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SHORT COMMUNICATION

Does the invasion intensity of *Erigeron annuus* (L.) Pers. and community invasibility increase as the number of plant species increases?

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Abstract

Habitats with different numbers of plant species (*S*) may exhibit varying levels of invasibility when invaded by invasive plants (IPS). Nevertheless, there are still doubts about the relationship between *S* and IPS' invasion intensity as well as the community invasibility. It is also unclear which environmental factor has the greatest influence on the community invasibility, especially in habitats with different *S*. A cross-plot comparison approach was employed to estimate the differences in IPS' relative abundance and invasion intensity, the community invasibility, and plant taxonomic diversity along a gradient of *S* under the invasion of *Erigeron annuus* (L.) Pers. Plant diversity, dominance, evenness, and richness evidently increased with increasing *S*. The relative abundance and invasion intensity of *E. annuus*, as also the mean, maximum, and minimum relative abundances of all plants, and the community invasibility significantly decreased with increasing *S*. The community invasibility was positively regulated by the relative abundance and invasion intensity of *E. annuus*, but negatively regulated by plant diversity, dominance, evenness, and richness. Therefore, protecting the diversity of native plants is crucial for enhancing the resistance to IPS' invasion.

Keywords: invasive plants, native plants, plant diversity, relative abundance

Introduction

Invasive plants (IPs) can result in significant modifications to the structure and function of native environments. In particular, IPS can cause a substantial decrease in the diversity of native plants in invaded habitats (Sato *et al.* 2021; Beshai *et al.* 2023; Swierszcz *et al.* 2024; Du *et al.* 2025). Thus, elucidating the mechanisms underlying IPS' invasion has recently become a research focus in the field of invasion ecology (Lu *et al.* 2020; Xu *et al.* 2023; Ahmad *et al.* 2025; Negesse *et al.* 2025).

After successfully expanding from their original distribution areas to new habitats, IPS will gradually undergo succession, and their relative abundance and/or relative coverage will also gradually change. This has led to varying degrees of IPS' invasion into invaded habitats (Fenouillas *et al.* 2021; Beshai *et al.* 2023; Xiao *et al.* 2024; Du *et al.* 2025). Progressive variations in IPS invasion degree have the potential to alter the invasion intensity of these IPS and the community invasibility (antonym: community resistance) by changing the pattern of growth competition between IPS and native plants. In addition, it is unclear which environmental factor has the greatest influence on the community invasibility, especially in habitats with different numbers of plant species (*S*). It is therefore vital to obtain an understanding of the influence of IPS' invasion intensity on the community invasibility, to get insight into the mechanisms driving IPS' invasion.

It is worth noting that there are differences in *S* in different habitats. Therefore, habitats with different *S* may have varying levels of resistance and invasibility to IPS' invasion mainly due to differences in *S*, community structure, and IPS' invasion intensity. Nevertheless, there are still doubts about the relationship between *S*

and community invasibility as well as IPS' invasion intensity. In general, the plant communities with a higher *S* may obtain a larger resistance to IPS' invasion, leading to a lower invasibility to IPS' invasion on a small scale (i.e., IPS' invasion intensity may be lower in plant communities with a higher *S* than in those with a lower *S*), and vice versa (Byun *et al.* 2013; Catford *et al.* 2019; Trevenen *et al.* 2024; Du *et al.* 2025). In contrast, plant communities with a greater *S* may be more vulnerable to IPS' invasion, leading to a higher invasibility on a larger scale (i.e., IPS' invasion intensity may be higher in plant communities with a higher *S* than in those with a lower *S*), and vice versa (Abella *et al.* 2012; Bartomeus *et al.* 2012; Ellis *et al.* 2012; Driscoll 2017). Of course, no obviously substantial correlation has been observed between *S* and IPS' invasion intensity as well as the community invasibility, even on a small scale (Meffin *et al.* 2010; Bart *et al.* 2015; Dong *et al.* 2015; Peng *et al.* 2019). It is therefore of great importance to analyze the relationship between *S* and IPS' invasion intensity as well as the community invasibility.

In this study, a cross-plot comparison approach was employed to evaluate the differences in IPS' relative abundance and invasion intensity, the community invasibility, and plant taxonomic diversity along a gradient of *S* under the invasion of *Erigeron annuus* (L.) Pers.

This study confirmed the following hypotheses: (I) the relative abundance and invasion intensity of *E. annuus*, as well as the community invasibility, may decrease as *S* increases, (II) the community invasibility may be positively regulated by the relative abundance and invasion intensity of *E. annuus*, while it may be negatively regulated by plant taxonomic diversity.

Materials and Methods

Study design

Plant communities under the invasion of *E. annuus* along a gradient of *S* were chosen from May to June 2024 in Zhenjiang, Jiangsu, Eastern China (longitude: 119.52–119.54° E; latitude: 32.11–32.12° N). *E. annuus* belong to the Asteraceae family and originated from North America (Yan *et al.* 2014; Wang *et al.* 2016; Hao and Ma 2023). *E. annuus* can frequently construct large-scale monodominant communities in East China (Fig. S1). *E. annuus* has been registered as a malignant IPS in China because it can cause serious ecological risks to native ecosystems, leading especially to the diversity loss of native plants (Liu *et al.* 2022; Wang *et al.* 2022; Zhang *et al.* 2025; Liu *et al.* 2026).

The surveyed plant communities were herbaceous communities without the growth of trees or shrubs. The habitat type of plant communities under examination was mainly wasteland, which may be disturbed by human activities. The most prevalent native plants in the inspected plant communities were *Acalypha australis* L., *Arthraxon hispidus* (Thunb.) Makino, *Commelina communis* L., *Digitaria sanguinalis* (L.) Scop., *Euphorbia helioscopia* L., *Lactuca indica* L., *Paspalum conjugatum* Bergius, *Polygonum perfoliatum* L., Pseudognaphalium affine (D. Don) Anderb., *Salvia plebeia* R. Br., *Stellaria aquatica* (L.) Scop., *Setaria viridis* (L.) P. Beauv., and *Trigonotis peduncularis* (Trevis.) Benth. ex Baker & S. Moore, etc.

The sampling plots (size: 1 m × 1 m) were comprised of the following categories with a gradient of *S*: (1) two species (n = 40); (2) three species (n = 72); (3) four species (n = 67); (4) five species (n = 94); (5) six species (n = 63); and (6) seven species (n = 31). The distance between sampling plots with different categories was ≥ 100 m. The distance between the sampling plots in each category was ≥ 50 m. Because this study aimed to evaluate the differences in the invasion intensity of *E. annuus* and the community invasibility along a gradient of *S* under the invasion of *E. annuus*, the plots with only native plants were not analyzed.

The number of individuals per plant species and *S* were counted across all sampling plots. The number of individuals of clonal species was evaluated by calculating the number of their ramets. This is because when a ramet of a clonal species and an individual of a non-clonal species has equal or similar stem height and stem diameter, there will not be evident differences in the space they occupy (Zhang *et al.* 2024; Du *et al.* 2025; Liu *et al.* 2026).

Method for determining plant community variables

The invasion intensity index (*III*) was calculated to analyze the invasion degree and intensity of *E. annuus*.

The community invasibility index (*CII*) was determined to evaluate the community susceptibility and invasibility under *E. annuus* invasion.

The Shannon's diversity index (*H'*), Simpson's dominance index (*D*), Pielou's evenness index (E_H), and Margalef's richness index (*F*) were evaluated to estimate plant taxonomic diversity.

The calculation of indices is presented in Table S1.

Statistical analysis

The differences in the values of variables with different *S* were evaluated using one-way analysis of variance (ANOVA) determined by Tukey's test.

The correlation between *S* and variables in the invaded communities was assessed using correlation analysis by calculating Pearson's coefficient

(*r*). Bonferroni correction was applied to adjust the *p*-value to decrease the probability of Type I errors.

The influences of *S* on the variables, as well as the influences of the variables on the community invasibility index in the invaded communities, were evaluated using path analysis by calculating the path coefficient (i.e., standardized path coefficient (i.e., standardized regression coefficient).

Statistical analyses were accomplished using IBM SPSS Statistics 26.0.

Results and Discussion

In this study, all measured plant taxonomic diversity variables were evidently enhanced with increasing *S* under *E. annuus* invasion ($p < 0.0001$; Table 1). The results of the correlation analysis also showed a substantial positive correlation between *S* and all measured plant taxonomic diversity variables ($p < 0.0001$; Table 2). Furthermore, the results of the path analysis exhibited that *S* significantly positively regulated the Shannon's diversity index, Pielou's evenness index, and Margalef's richness index ($p < 0.0001$; Fig. 1). Therefore, as *S* increases, plant diversity, dominance, evenness, and richness may also progressively upsurge. This phenomenon aligns with common expectations. The increased plant diversity, dominance, evenness, and richness may lead to higher levels of ecological functions (such as biomass production, stress resistance, and disturbance resistance), which may result in a higher resistance to IPS' invasion, leading to a lower invasibility to IPS' invasion as *S* increases. The relevant key mechanisms may contain the following effects: (I) the covariance effect: compared to the monocultured species, the relative abundance of the competing species gradually becomes negative covariance in cases of multi-species; (II) the species asynchrony effect: compared to the monocultured species, the down-regulation of relative abundance of certain species can be momentarily offset by the upregulation of relative abundance of another species in cases of multi-species; (III) the high yield effect: due to the compensatory fluctuations, the average biomass production level increases relative to time changes, and the average yield of multi-species communities with the asynchronous populations becomes more stable over time in cases

Table 1. Differences in the measured plant community variables with different numbers of plant species in the invaded communities. Data (mean & standard error) with different lowercase letters in a vertical column indicate statistically significant differences ($p \leq 0.05$)

S	P_{EA}	$MeanP_i$	$MaxP_i$	$MinP_i$	*III*	*CII*	*H'*	*D*	E_H	*F*
Two	0.882 ± 0.017a	0.500 ± 0.000a	0.882 ± 0.017a	0.118 ± 0.017a	0.885 ± 0.017a	0.886 ± 0.017a	0.318 ± 0.027e	0.187 ± 0.020e	0.458 ± 0.039c	0.185 ± 0.001f
Three	0.747 ± 0.026b	0.333 ± 0.000b	0.778 ± 0.019b	0.056 ± 0.007b	0.762 ± 0.026a	0.766 ± 0.026b	0.567 ± 0.030d	0.319 ± 0.021d	0.516 ± 0.028c	0.403 ± 0.007e
Four	0.554 ± 0.030c	0.250 ± 0.000c	0.633 ± 0.020c	0.036 ± 0.004bc	0.595 ± 0.032b	0.624 ± 0.023c	0.891 ± 0.031c	0.489 ± 0.019c	0.643 ± 0.022b	0.642 ± 0.011d
Five	0.381 ± 0.024d	0.200 ± 0.000d	0.532 ± 0.016d	0.028 ± 0.003c	0.428 ± 0.027c	0.492 ± 0.024d	1.169 ± 0.027b	0.592 ± 0.015b	0.726 ± 0.017ab	0.838 ± 0.011c
Six	0.372 ± 0.032d	0.167 ± 0.000e	0.526 ± 0.023d	0.017 ± 0.002c	0.386 ± 0.033c	0.410 ± 0.032d	1.195 ± 0.035b	0.592 ± 0.019b	0.657 ± 0.022ab	1.023 ± 0.013b
Seven	0.287 ± 0.032d	0.143 ± 0.000f	0.436 ± 0.022e	0.017 ± 0.003c	0.435 ± 0.049c	0.628 ± 0.032c	1.467 ± 0.037a	0.701 ± 0.015a	0.754 ± 0.019a	1.184 ± 0.016a
F	56.661	> 1000.000	56.620	28.732	38.025	37.479	138.815	78.547	19.178	916.047
P	**< 0.0001**	**< 0.0001**	**< 0.0001**	**< 0.0001**	**< 0.0001**	**< 0.0001**	**< 0.0001**	**< 0.0001**	**< 0.0001**	**< 0.0001**

"ns" indicates no statistically significant differences ($p > 0.05$). $p \leq 0.05$ are shown in bold. Abbreviations: *S*, the number of plant species; P_{EA}, the relative abundance of *Erigeron annuus* (L.) Pers.; $MeanP_i$, the mean of the relative abundance of all plants; $MaxP_i$, the maximum relative abundance of all plants; $MinP_i$, the minimum relative abundance of all plants; *III*, the invasion intensity index of *E. annuus*; *CII*, the community invasibility index; *H'*, the Shannon's diversity index; *D*, the Simpson's dominance index; E_H, the Pielou's evenness index; *F*, the Margalef's richness index

Table 2. Correlations (*r*, the Pearson's coefficient) between the number of plant species and the measured plant community variables in the invaded communities

	P_{EA}	$MeanP_i$	$MaxP_i$	$MinP_i$	*III*	*CII*	*H'*	*D*	E_H	*F*
R	–0.636***	–0.933***	–0.639***	–0.462***	–0.547***	–0.491***	0.790***	0.690***	0.399***	0.960***
P	**< 0.0001**	**< 0.0001**	**< 0.0001**	**< 0.0001**	**< 0.0001**	**< 0.0001**	**< 0.0001**	**< 0.0001**	**< 0.0001**	**< 0.0001**

*** indicates statistically significant differences at the 0.001 probability levels. *p* values equal to or lower than the corrected *p* value (corrected value = 0.05 / (10 * 9 / 2) = 0.001111) by using Bonferroni correction are shown in bold. Abbreviations same as in Table 1

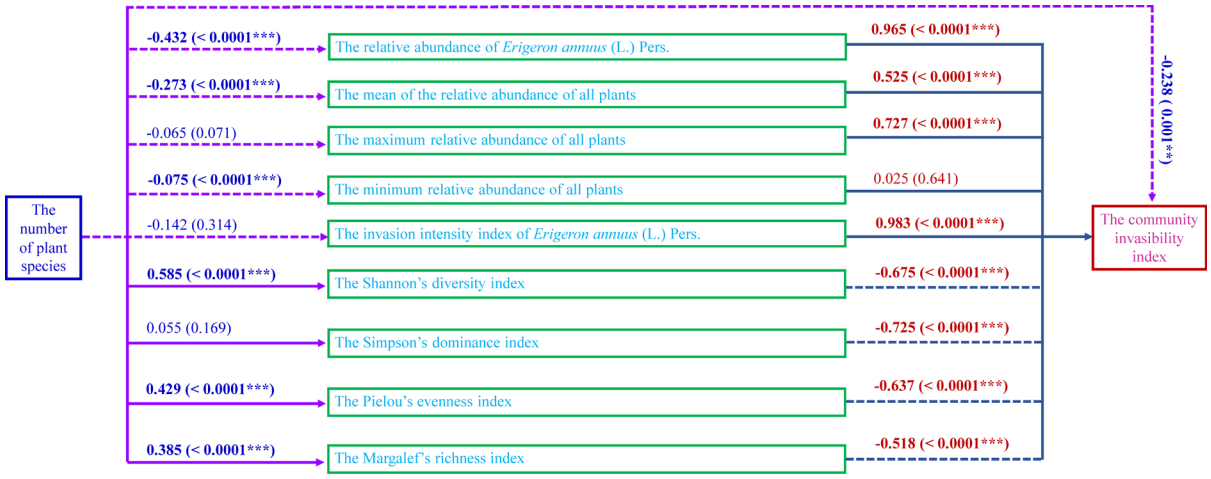

Fig. 1. Schematic diagram of influences of the number of plant species on the variables as well as influences of the variables on the community invasibility index in the invaded communities. The blue numbers represent the influences of the number of plant species on the variables. The purplish red numbers represent the influences of the variables on the community invasibility index. Positive values (solid lines) indicate positive influences, while negative values (dashed lines) indicate negative influences. The stronger the influence, the greater the deviation from 0; and vice versa. The *p*-value is displayed in parentheses. Asterisks (*, **, and *** indicate statistically significant differences at the 0.05, 0.01, and 0.001 probability levels) indicate significant path coefficients. $p \leq 0.05$ are shown in bold

of multi-species compared to the monocultured species; (IV) the complementary effect: compared to the growth performance of the monocultured species, if species interactions increase niche allocation or decrease selection effect, cocultured multiple-species can achieve stronger and better growth performance by enhancing a complementary effect, especially by enhancing ecological resource utilization efficiency, when growing together (Hector *et al.* 2010; Rastogi *et al.* 2023; Ahmad *et al.* 2025; Liu *et al.* 2026).

In this study, the relative abundance and invasion intensity of *E. annuus*, the mean, maximum, and minimum relative abundances of all plants, and the community invasibility significantly decreased with increasing *S* under *E. annuus* invasion ($p < 0.0001$; Table 1). The results of the correlation analysis also presented that *S* was significantly negatively correlated with the relative abundance and invasion intensity of *E. annuus*, the mean, maximum, and minimum relative abundances of all plants, and the community invasibility index ($p < 0.0001$; Table 2). Furthermore, the results of the path analysis revealed that *S* significantly negatively affected the relative abundance of *E. annuus*, the mean and minimum relative abundances of all plants, and the community invasibility index ($p < 0.0001$; Figure 1). The decreased relative abundance of *E. annuus* as well as the mean, maximum, and minimum relative abundances of all plants may be ascribed to the limited occupation of living space and ecological resources by each species with increasing *S*. This may affect the growth performance of each species and gradually reduce their relative abundance in a given community. The weakened invasion intensity of *E. annuus* with increasing *S* may be due to the gradual decrease in the relative abundance of *E. annuus* and/or the progressive increase in plant diversity, dominance, evenness, and richness. This result validates the first hypothesis.

The results of the path analysis presented that the community invasibility was mainly positively regulated by the relative abundance and invasion intensity of *E. annuus*, but negatively regulated by plant diversity, dominance, evenness, and richness ($p < 0.05$; Figure 1). Thus, there was a noteworthy positive correlation between the community invasibility and the relative abundance as well as the invasion intensity of *E. annuus*, but the community invasibility was significantly negatively correlated with plant diversity, dominance, evenness, and richness (Byun *et al.* 2013; Catford *et al.* 2019; Trevenen *et al.* 2024; Du *et al.* 2025). Therefore, IPS' relative abundance and invasion intensity (generate positive influence), as well as plant diversity (produce negative influence), may be the main key factors affecting the community invasibility by influencing the structural composition and ecological functions of plant communities, especially the pattern of growth competition between IPS and native plants. This phenomenon may be due to the fact that the plant communities with a higher *S* can obtain a higher resistance to IPS' invasion but a lower invasibility to IPS' invasion by increasing plant diversity, dominance, evenness, and richness via the intensified covariance effect, species asynchrony effect, high yield effect and complementary effect (Hector *et al.* 2010; Rastogi *et al.* 2023; Ahmad *et al.* 2025; Liu *et al.* 2026). This result validates the second hypothesis.

Based on the above content, a theoretical framework is recommended, namely "the hypothesis of the number of plant species regulating the community invasibility", to illuminate the relationship between *S* and community invasibility, as well as the possible mechanism of *S* regulating the community invasibility. The specifics of this hypothesis are as follows: (I) The community invasibility decreases as *S* increases. (II) The community invasibility may be positively regulated by IPS' relative abundance and invasion intensity, but may be negatively regulated by plant diversity, dominance, evenness, and richness. (III) The plant communities with a wider variety of plant species can get a stronger resistance to IPS' invasion but are less vulnerable to IPS' invasion by increasing plant diversity, dominance, evenness, and richness via the intensified covariance effect, species asynchrony effect, high yield effect, and complementary effect, ultimately leading to a weaker susceptibility and invasibility, and vice versa.

It should be noted, however, that the experimental design of this study is subject to certain restrictions. The present study did not evaluate the effects of the external interference on the interaction between IPS and native plant communities. Therefore, the experimental design must be further refined, particularly with regard to the examination of the influence of the external interference with different intensities and types on the invasion intensity of *E. annuus* and community invasibility, especially along a gradient of *S*.

Conclusions

As *S* increases, plant diversity, dominance, evenness, and richness significantly increase. The relative abundance and invasion intensity of *E. annuus*, the mean, maximum, and minimum relative abundances of all plants, and the community invasibility significantly decreased with increasing *S*. The community invasibility was mainly positively regulated by the relative abundance and invasion intensity of *E. annuus*, but negatively regulated by plant diversity, dominance, evenness, and richness. Consequently, it is vital to protect the diversity of native plants to decrease or even prevent IPS' reproduction and expansion by downregulating IPS' relative abundance and invasion intensity, but enhancing the resistance to IPS' invasion.

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