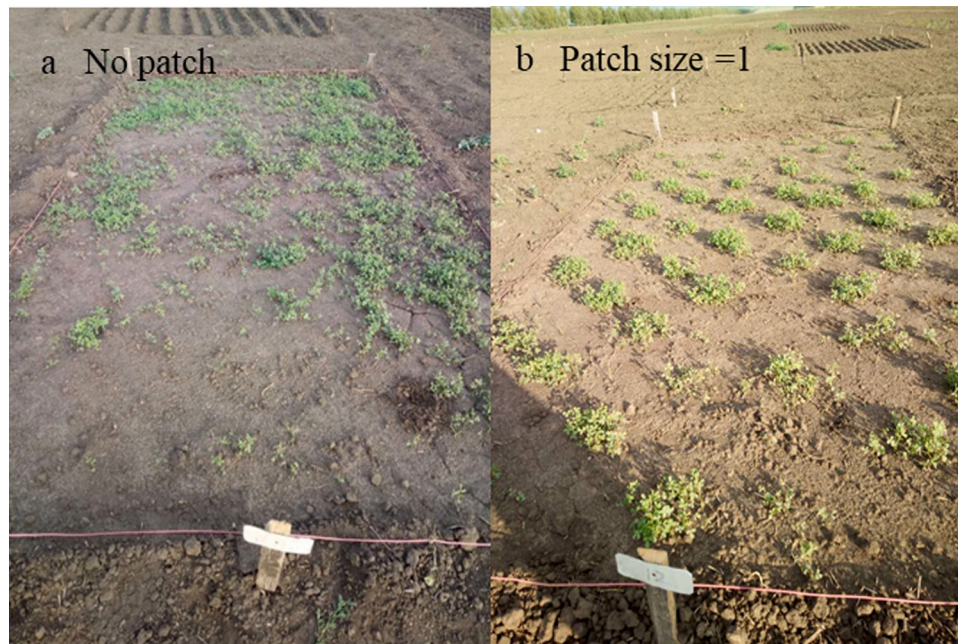


Fig. 1. View of the experimental fine-scale species patch seeding pattern. Legume-grass mixture between square patches with (a) side long > 0 (species mixed with no patch) and (b) side long = 1. Photos were taken in May 2017 when the plants had grown for more than one month.

Another method to calculate the direction and intensity of the response of species i in each monoculture and mixed community was used to compare the interspecific interactions among neighbors. Specifically, the response of species i in mixed community ij was assessed using the neighbor effect intensity index with commutative symmetry (NIntC):

$$NIntC_{net(i/ij)} = 2(B_{i/ij} - B_i) / [(B_{i/ij} + B_i) + |B_{i/ij} - B_i|] \quad (2)$$

$NIntC_{net}$ quantifies the relative change of the biomass of species i in a mixture compared to its biomass in monoculture. Comparisons of $NIntC_{net}$ among monocultures and mixtures indicates differences in the net outcome of species interactions on productivity. $NIntC$ values range from -1 to 1 . Positive $NIntC$ values indicate net positive (facilitative) interactions while negative values indicate net negative (competitive) interactions; 1 and -1 are extreme values indicating the strongest effect sizes (Diaz-Sierra et al., 2017). Higher NEI and $NIntC$ indicate better species coexistence and a more stable community.

2.3. Statistical analysis

We used legume biomass, grass biomass, total biomass, NEI, and $NIntC_{net}$ as response variables to species patch size treatments of the planted communities. Soil properties include: soil nitrate nitrogen (SNN), soil ammonia nitrogen (SAN), soil available phosphorus (SAP), soil moisture (SM). MAP and MAT were compared among years using a T-test to determine the abiotic effects of years on plant biomass. The variation of SAN and SAP were also tested in the different species patch size treatments. Generalized linear mixed-effects models using restricted maximum likelihood estimation were applied and we assessed the significance of the fixed effects using repeated measures analysis of variance (ANOVA) and F tests with adjusted error terms. Block was set as a random factor and conspecific patch size treatment, year, and their interactions were set as model terms. All statistical analyses were performed using SAS Version 9.4 (SAS Institute Inc., Cary, NC, USA).

3. Results

Biomass at species and community levels and NEI significantly

varied with different species and species patch size treatments over the three experimental years. NEI had no significant variation among years (Table 1; Figs. 1 and 2). *M. sativa* always showed higher biomass than *F. arundinacea* within all species patch size treatments from 2016 to 2018. As species patch size decreased, species biomass increased significantly, except in the first experimental year (2016). Compared with the control, species had similar biomass when the conspecific patch size was equal to 1 m^2 and 0.25 m^2 area (Fig. 2). Community total biomass increased with decreasing species patch size and decreased in the control treatment (Fig. 2). Community total biomass was negatively correlated with soil available nitrogen ($R^2 = 0.22$, $P \leq 0.05$) but was not significantly associated with soil available phosphorus ($R^2 = 0.04$, $P > 0.05$) as species patch size increased (Fig. S2 and Table 2), which indicates higher nutrition availability in smaller species patch sizes. Plant communities had similar total biomass in the no patch mixture and the species patch size $P = 0.5 \text{ m}$. Total biomass significantly differed among years within the same patch size. On average, total biomass was higher in 2017 than in 2018 and was the lowest in 2016, except for the control, which had the highest biomass in 2018.

To quantify plant-plant interactions, we selected two well-known indexes, NEI and $NIntC$. Both indexes significantly varied with different species and species patch size treatments over the three experimental years, but had no significant variation among years and

Table 1

Repeated measures ANOVA analyses of species patch treatment on neighbor effect intensity (NEI), neighbor-effect intensity index with commutative symmetry ($NIntC$), species biomass (SB) and community total biomass (TB). Values are F-statistics and degrees of freedom, which were reduced for variables with three growing seasons of data.

Source	df	SB	NEI	$NIntC$	TB
Year (Y)	2	9.03***	0.60ns	0.85ns	18.64**
Patch (P)	3	13.22***	18.30***	19.44***	20.52***
Species (S)	1	196.37***	0.34ns	0.63ns	
Y*P	6	2.93*	1.97ns	2.42ns	2.37*
Y*S	2	11.17***	1.23ns	1.74ns	
P*S	3	13.29***	1.61ns	1.95ns	
Y*P*S	6	2.51*	1.05ns	1.62 ns	

Note: * $P \leq 0.05$, ** $P \leq 0.01$, or *** $P \leq 0.001$.

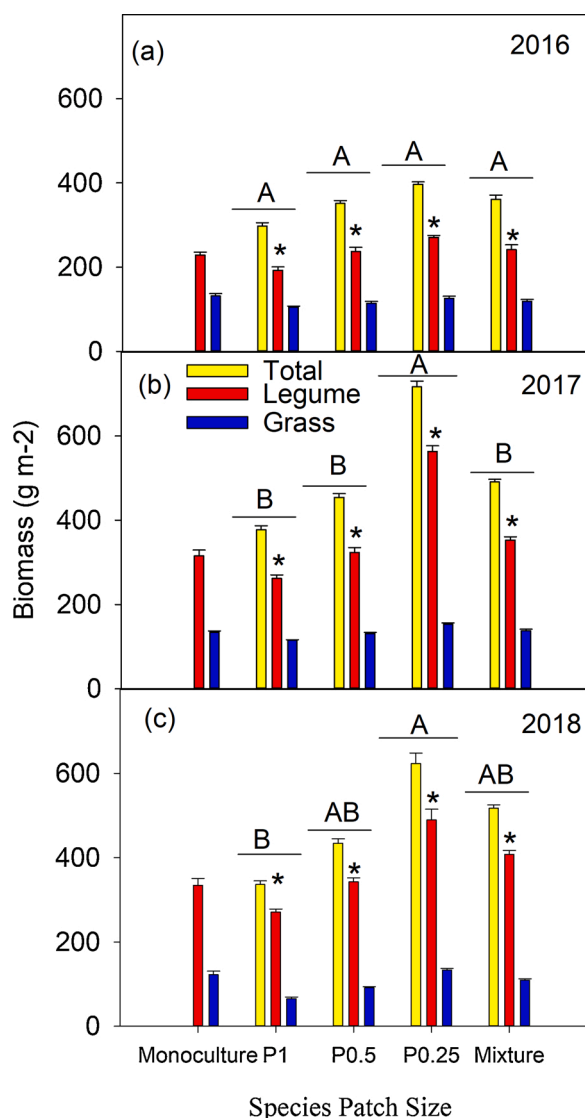


Fig. 2. Effect of conspecific patch size on species biomass and community total biomass in three growing seasons (2016–2018). Species patches were squares (with one species per square), and patch size refers to the length in meters of one side of the square. Bar groups with different capital letters indicate a significant difference among patch size treatments within legume or grass species or community total biomass, and * indicates a significant difference between legume and grass species within the same patch size. Values are means (+ standard error, n = 10). * indicates $P \leq 0.05$.

Table 2
Available nitrogen and phosphorus in soil cultivated with different species patch size treatments.

Soil properties	P1 soil	P0.5 soil	Mixture soil	P0.25 soil
SAN(mg/kg)	35.5 ± 5.1a	31.4 ± 1.8a	24.4 ± 2.0b	21.5 ± 1.4b
SAP(mg/kg)	6.57 ± 0.62a	3.79 ± 0.75b	4.60 ± 0.65ab	4.86 ± 0.44ab

Note: SAN: soil available nitrogen; SAP: soil available phosphorus.

the plant-plant interactions (Table 1). NInC quantifies changes in species biomass in net facilitation (+) versus net competition (-) with changing species patch size by comparing $NIntC_{facilitation}$ and $NIntC_{competition}$ among mixed communities. Increasing (i.e., less negative) $NIntC_{competition}$ indicated decreasing net competition and likely increasing niche differentiation and vice versa, whereas increasing $NIntC_{facilitation}$ likely

indicated increasing facilitation intensity and vice versa. Mixed species encountered stronger negative effects from interspecific neighbors in the largest species patch size treatments ($P = 1$), but showed positive effects in the smaller patch size treatments ($P = 0.5$ m, 0.25 m or mixture) (Fig. 3). Species had their highest NEI and NInC values in the smallest species patch size treatments ($P = 0.25$ m). In the mixture with no patch size and a patch size of $P = 0.5$ m per plot, there were no significant differences in species NEI and NInC values.

4. Discussion

Numerous studies have described a direct relationship between species diversity and ecosystem productivity through facilitation or resource partitioning (Loreau et al., 2001; Grace et al., 2007; Jesch et al., 2018). However, fewer studies have determined how these interactions take place in space and time. This represents a gap in knowledge because it limits our ability to design long-term agricultural production and restoration systems. Our results showed that plant communities with smaller patch size had stronger NEI and NIntC as well as higher community productivity and higher nutrition availability (lower SAN and SAP; Table 2; Fig. S2). This effect was not present immediately but in the subsequent growing year; therefore, the time effect of species patch size needs to be considered when planning agroecosystems. The effects of abiotic factors, such as climate (MAP, MAT) and soil properties (SAN, SAP, SM) on community productivity throughout the study were excluded, as there was no significant difference found over the course of the study (Table S1). These findings indicate that a larger patch size with smaller interspecific interactions occur more within a species rather than between different species. In small patches, the likelihood of a close neighbor being conspecific is reduced (in particular at the edges of the patch where there are interspecific neighbors). As patch size (length of the edge of the square) increases, the number of seeds surrounded by the same species increases non-linearly (e.g., in patches of $3 \times 3 = 9$ seeds it is only 1 seed, in a patch of $5 \times 5 = 25$ it is 9 seeds and so on). As intraspecific competition is assumed to be greater than intraspecific competition, this would explain greater mixture effects with smaller patch size. Plants that responded negatively to a larger species patch size experienced stronger competition, as reflected by the negative NEI value, and low NIntC value. These indices are highly useful as a result of distinguishing between mutual interference, facilitation interactions, and the competitive advantage of one species over the other. *M. sativa*,

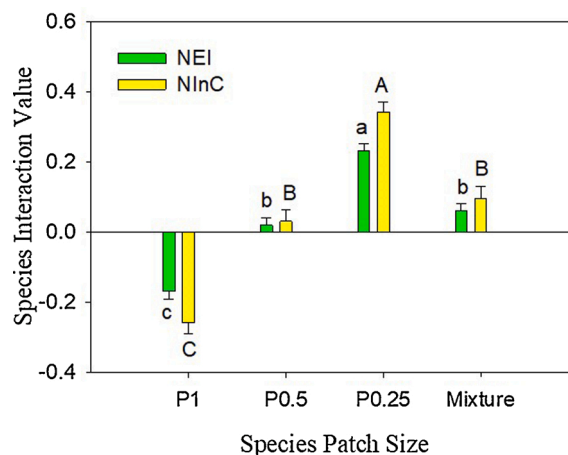


Fig. 3. Effect of conspecific patch size on species interaction neighbor effect intensity (NEI) and neighbor-effect intensity index with commutative symmetry (NIntC) in three growing seasons (2016–2018). Species patches were squares (with one species per square), and patch size refers to the length in meters of one side of the square. Groups with different letters indicate a significant difference among patch size treatments between NEI and NInC values. Values are means (+ standard error, n = 10) and are averaged over patch size.

an allelopathic plant, imposed a stronger NEI effect than grass on its interspecific neighbor. One of the advantages of a grass/legume mixture in plant communities is the ability of the component species to make use of different sources of N (Carlsson and Huss-Danell, 2003; Xi et al., 2017). While grasses may be more competitive than legumes for soil mineral N, legumes can satisfy their own nutrient needs by fixing nitrogen.

Previous studies have shown that plants suffer stronger competitive interactions from their neighbors at higher resource levels by shaping their functional traits (Callaway and Walker, 1997; Fajardo and McIntire, 2011; Liu et al., 2013). Legume species, as potential nitrogen sources, strongly influence plant aboveground competition (Marquard et al., 2009) and in general a combination of legume and grass plants is usually recommended to increase grassland productivity or reconstruct degraded lands. Our results indicated that *M. sativa* had stronger interspecific competition with *F. arundinacea*. Compared with the conventional mixture pattern, structured legume-grass mixtures with smaller patch size significantly increased productivity and species establishment.

Monoculture cropping can reduce the intensity of competition by increasing intraspecific niche differentiation, while mixed cropping could increase facilitative interactions and also interspecific niche differentiation (Brooker et al., 2016). In addition, more effective niche partitioning could help support species coexistence (Turnbull et al., 2013; Mordecai et al., 2016; Chesson, 2018). Thus, integrating the pattern of species patches into contemporary niche theory may enhance our ability to predict the structure of plant communities. In light of the current decline in natural and agricultural biodiversity (Pereira et al., 2010; Duffy et al., 2017; Garcia-Palacios et al., 2018), this study has substantial implications for environmental sustainability and long-term agricultural management of grasslands (Schob et al., 2018). A key novelty of our study was to quantify NEI at different species patch sizes in order to distinguish between niche differentiation or facilitation in mixed cropping. In addition to different species patch sizes, we assessed the competition intensity of species to explore the balance between interspecific- and intraspecific competition. Significant differences between NEI and NIntC in the different species patch size indicate dynamic balance and stability among plant species (Letten et al., 2017).

Understanding the exact scales of inter- and intraspecific competition can allow for the determination of niche differentiation and facilitation, and further facilitate preemptive management. Previous studies have confirmed, that patchy spatial patterns limit species dominance and maintain community stability by decreasing interspecific interactions and increasing intraspecific aggregation (Porensky et al., 2012; Houseman, 2014, Sehra et al. 2016). In an agronomic setting, such as our study site, designing mixed patch size plots that maximize some aspect of production at the end of the growing season results from an initial size advantage related to species' competitive dominance. Different species' patch size at seeding as a result of the edge/area ratio in mixtures may change light use efficiency, e.g., phenotypic plasticity of the shaded species could increase radiation use efficiency and mitigate the decrease in light interception (Bedoussac and Justes, 2011; Gou et al., 2017). Depending on the architecture of the plants, light interception in the mixed stands may have been very different between different patch sizes. In intercropped strips, shading effects of taller species may extend over multiple rows of a companion species (Wang et al., 2016; Letten et al., 2017; Liu et al., 2017), and thus weakening the effects of mixing species as strips become increasingly wider (van Oort et al., 2020). In the current study, a patchy legume-grass mixture of 0.25 m length reached maximal facilitation intensity, minimized species competitive exclusion, and maximized community productivity. It may be also reasonable to assume that 0.25 m long patches, as an intermediate size, maximized light interception. Sehra et al. (2016) showed a similar result and concluded that seeding species with 0.5 to 0.25 m edge sizes are likely to have formative interactions and enhance the success of restoration. In agronomy, intercropped strips have been

promoted to limit plant diseases (Ma et al., 2007). Intermediate patch sizes might be advantageous because very large patches do not provide sufficient barriers or dilution effects within the patch, while distances for disease propagules to travel from host to host might not be large enough to reduce disease spread in very small patches; This may also be relevant to belowground diseases. Considering species competition in mixtures may provide more options for agricultural systems than the conventional mixed seeding pattern.

In conclusion, we showed that the intensity of species competition in mixtures allowed for a better description of how plants partition their ecological niches and their fitness. We showed that the spatial patch size of plant species induces changes in the NEI and NIntC of species with direct implications for plant-plant coexistence. We also showed that mixed plant communities with smaller patch size patterns better partitioned their ecological niches. Resource availability has impacts on species interactions (Seneviratne et al., 2010; Roscher et al., 2016; Slade et al., 2017). Fine-scale seeding of mixed legume-grasses may help support the development of sustainable agricultural systems through mixed cropping. Finally, our work underscores how integrating key species interactions is important to understand plant community dynamics, maintenance, and stable coexistence, presenting opportunities for manipulating interspecific competition to increase productivity.

Data availability statements

All data generated or analyzed during this study are included in this published article (and its supplementary information files)

CRediT authorship contribution statement

Haiyan Ren: Conceptualization, Methodology, Formal analysis, Writing - original draft, Supervision, Project administration. **Anran Cai:** Visualization, Investigation. **Jorge L. Mazza Rodrigues:** Writing - review & editing. **Xinwei Wu:** Writing - review & editing. **Lifeng Wang:** Software, Validation. **Jiechao Chang:** Software, Validation. **Xiuyang Wu:** Visualization. **Quanping Zhou:** Resources. **Yuehua Jiang:** Resources. **Shuijin Hu:** Project administration.

Declaration of Competing Interest

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

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Appendix A. Supplementary data

Supplementary material related to this article can be found, in the online version, at doi:<https://doi.org/10.1016/j.eja.2021.126342>.

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