



## Seed density is as important as limiting similarity, diversity effect, and propagule pressure in plant restoration to control invasion



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### ABSTRACT

Restoring invasion-resistant plant communities is critical for the successful control of invasive plant species. It is based on ecological principles, such as limiting similarity, and the diversity–invasibility hypothesis, which can be used to select optimal combinations of species and determine appropriate plant density for the effective suppression of invasion due to propagule pressure. However, no attempt has been made to combine these factors in a single research framework. Here, we show for the first time the relative importance of all significant factors, including seed density, limiting similarity, diversity effect, and propagule pressure, in the invasion mechanism of *Sicyos angulatus*, an invasive plant species. Our results suggest that seed density, rarely explored in previous studies, is as important a determinant of invasion success as limiting similarity, diversity effect, and propagule pressure. Thus, the density-mediated mechanism must be given careful consideration for the restoration of strong invasion-resistant native plant communities.

### 1. Introduction

Biotic resistance refers to the ability of a community to limit intrusion by invaders (Catford et al., 2009; Levine et al., 2004). Knowledge of the mechanism of biotic resistance is central to our understanding of community invasibility (Byun et al., 2013). However, biotic resistance has not been emphasized in the restoration guidelines for invasive species control (Guo et al., 2019; Kettenring and Adams, 2011), and the basis of selection or combination of species, as well as the number of seeds required for the control of invasive plant species, remain largely unknown. Investigation of the factors that contribute to biotic resistance (Levine et al., 2004) has led to several ecological theories, which are particularly relevant to how species assemble and control invasion (Funk et al., 2008; Shea and Chesson, 2002), and to the identification of factors that determine biotic resistance to plant invasion, including limiting similarity (Price and Pärtel, 2013), functional group composition (Byun et al., 2013; Drenovsky et al., 2012; Hooper and Dukes, 2010), diversity effect (Elton, 1958; Levine, 2000; Levine and D'Antonio, 1999), and seed density (MacLaren et al., 2019; Yannelli et al., 2018).

Limiting similarity suggests that competitive exclusion limits coexistence between functionally similar species (MacArthur and Levins, 1967; Price and Pärtel, 2013). Niche opportunities are narrow for

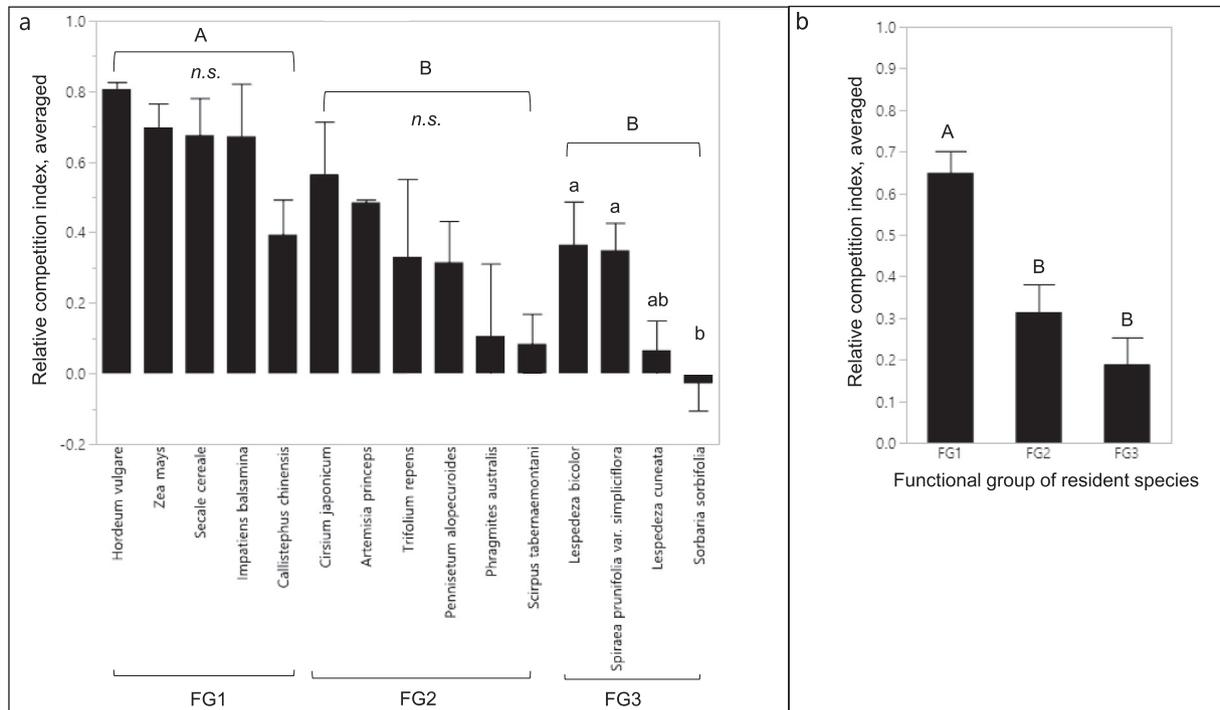
invading species, especially when their niche overlaps with that of resident species (Shea and Chesson, 2002). The pattern of limiting similarity has been observed in many case studies (Divišek et al., 2018; Larson et al., 2013; Petruzzella et al., 2018; Turnbull et al., 2005). Additionally, Walder and colleagues reported that limiting similarity is much more important than biotic resistance via the diversity effect (Walder et al., 2019).

The functional composition of a community affects biotic resistance to invasion (Fox and Brown, 1993; Gooden and French, 2015; Hooper and Dukes, 2010) because a functional group, comprising species with similar functional traits, exhibits selective resistance against an individual invader (Funk et al., 2008). For example, early growing annual plants most effectively resist perennial invaders, such as common reed (*Phragmites australis*) (Byun et al., 2013) and white snakeroot (*Ageratina altissima*) (Byun and Lee, 2017), through niche pre-emption or priority effect (first-come, first-served effect) (Stuble and Souza, 2016).

According to the diversity–invasibility hypothesis (Elton, 1958), species diversity regulates biotic resistance to invasion (Abernathy et al., 2015; Henriksson et al., 2016) because species in diverse communities partition their niches for efficient resource uptake (Shea and Chesson, 2002). Species-rich communities usually exhibit higher functional diversity, which promotes invasion resistance (Ammond and Litton, 2012; Pokorný et al., 2005; Symstad, 2000).

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**Fig. 1.** Effect of resident species on *Sicyos angulatus* (invasive species), estimated as the average relative competition index (RCI<sub>avg</sub>), in monoculture treatments. **a**, Effect of each resident plant species on *S. angulatus*. Each resident species was grouped into three functional groups (FG1–3). **b**, Effect of each functional group on *S. angulatus*. Data represent mean  $\pm$  standard error (SE) with sample size is three per mean. Different uppercase letters in **A** and **B** indicate significant differences among functional groups. Different lowercase letters in **a** indicate significant differences among individual resident species with each functional group. *n.s.* indicates no significant difference.

Seed density also controls biotic resistance to invasion (Adomako et al., 2019; Nemeč et al., 2013; Reinhardt Adams and Galatowitsch, 2008) because species planted at a high density create a dense and complex canopy that blocks sunlight, which controls the growth of invasive alien species (Lindig-Cisneros and Zedler, 2002a; Lindig-Cisneros and Zedler, 2002b). Although the effect of seed density on biotic resistance has not been thoroughly investigated in previous studies, recent evidence suggests that seed density is more important than limiting similarity (Yannelli et al., 2018). Furthermore, the application of seed density for species restoration has practical implications because of the associated cost.

In addition to biotic resistance, propagule pressure also determines invasion success (Simberloff, 2009). Propagule pressure refers to the number of released individual invaders and the frequency of release events at a single location (Lockwood et al., 2005). In some cases, propagule pressure overwhelmingly determines invasion success, regardless of ecological resistance (Eschtruth and Battles, 2009; Eschtruth and Battles, 2011; Holle and Simberloff, 2005). Therefore, it is very important to incorporate propagule pressure along with biotic resistance in a single research framework.

Oneseed bur cucumber (*Sicyos angulatus*) is one of the most notorious invasive plant species found in wetlands, along riversides, and in floodplains around the world, especially Asia (Lee et al., 2015; Uchida et al., 2012). It is an annual vine in the gourd family (Cucurbitaceae) and is native to eastern North America. *S. angulatus* spreads throughout the invaded area by creeping on other plants and small trees. Effective control of *S. angulatus* is difficult; if the vines of *S. angulatus* are cut and removed from the plants of resident species, the community is invaded by other invasive plant species (Hashimoto, 2010). Therefore, restoration of alternative plants is very important to increase biotic resistance to *S. angulatus*. However, no studies have yet been conducted to examine the possibility of restoration of native plant communities invaded by *S. angulatus*.

In this study, we aimed to identify the determinants of biotic resistance to *S. angulatus*. We tested the effects of resident species grown in monoculture or in a mixture at different seed densities on the growth of *S. angulatus*. We also investigated the effect of propagule pressure of *S. angulatus* on invasion success. To estimate the contribution of each factor to invasion, we applied the structural equation model (Grace, 2006; Grace et al., 2010, 2012). Our results suggest that seed density is a critical factor affecting the successful invasion of resident species by *S. angulatus*.

## 2. Material and methods

### 2.1.1. Species selection and functional classification

A total of 37 plant species were initially selected. Data on the leaf area, canopy height, life form, growth habit, woodiness, relative growth rate, and leaf dry matter content of the study species (Supplementary Table 1) were obtained from the TRY plant trait database (Kattge et al., 2011). These functional traits are relevant to the list of common core plant traits related to dispersal, establishment, and persistence (Weiher et al., 1999), and to competitive ability and growth (Funk et al., 2008). To build a species–trait matrix, the median value of a measured trait of each species was used to determine data consistency. Cluster analysis was performed using the ward option in the *hclust* function of the R program (Supplementary Fig. 1) to categorize the plant species into functional groups. To determine the similarity among species, all traits were standardized and equally weighted, and the Gower's similarity coefficient was calculated using the *gowdis* function in the R program (Gower, 1971; Podani, 1999).

A total of 22 out of 37 species were selected for further analysis, based on expert opinion and seed availability. Among these 22 species, four species (*Ambrosia trifida*, *Ageratina altissima*, *Sicyos angulatus*, and

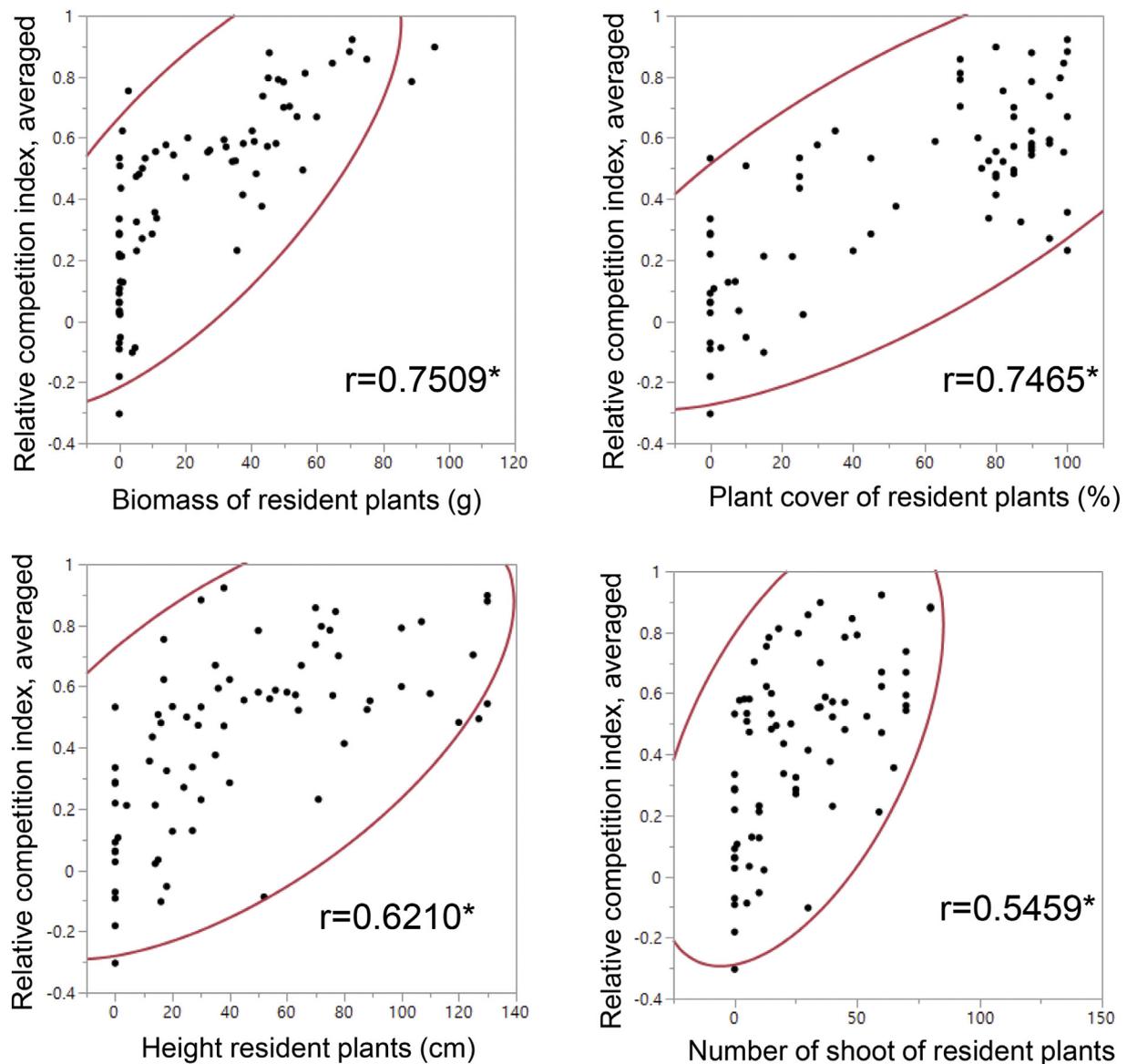


Fig. 2. Effect of the biomass, cover, height, and shoot number of native species on *S. angulatus*, estimated as the average relative competition index ( $RCI_{avg}$ ). Values of the Pearson's correlation coefficient ( $r$ ) are indicated. Asterisks indicate significance ( $P < .05$ ).

*Aster pilosus*) were considered invasive in South Korea.

### 2.1.2. Experimental setup and seed preparation

A pot experiment was set up in the greenhouse facility of the School of Biological Sciences at Seoul National University (Supplementary Fig. 2). The experiment was designed to simulate a scenario where seeds of *S. angulatus* reach bare soil after a biological disturbance.

Seeds of *S. angulatus* were collected from the riverside of the Han River, Seoul in November 2018, while the seeds of most native plants were purchased from seed suppliers. To determine seed viability, all seeds were cold stratified at 3 °C, as described previously (Lindig-Cisneros and Zedler, 2001). To test seed germination, 100 seeds of each species were placed in a Petri dish lined with filter paper (Whatman® No. 1) and moistened with 6 mL distilled water. The plates were incubated under fluorescent light for 3 weeks. Germination tests were conducted in three replicates for each species. Species with germination rate < 3% were excluded from the study. Among the 22 species, 15 species showed germination rate > 3%. Viable seeds (not seedlings) of each species among 15 species were sown in pots (22 cm diameter and 30 cm in height) that were filled with fertile agricultural soil.

### 2.1.3. Design of competition test

An additive competition design was used to test the competitive effect of resident species on *S. angulatus* (Connolly et al., 2001; Keddy et al., 1994; Snaydon, 1991). A total of 15 monoculture, eight mixed, and 12 density treatments were conducted. In monoculture treatments, seeds of each resident species were sown in separate pots. In mixed treatments, four randomly selected resident plant species were sown together in each pot. In monoculture and mixed treatments, each pot contained 20 viable seeds of the resident species and five viable seeds of *S. angulatus*. Density treatments were conducted using four resident species (*Hordeum vulgare*, *Secale cereale*, *Trifolium repens*, and *Lespedeza cuneate*), each sown at different densities (control, low, medium, and high [0, 20, 100, and 500 viable seeds  $\text{pot}^{-1}$ , respectively]), along with *S. angulatus* at three different densities (low, medium, and high [3, 9, and 27 viable seeds  $\text{pot}^{-1}$ , respectively]) in separate pots. Control pots, containing five viable seeds of *S. angulatus* only, were included in each treatment. All treatments were sown in early March 2019. Pots were arranged in a randomized complete block design, with three replicates per treatment (three blocks).

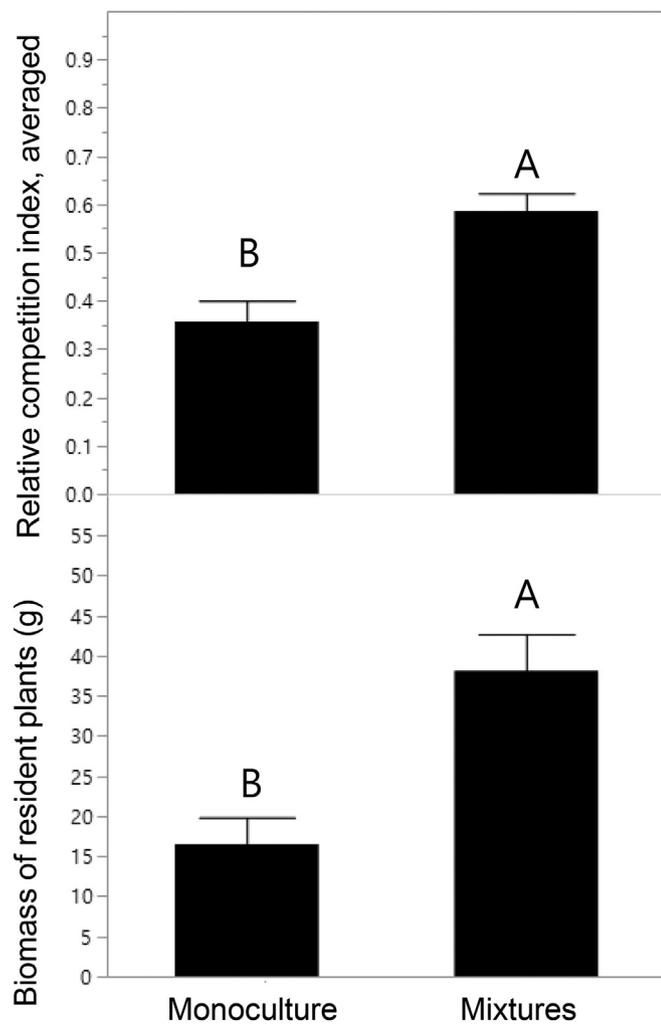


Fig. 3. Comparisons of the average relative competition index ( $RCI_{avg}$ ) and resident plant biomass between monoculture and mixed treatments. Data represent mean  $\pm$  SE with sample size = 3. Different uppercase letters indicate significant differences between means.

#### 2.1.4. Measurements of plant growth parameters

The shoot number, aboveground biomass, plant height, and plant cover of *S. angulatus* in each treatment and control pot were measured in early July 2019 to calculate the primary response variable (see below). Additionally, the plant cover, plant height, and aboveground biomass of all resident plant species were measured to correlate these variables with the response variables. To determine aboveground biomass, the aboveground portion of plants was harvested in early July, dried at 80 °C for 48 h, and weighed. Plant height was estimated for each species to the closest 0.5 cm. The value of RCI was calculated using the following equation (Weigelt and Jolliffe, 2003):

$$RCI_Y = \frac{Y_{control} - Y_{treatment}}{Y_{control}} \quad (1)$$

where RCI is the relative competition effect of a resident plant on *S. angulatus* in either monoculture or mixed treatment; Y represents a specific variable of *S. angulatus* such as shoot number, aboveground biomass, and plant cover;  $Y_{control}$  is the performance of *S. angulatus* in the control; and  $Y_{treatment}$  is the performance of *S. angulatus* in a treatment. Because  $RCI_{shoot\ number}$ ,  $RCI_{biomass}$ , and  $RCI_{plant\ cover}$  were highly correlated with one another,  $RCI_{avg}$  was calculated as the mean of these three RCIs and used as the primary response variable in all analyses.  $RCI_{height}$  was excluded from the calculation of  $RCI_{avg}$  because *S. angulatus* is a creeper with tendrils; therefore, the height of *S. angulatus*

plants was correlated with that of resident plants ( $r = +0.3384$ ;  $P < .001$ ), regardless of *S. angulatus* performance.  $RCI_{avg} = 0$  indicates no competitive effect of the resident species on *S. angulatus*;  $RCI_{avg} = 1$  indicates complete competitive exclusion of *S. angulatus*;  $RCI_{avg} < 0$  indicates that the establishment and growth of *S. angulatus* are facilitated by resident plants.

#### 2.1.5. Statistical data analysis

In monoculture treatments, the effects of functional group identity and species identity (within each functional group) on  $RCI_{avg}$  were tested using ANOVA. A generalized linear mixed model (REML; *F*-test) was used to account for the random block effect (Bolker et al., 2009). Normality of residuals and homoscedasticity were evaluated, and the response variables were transformed when necessary. When a significant functional group effect was detected, the means of functional groups were compared using a contrast test on each pair of functional groups. When a significant species identity effect was detected within each functional group, Tukey's honestly significant difference (HSD) multiple comparison test was used to compare means. ANOVA was used to determine the significance of the difference between monoculture and mixed treatments. In the density treatments, two-way ANOVA was used to test the main effect of each treatment (propagule pressure of *S. angulatus* and seed density of resident plants) as well as their interaction effect. Significant main effects were further compared using Tukey's HSD multiple comparison test.

To synthesize all factors together, structural equation models (Grace, 2006; Grace et al., 2010, 2012) were used to determine the contributions of various factors to biotic resistance. For example, three factors (seed density, limiting similarity, and diversity effect) may have an effect on the performance of resident plants (aboveground biomass or number of shoots), which may affect invasion success (aboveground biomass or number of shoots of *S. angulatus*). Propagule pressure (number of sown viable seeds of *S. angulatus*) may also have an effect on invasion success. To disentangle these complex relationships, a structural equation model was built using the *sem* function in the *lavaan* package of R, with maximum likelihood.

All ANOVA tests and correlation analyses were conducted using the JMP software (© SAS Institute Inc., Cary, NC, USA). Cluster analysis and structural equation model analysis were conducted using the R program (R Development Core Team, 2015).

### 3. Results

#### 3.1.1. Functional group classification

Species were classified into three functional groups (FG1–3), based on trait similarity. The functional groups differed from one another primarily by life span and woodiness traits; FG1, FG2, and FG3 comprised annual plants, perennial herbaceous plants, and perennial woody plants, respectively (Supplementary Table 1).

#### 3.1.2. Monoculture treatments

In monoculture treatments, the biotic resistance of resident plants to *S. angulatus* was primarily related to their functional group identity, whereas the species identity effect was redundant within each functional group, except FG3 (Fig. 1).

We estimated the relative competition index (RCI) to determine the effect of resident plants on *S. angulatus*. The average RCI ( $RCI_{avg}$ ) of 15 resident plants varied significantly among the three FGs ( $F_{2,40} = 12.83$ ;  $P < .001$ ). FG1 (annual plants) showed the highest  $RCI_{avg}$  value, followed by FG2 and FG3 ( $RCI_{avg} = 0.649, 0.314,$  and  $0.188$ , respectively; Fig. 1). Species functionally similar to *S. angulatus* in FG1 showed the highest resistance to *S. angulatus*. Among the species in FG1, *Hordeum vulgare* showed the highest  $RCI_{avg}$  ( $\bar{Y} = 0.8068$ ), followed by *Zea mays* ( $\bar{Y} = 0.6975$ ), *Secale cereale* ( $\bar{Y} = 0.6756$ ), and *Impatiens balsamina*

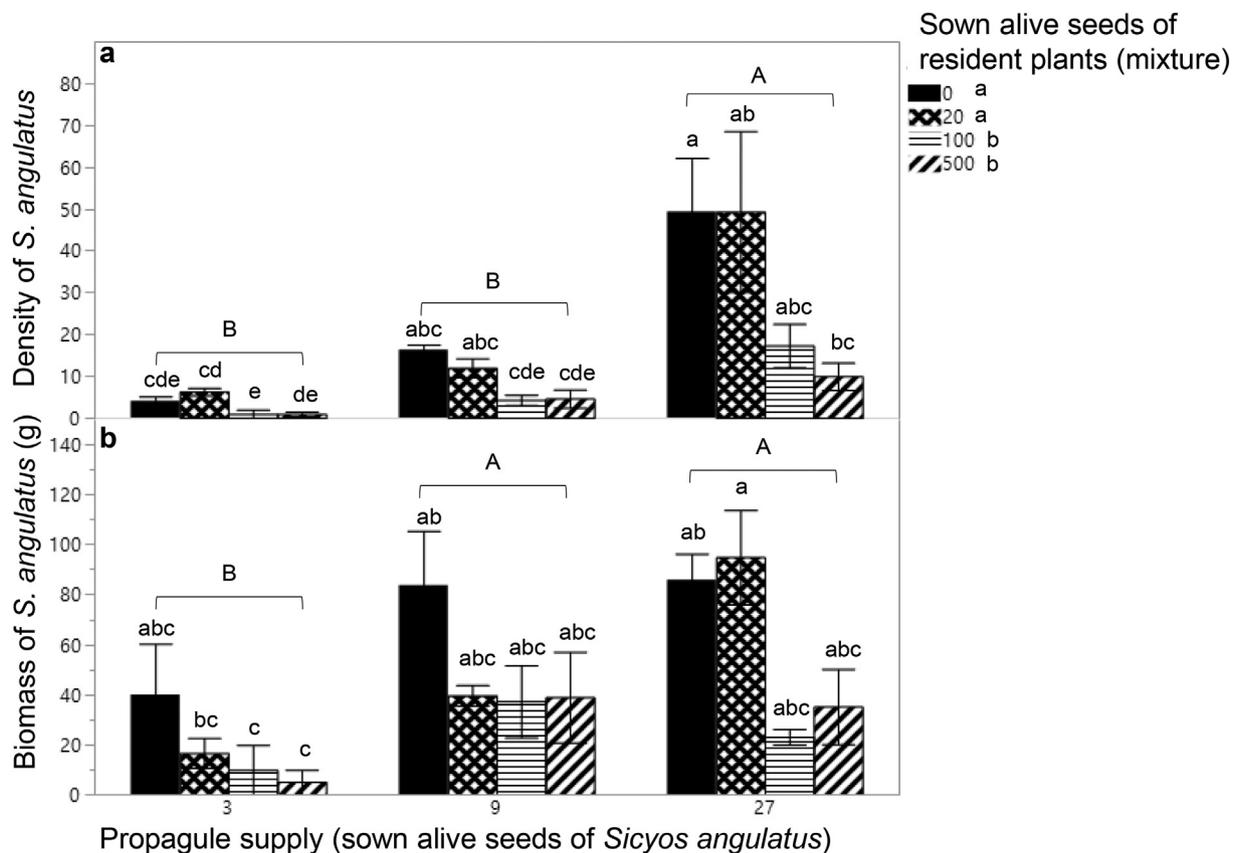


Fig. 4. Effect of propagule supply of *S. angulatus* on invasion success at four seeding densities of resident species (0, 20, 100, and 500 seeds  $\text{pot}^{-1}$ ). **a** and **b**, Correlation of propagule supply of *S. angulatus* at three levels (3, 9, and 27 seeds  $\text{pot}^{-1}$ ), with its density (**a**) and biomass (**b**) at four seeding densities of resident species. Different uppercase letters indicate significant differences among different propagule supply treatments ( $P < .05$ ; Tukey's HSD test). Different lowercase letters indicate significant differences among different seeding densities of resident species ( $P < .05$ ; Tukey's HSD test).

( $\bar{Y} = 0.6722$ ). No significant differences were detected in the  $\text{RCI}_{\text{avg}}$  of species within FG1 ( $F_{4,8} = 2.56$ ;  $P = .1201$ ) and FG2 ( $F_{5,10} = 2.40$ ;  $P = .1109$ ). However, the  $\text{RCI}_{\text{avg}}$  of species within FG3 showed significant differences ( $F_{3,6} = 8.02$ ;  $P = .0160$ ); within FG3, the  $\text{RCI}_{\text{avg}}$  of *Sorbaria sorbifolia* var. *stellipila* ( $\bar{Y} = -0.0282$ ) was significantly lower than that of the other three species (*Lespedeza bicolor*, *Spiraea prunifolia* var. *simpliciflora*, and *Lespedeza cuneata*).

Estimation of Pearson's correlation coefficient ( $r$ ) indicated that the  $\text{RCI}_{\text{avg}}$  of resident plants was significantly positively correlated with the biomass ( $r = 0.751$ ;  $P < .0001$ ), cover ( $r = 0.747$ ;  $P < .0001$ ), height ( $r = 0.621$ ;  $P < .0001$ ), and shoot number ( $r = 0.546$ ;  $P < .0001$ ) of resident plants (Fig. 2).

### 3.1.3. Mixed treatments

The  $\text{RCI}_{\text{avg}}$  of mixed treatments was significantly higher than that of monocultures ( $F_{1,71} = 10.92$ ;  $P = .0015$ ; Fig. 3), indicating that mixed treatments were more resistant to *S. angulatus* invasion than monocultures. The aboveground biomass of resident species was also significantly higher in mixed treatments than in monoculture treatments ( $F_{1,71} = 13.97$ ;  $P = .0004$ ; Fig. 3).

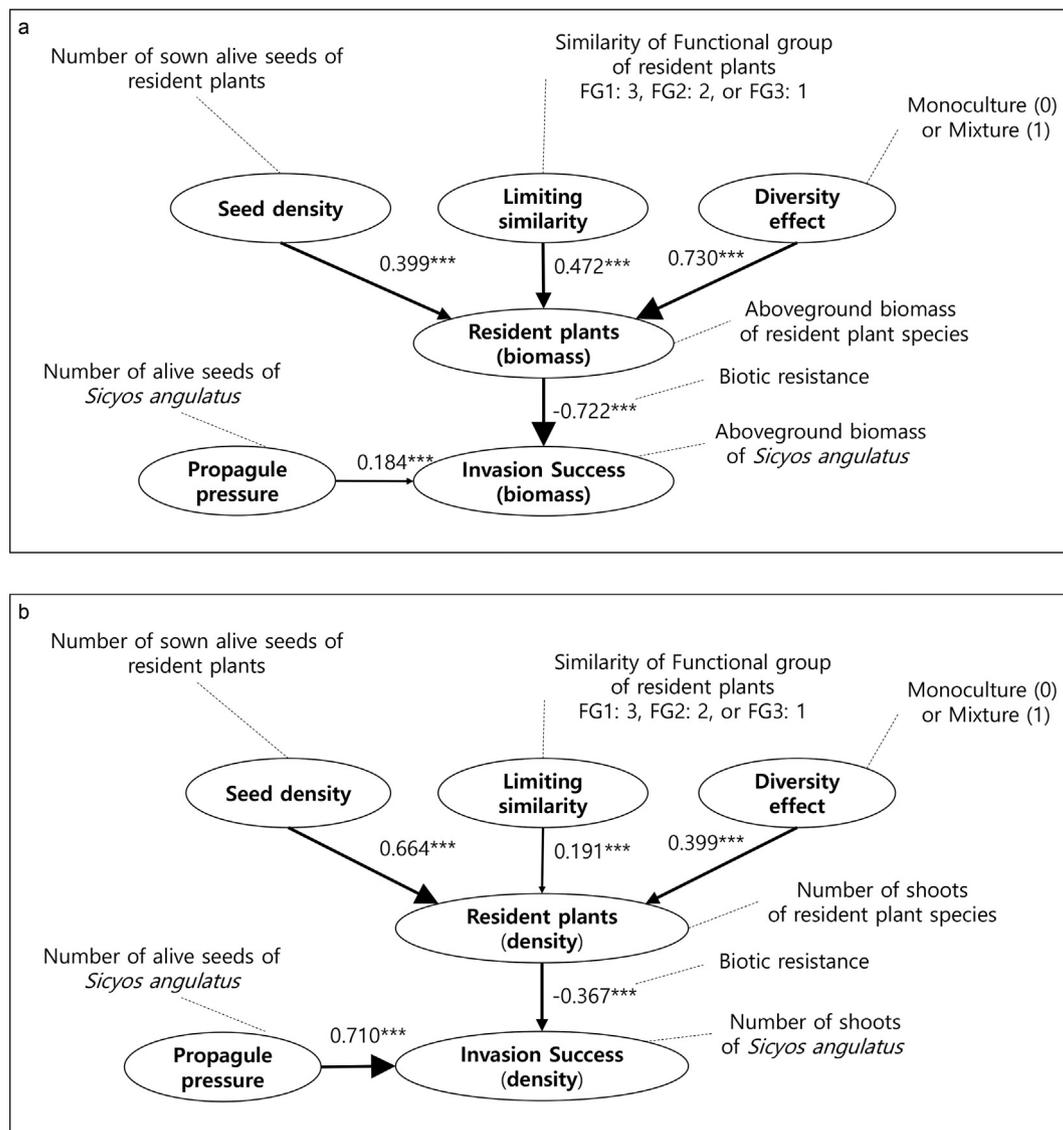
### 3.1.4. Density treatments

We determined the effects of propagule supply of *S. angulatus* and seeding density of resident species on invasion success, based on the shoot number and biomass of *S. angulatus*. Two-way analysis of variance (ANOVA) of shoot numbers (log-transformed data) revealed significant effects of propagule pressure ( $F_{2,22} = 49.13$ ;  $P < .001$ ) and seed density ( $F_{3,22} = 16.96$ ;  $P < .001$ ), although the interaction between the main effects showed no significant effects ( $F_{6,22} = 0.58$ ;  $P = .7364$ ; Fig. 4a). Similarly, two-way ANOVA of the biomass of *S.*

*angulatus* revealed significant effects of propagule pressure ( $F_{2,22} = 9.70$ ;  $P = .0010$ ) and seed density ( $F_{3,22} = 7.24$ ;  $P = .0015$ ) but non-significant effects of the interaction variable ( $F_{6,22} = 1.52$ ;  $P = .2169$ ; Fig. 4b). The invasion success *S. angulatus* (in terms of both shoot number and biomass) increased with the propagule supply of *S. angulatus* but decreased with the seeding rate of resident plants. The effect of the seeding density of resident plants on the relationship between propagule supply and invasion success (number of shoots of *S. angulatus*) suggests clear benefits in investing  $> 100$  seeds  $\text{pot}^{-1}$  (equivalent seed density =  $\sim 2500$  live seeds  $\text{m}^{-2}$ ), but not any more increase benefit. Additionally, despite high propagule pressure, invasion success was reduced when a resident plant cover was present compared with no cover. Conversely, invasion success increased with propagule pressure at the fastest rate and to the highest level in the absence of competing resident species.

### 3.1.5. Estimation of main factor effects using the structural equation model

While the direct positive effects of three main factors (seed density, limiting similarity, and diversity effect) on the performance of resident plants (in terms of biomass and shoot number) were significant, biotic resistance of resident plants had negative effects on invasion success, and propagule pressure always had positive effects on invasion success (Fig. 5). For instance, the biomass of resident plants increased as a result of seed density ( $\beta = 0.399$ ;  $P < .001$ ), limiting similarity ( $\beta = 0.472$ ;  $P < .001$ ), and diversity effect ( $\beta = 0.730$ ;  $P < .001$ ). Thus, seed density was as important as limiting similarity and diversity effect. Additionally, biotic resistance of resident plants decreased invasion success ( $\beta = 0.722$ ;  $P < .001$ ), whereas propagule pressure increased invasion success ( $\beta = 0.184$ ;  $P < .001$ ).



**Fig. 5.** Determination of the effects of the seeding density, limiting similarity, and diversity of resident species on invasion by *S. angulatus* using the structural equation model. **a and b**, Effects of the seeding density, limiting similarity, and diversity of resident species on the biomass (a) and shoot number (b) of the resident species and *S. angulatus*. Numbers represent covariance; '+' and '-' signs indicate positive and negative effects, respectively. Arrows represent significant effects ( $P < .05$ ; Student's *t*-test), and arrow width indicates the magnitude of the effect.

#### 4. Discussion

In this study, we demonstrated that the functional group identity determined biotic resistance to *S. angulatus* invasion, whereas the species identity effect was redundant within each functional group (Fig. 1). This finding is consistent with previous studies on *Phragmites australis* (Byun et al., 2013), *Ageratina altissima* (Byun and Lee, 2017), *Taeniatherum caput-medusa* (Sheley and James, 2017), and other invaders (Wang et al., 2013). The most resistant species belonged to the early establishing FG1 (short annual plants), thus indicating the importance of limiting similarity (Macarthur and Levins, 1967) and priority effect (Stuble and Souza, 2016; Wilsey et al., 2015) or niche pre-emption (Mwangi et al., 2007). These factors were considered as the most effective in determining the ecological resistance to invasive plant species (Byun et al., 2018). Additionally, we showed a positive correlation between performance traits, such as plant biomass, cover, height, and density, and biotic resistance to invasion by *S. angulatus* (Fig. 2). This is consistent with previous studies showing that biotic resistance is directly correlated with the plant cover (Bakker and Wilson, 2004; Gerhardt and Collinge, 2003), height (Schamp and Aarssen, 2010), and

biomass (Lulow, 2006; Rinella et al., 2007) of native species. Additionally, our results support the diversity-invasibility hypothesis (Elton, 1958), as the resistance to invasion by *S. angulatus* was higher in the mixed treatments than in the monoculture treatments (Fig. 3). Many small-scale studies provide empirical evidence in support of this hypothesis (Fargione and Tilman, 2005; Henriksson et al., 2016; Kennedy et al., 2002; Levine, 2000; Naeem et al., 2000; Nemeček et al., 2013; Zhu et al., 2015); however, conflicting results are found in relatively large-scale studies (Rinella et al., 2007). In addition, we found a threshold effect of seed density on invasion resistance: seed density > 100 seeds per pot (2500 viable seeds  $m^{-2}$ ) did not cause a further increase in invasion resistance (Fig. 4). This is consistent with previous studies, which reported seed density as a strong determinant of plant resistance to invasion (Byun et al., 2015; MacLaren et al., 2019; Nemeček et al., 2013; Reinhardt Adams and Galatowitsch, 2008; Yannelli et al., 2018). Furthermore, propagule pressure played an important role in determining invasion success in our study, as both the density and biomass of *S. angulatus* plants increased with the increase in seeding density. Many case studies reported that propagule pressure strongly increases invasion success (Byun et al., 2015; Eschtruth and Battles,

2009; Eschtruth and Battles, 2011; Holle and Simberloff, 2005; Simberloff, 2009). The most important finding of our study was the identification of the relative importance of seed density, limiting similarity, diversity effect, and propagule pressure in the invasion mechanism (Fig. 5). To date, no studies have attempted this synthesizing approach. Although seed density did not receive much attention until now, we showed that seed density is as important as diversity effect and limiting similarity in determining biotic resistance (Fig. 5b). Thus, creating a highly dense plant cover by sowing mixtures of seeds in optimal quantities is a promising approach for the restoration of invasion-resistant native plant communities, regardless of species selection and combination.

### Authors' contributions

CB and HK conceived the study. CB designed the experiments, analyzed the data, and wrote the manuscript. CB and MO performed the experiments. All authors revised the manuscript and approved the final version.

### Data availability statement

The data supporting the results will be archived in an appropriate public repository (Figshare).

### Declaration of Competing Interest

The authors declare no competing interests.

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### Appendix A. Supplementary data

Supplementary data to this article can be found online at <https://doi.org/10.1016/j.ecoeng.2019.105712>.

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