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Report

A method for quantifying relative competitive advantage and the combined effect of co-invasion for two invasive plants

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Invasive plants affect the composition of native habitats, often triggering the loss of biodiversity (Kuebbing et al., 2014, 2016; Wang et al., 2021a, 2021b). Hence, understanding the mechanisms that underlie successful biological invasion has become a major issue in invasion ecology.

The invasion of one habitat by two or more invasive plants is referred to as co-invasion (Sheppard, 2019; Wang et al., 2020, 2022; Wei et al., 2020a). The invasional meltdown hypothesis posits that the successful colonization of one invasive plant can create a favorable environment for the successful colonization of a second invasive plant (Simberloff, 2006; Green et al., 2011; Kuebbing et al., 2016; Braga et al., 2017). Current research on the combined effect of co-invasion is mainly focused on the structure and function of ecosystems mediated by two or more invasive plants (Kuebbing et al., 2014, 2016; Lenda et al., 2019; Sheppard 2019). However, there is currently no method that quantifies the combined effect of co-invasion mediated by two or more invasive plants. More importantly, methods that quantify the relative competitive advantage of different invasive plants during co-invasion are inadequate.

The aim of this study is to quantify the relative competitive advantage and the combined effect of co-invasion for two invasive plants, *Erigeron annuus* (L.) Pers. and *Solidago canadensis* L. These two invasive plants often co-invade the same habitat (mostly wasteland) in eastern China (Wang et al., 2020, 2022; Wei et al., 2020a, 2020b) (Fig. S1). Both invasive plants have been designated the two most aggressive invasive plants in China owing to the severe risk they pose to the biological security of native habitats, particularly biodiversity (Wang et al., 2020, 2022; Wei et al., 2020b). Both invasive plants belong to Asteraceae, which contains the highest number of invasive plant species in China at the family level, i.e., the Asteraceae comprises 104 invasive plant species, approximately 25% of all invasive plant species in China (Hao and Ma, 2023).

Communities co-invaded by *Erigeron annuus* and *Solidago canadensis* were randomly selected in late June 2019 in Zhenjiang, Jiangsu Province, China (longitude and latitude: 32.117–32.120°N, 119.526–119.530°E). The communities consisted of weedy habitat without shrubs or trees, in which most of the native plant species were annual herbs (mainly *Pterocypsela laciniata* (Houtt.) Shih, *Setaria viridis* (L.) Beauv., *Arthraxon hispidus* (Trin.) Makino, and *Digitaria sanguinalis* (L.) Scop.). The only invasive plant species in the selected communities were *E. annuus* and *S. canadensis*.

A total of 36 quadrats were sampled. Specifically, we randomly surveyed twelve quadrats (size: 2 m × 2 m) invaded by *Erigeron annuus* alone, twelve quadrats (size: 2 m × 2 m) invaded by *Solidago canadensis* alone, and twelve quadrats (size: 2 m × 2 m) co-invaded by both invasive plants. Functional traits and community-weighted trait values of the two invasive plants were measured, and the number of plant species and the number of individuals per plant species were recorded. Quadrats with different invasion conditions were separated by more than 100 m.

The results of the functional traits (i.e., plant height, ground diameter, leaf length, leaf width, green leaf area, and leaf chlorophyll and leaf nitrogen concentrations) and community-weighted trait values of the two invasive plants have been described in a previous study (Wang et al., 2020).

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The relative competitive advantage of the two invasive plants under co-invasion was assessed by computing the relative competitive advantage index of invasive plants under co-invasion (*RCAI*) as $RCAI = \Sigma(P_x X_x)/(P_i X_i)$, where P_x is the relative abundance of IPS x and X_x is the average of the assayed functional traits of invasive plant x in one quadrat, respectively; P_i is the sum of the relative abundance of all invasive plants and X_i is the average of the assayed functional traits of all invasive plants in one quadrat, respectively. The *RCAI* value will range between zero and one; high *RCAI* values indicate higher relative competitive advantage of an invasive plant.

The combined effect of co-invasion of two invasive plants was evaluated by computing the co-invasion combined effect index of two invasive plants (*CCEI*) as $CCEI = CAI_{xy}/(CAI_x + CAI_y)$, where CAI_x is the competitive advantage index of invasive plant x and CAI_y is the competitive advantage index of invsiave plant y under the independent invasion, respectively; CAI_{xy} is the sum of the competitive advantage index of invasive plant x and invasive plant y under co-invasion. The index represents a synergistic effect when the value is higher than two; the index represents an additive effect when the value is equal to two; the index represents a competitive effect when the value is higher than one and less than two; the index represents a neutral effect when the value is equal to one; and the index represents an antagonistic effect when the value is higher than zero and less than one. The method for determining the competitive advantage index of an invasive plant follows a previous study (Wang et al., 2021a). The methods for determining the relative competitive advantage index of invasive plants under co-invasion and the co-invasion combined effect index of two invasive plants proposed in this study were first described by the authors of this study.

Deviations from normality and homogeneity of the variances were assessed by using Shapiro–Wilk's test and Bartlett's test, respectively. Differences in the values of the relative competitive advantage index of invasive plants under co-invasion and the competitive advantage index of the two invasive plants under different invasion conditions were evaluated using one-way analysis of variance (ANOVA) with Tukey's test. The contribution of functional traits of the two invasive plants to their relative competitive advantage under co-invasion was judged using path analysis. Statistical analyses were conducted using IBM SPSS Statistics 26.0.

The relative competitive advantage index of *Solidago canadensis* was significantly greater than that of *Erigeron annuus* under co-invasion (Fig. 1A; $P < 0.0001$). The competitive advantage index of invasive plants under different invasion conditions significantly decreased in the following order: independent invasion of *S. canadensis* > co-invasion of the two invasive plants > independent invasion of *E. annuus* (Fig. 1B; $P < 0.0001$). The co-invasion combined effect index of the two IPS was about 0.563 (Fig. 1B).

The direct path coefficient of leaf width, green leaf area, and leaf chlorophyll and leaf nitrogen concentrations of the two invasive plants on their relative competitive advantage index under co-invasion were obviously greater than those of other measured functional traits (Table 1).

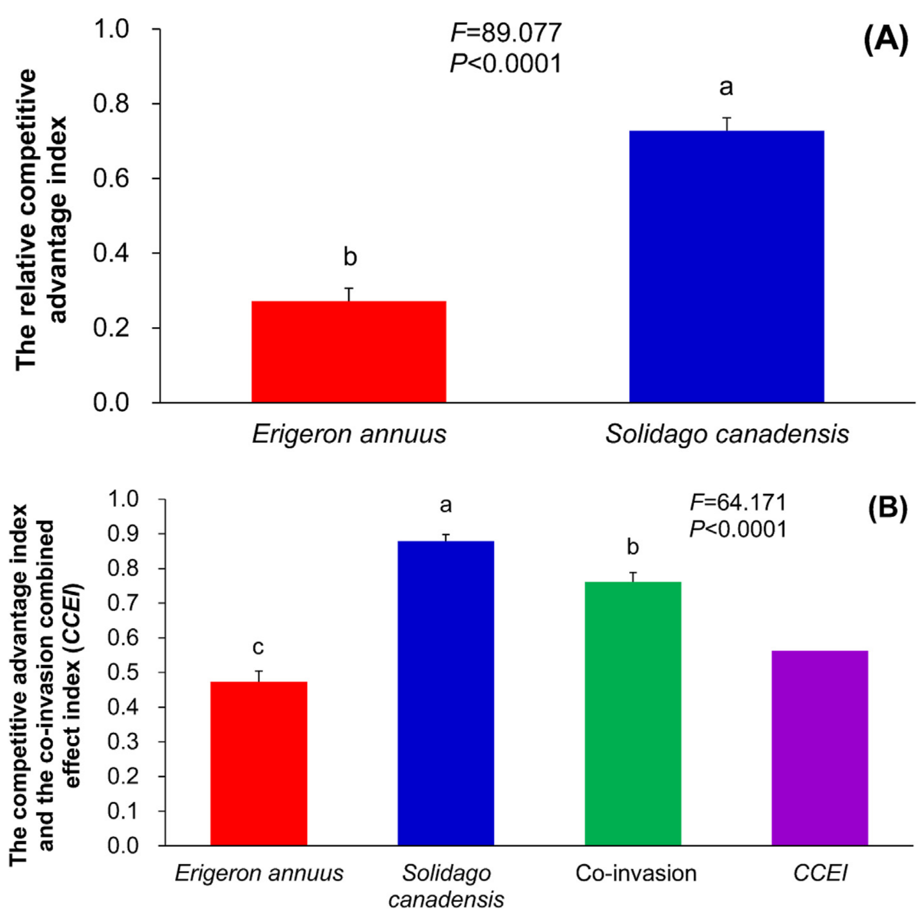

Fig. 1. Differences in the relative competitive advantage index of two invasive plants during co-invasion (A), the competitive advantage index of the two invasive plants under different invasion conditions (B), and the co-invasion combined effect index (*CCEI*) of the two invasive plants (B). Bars (mean & standard error, $n = 12$) with different lowercase letters mean statistically significant differences ($P < 0.05$).

Table 1
The contribution of functional traits of the two invasive plants to their relative competitive advantage index under co-invasion. Abbreviation: *p*, direct path coefficient (using the absolute value of the standardized regression coefficient).

	p (*Erigeron annuus*)	*p* (*Solidago canadensis*)
Plant height	0.096	0.372
Ground diameter	0.051	0.396
Leaf length	0.068	0.869
Leaf width	6.996	3.380
Green leaf area	1.246	4.591
Leaf chlorophyll concentration	7.232	6.376
Leaf nitrogen concentration	4.499	2.328
Community-weighted trait values	1.027	1.053

The relative advantage of the two invasive plants differed during co-invasion. Specifically, the relative competitive advantage of *Solidago canadensis* was significantly greater than that of *Erigeron annuus* under co-invasion (Fig. 1A). The differences in the relative competitive advantage of the two invasive plants under co-invasion may be largely attributed to the differences in the invasive plant identity, particularly their growth competitiveness. In this study, the competitive advantage index of *S. canadensis* was significantly greater than that of *E. annuus* under independent invasion (Fig. 1B). Moreover, the community-weighted trait value, the invasion intensity, and the relative invasiveness of *S. canadensis* were also significantly higher than those of *E. annuus* under independent invasion (Wang et al., 2020). Thus, the relative competitive advantage of the two invasive plant species during co-invasion was not symmetrical.

In this study, the relative competitive advantage of the two invasive plants under co-invasion was mainly attributable to their leaf width, green leaf area, and leaf chlorophyll and leaf nitrogen concentrations (Table 1). These functional traits may be crucial to the level of photosynthetic area and the degree of photosynthetic capacity. In particular, light is one of the most critical influences affecting plant growth (Sun et al., 2006; Yang et al., 2013; Meng et al., 2014; Xiao et al., 2015). More importantly, previous findings have shown that invasive plants with a higher level of photosynthetic area and a greater degree of photosynthetic capacity can often show stronger growth performance, which is beneficial to their invasion success (Feng et al., 2007; van Kleunen et al., 2010; Zunzunegui et al., 2020).

In nature, two or more invasive plants can co-invade the same habitat (Lenda et al., 2019; Sheppard, 2019; Wang et al., 2020; Wei et al., 2020a, 2020b). However, two or more invasive plants can create a range of co-invasion combined effects (including synergistic, additive, competitive, neutral, and antagonistic) possibly owing to differences in the invasion phase of invasive plant species, the invasion history of the invasive plants, the arrival order of the invasive plants into the invaded plant community, the invasive plant identity, the composition of the invaded plant community, the availability level of soil nutrients in the invaded plant community, the intensity and frequency of external interference in the invaded plant community, and/or the experimental period. In this study, the co-invasion combined effect index of the two invasive plants was greater than zero and less than one (Fig. 1B). Thus, the combined effect of co-invasion of the two invasive species was antagonistic. This phenomenon may be due to the gradually increased intraspecific competition and interspecific competition during co-invasion because of the limited living space and the available resources (Wang et al., 2020, 2022). Moreover, the community-weighted trait value and the invasion intensity of the two invasive plants under co-invasion were significantly greater than those of *Erigeron annuus* under independent invasion but significantly less than those of *Solidago canadensis* under independent invasion (Wang et al., 2020). This phenomenon may also be because the competitive advantage of the two invasive plants under co-invasion was significantly greater than that of *E. annuus* under independent invasion but significantly less than that of *S. canadensis* under independent invasion in this study (Fig. 1B). Previous studies also show that there is an antagonistic combined effect of two invasive plants during co-invasion, i.e., the overall performance of two invasive plants may be decreased during co-invasion through the invasional interference potentially mediated by resource competition (Belote and Weltzin, 2006; Lenda et al., 2019; Wang et al., 2020, 2022).

In summary, this study first describes methods for determining the relative competitive advantage index of invasive plants under co-invasion and the co-invasion combined effect index of two invasive plant species. This study has shown that the relative competitive advantage of *Solidago canadensis* was significantly greater than that of *Erigeron annuus* under co-invasion, the relative competitive advantage of the two invasive plants under co-invasion can be explained by their leaf width, green leaf area, and leaf chlorophyll and leaf nitrogen concentrations, and the combined effect of co-invasion of the two invasive plants was antagonistic.

Authors contributions

CYW and DLD conceived and designed research; YL, CL, SSZ, ZLX, and YLY collected data and performed analysis. All authors contributed critically to the drafts and gave final approval for publication.

Declaration of competing interest

All authors declare that they have no competing interests and personal relationships and agree on the contents of the paper.

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Appendix A. Supplementary data

Supplementary data to this article can be found online at https://doi.org/10.1016/j.pld.2023.01.005.

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