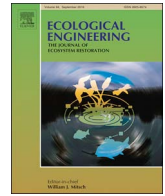




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Moderate and heavy *Solidago canadensis* L. invasion are associated with decreased taxonomic diversity but increased functional diversity of plant communities in East China



Congyan Wang^{a,b,*}, Kun Jiang^a, Jun Liu^a, Jiawei Zhou^a, Bingde Wu^a

^a Institute of Environment and Ecology, Academy of Environmental Health and Ecological Security & School of the Environment and Safety Engineering, Jiangsu University, Zhenjiang 212013, PR China

^b Ministry of Education Key Laboratory for Biodiversity Science and Ecological Engineering, Institute of Biodiversity Science, Fudan University, Shanghai, 200433, PR China

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ABSTRACT

Clarifying the effects of invasive plant species (IPS) on the taxonomic and functional diversity of native communities provides insight into the mechanisms underlying successful plant invasion. This study aims to determine the effects of an IPS (*Solidago canadensis* L.) at different invasion degree on the taxonomic and functional diversity of plant communities by using a comparative analysis. The degree of *S. canadensis* invasion was divided into several categories—uninvaded (0%), low (< 35%), moderate (35%–75%), and heavy (> 75%)—on the basis of the relative abundance of the species in the invaded ecosystems. Forty quadrats (2 m × 2 m) were surveyed per invasion to assess the degree of *S. canadensis* invasion. The taxonomic diversity of plant communities was calculated using the Shannon–Wiener diversity and Margalef's richness indices. The functional diversity of plant communities was estimated using community-weighted mean trait values, Mason's α and β functional diversity, and Rao's quadratic entropy. The taxonomic diversity indices of plant communities significantly decreased under moderate and heavy degree of *S. canadensis* invasion conditions. Most of the functional diversity indices of plant communities significantly increased under all degree of *S. canadensis* invasion conditions (especially under moderate and heavy degree of invasion conditions). The increased functional diversity of plant communities under *S. canadensis* invasion conditions (especially under moderate and heavy degree of invasion conditions) may lead to a more efficient use of resources at the interspecific level via niche complementarity.

1. Introduction

Invasive plant species (IPS) have had apparent impacts on the structure and function of native ecosystems (Powell et al., 2013; Wang et al., 2016a, 2017a, 2017b; Martín-Forés et al., 2017). Because coexisting IPS and native plant species (NPS) suffer similar or even identical environmental selective pressures, the differences in the functional traits between IPS and NPS are considered to be one of the main drivers of successful plant invasion (van Kleunen et al., 2010; Gross et al., 2013; Wang et al., 2016b, 2017c). IPS can colonize ecosystems after their propagules are transported far from their original ranges (Wilson and Pinno, 2013). Accordingly, IPS can demonstrate different invasion degree in colonized habitats (Wang et al., 2017a, 2017b, 2018). Thus, understanding the differences in functional traits between IPS and coexisting NPS across different invasion degree is important for

understanding the mechanisms underlying successful plant invasion.

Recent research has revealed a scale-dependent relationship between NPS and IPS (Lilley and Vellend, 2009; Powell et al., 2013). Generally, IPS invasion can reduce plant diversity at fine spatial scales, i.e., native–invasive richness relationships may be negative, as higher native richness confers resistance to IPS invasion (Vilà et al., 2011; Byun et al., 2013; Gornish and dos Santos 2015). However, IPS invasion can enhance plant diversity at broad spatial scales, i.e., native–invasive richness relationships may be positive if IPS and NPS respond similarly to extrinsic factors (Ellis et al., 2012; Driscoll 2017; Martín-Forés et al., 2017). Nevertheless, no relationship may also be observed for native–invasive richness (Higgins and Richardson, 1998; Bart et al., 2015). Thus, the signification of threats posed by IPS invasion is still hotly debated owing to conflicting findings (Dong et al., 2015).

Numerous studies have shown IPS impacts plant diversity. In

* Corresponding author at: Institute of Environment and Ecology, Academy of Environmental Health and Ecological Security & School of the Environment and Safety Engineering, Jiangsu University, No. 301, Xuefu Road, Zhenjiang, 212013, PR China.

E-mail address: liuyexue623@163.com (C. Wang).

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contrast, very few studies have investigated the response of functional diversity of plant communities to IPS invasion. However, ecosystem functions may mainly be driven by functional diversity of plant communities, including functional trait values weighted by abundance (i.e., community-weighted mean, *CWM*) and variation in functional trait values (Butterfield and Suding, 2013; Zuo et al., 2016; Zhang et al., 2017). The *CWM* effects may primarily be attributed to the abundance of plant species, i.e., the most abundant species have the strongest effects on ecosystem processes and properties (Conti and Díaz, 2013; Lavorel 2013; Butterfield and Suding, 2013). In contrast, functional trait effects may support the niche complementarity hypothesis (Gross et al., 2007; Gamfeldt et al., 2008; Zhang et al., 2017), i.e., higher functional diversity may reflect the coexistence of different functional strategies and an increase in niche-complementarity among plant species (Gross et al., 2007; Schleicher et al., 2011; Spasojevic et al., 2014; Zhang et al., 2017). More importantly, recent studies have shown that ecosystem processes are more closely associated with plant functional diversity than plant taxonomic diversity (Zhang et al., 2015, 2017; Tobner et al., 2016). Moreover, functional diversity of plant communities is more closely related to the invasibility of plant communities (Symstad 2000; Schamp and Aarssen, 2010). In particular, assemblages with lower levels of species and functional diversity are more heavily invaded than assemblages with greater species and functional diversity (Maron and Marler, 2007). Thus, understanding the effects of IPS invasion on the taxonomic and functional diversity of plant communities is also important for understanding the mechanisms underlying successful plant invasion.

The present study aims to determine the differences in the functional traits between the East China IPS (*Solidago canadensis* L.) and coexisting NPS as well as the effects of *S. canadensis* invasion on taxonomic and functional diversity of plant communities across different degree of *S. canadensis* invasion. The degree of *S. canadensis* invasion is divided into uninvaded (0%, CK), low (< 35%, L), moderate (35%–75%, M), and heavy (> 75%, H) on the basis of its relative abundance in the invaded ecosystems. *S. canadensis* is an herbaceous perennial plant that is native to North America. *S. canadensis* was introduced to Shanghai, China as a horticultural plant in the early 1930s. Currently, the species has become invasive across a great part of China and it is listed as one of the most destructive and widespread IPS in China (Abhilasha et al., 2008; Yang et al., 2008; Zhao et al., 2015).

This study tests the following hypotheses: (1) *S. canadensis* may be more likely to display a higher value of functional traits than coexisting NPS; and (2) taxonomic and functional diversity of plant communities decrease as the degree of *S. canadensis* invasion increases.

2. Materials and methods

2.1. Study design

S. canadensis was chosen as the target IPS. From early August to early September 2016, samples of *S. canadensis* and coexisting NPS were surveyed across two adjacent sampling sites (32.117–32.120°N, 119.526–119.530°E, a total size of approximately twelve hectares; 32.159–32.162°N, 119.528–119.533°E, a total size of approximately fifteen hectares) in Zhenjiang, characterized by a subtropical and humid climate. The annual mean temperature is approximately 15.9 °C, with the monthly mean temperatures reaching a maximum of 28 °C in July and a minimum of 2.9 °C in January. The annual precipitation of the study area is approximately 1101.4 mm with the monthly mean precipitation accumulation reaching a maximum of 205.6 mm in July and a minimum of 33.4 mm in January. The annual sunshine time is approximately 1996.8 h, and the monthly mean sunshine time reaches a maximum of approximately 201.1 h in August and decreases to a minimum of approximately 137.0 h in December. The site climate summaries were determined from local records (Hang and Wu 2016). The two adjacent sample sites have identical climatic conditions, soil

types, and plant community types. Thus, this study does not consider the effects of the spatial distribution of the sample sites on the results.

The plant communities in the sampling site were herbaceous weed communities lacking invasive species (i.e., there are no other IPS except for *S. canadensis*). The degree of *S. canadensis* invasion was evaluated according to its relative abundance in the invaded sites and was divided into one of four levels for each quadrat: uninvaded (0%, CK), low (< 35%, L), moderate (35%–75%, M), and high (> 75%, H). The relative abundance of *S. canadensis* was calculated as the ratio of the number of *S. canadensis* individuals to the number of individuals of all plant species in the surveyed area. Forty quadrats (2 m × 2 m) were surveyed per degree of *S. canadensis* invasion estimate. Three plant sample replicates of the same plant species (including *S. canadensis* and all coexisting NPS) from the same quadrat were selected randomly to determine plant functional traits. All quadrats were checked to determine the number of individuals of all plant species, the number of individuals per plant species, and the number of plant species. In particular, the number of individuals among clonal plant species was determined mainly by assessing the number of ramets.

2.2. Determination of plant functional traits

Ten functional traits related to plant performance and fitness were surveyed. In particular, the value of one functional trait of *S. canadensis* in one quadrat was determined by using the mean of the values of the same functional trait of three *S. canadensis* individuals in the same quadrat. The value of one functional trait of NPS that coexisted with *S. canadensis* in one quadrat was determined by using the mean of the values of the same functional trait of all native species in the same quadrat.

Plant height was determined by measuring the distance between the base of the stem and the apical shoot with a ruler to an accuracy of 0.1 cm (Wang et al., 2017a, 2017b, 2017c). Ground diameter and petiole diameter were determined using a Vernier caliper to an accuracy of 0.01 mm (Xiao et al., 2015; Wang et al., 2016c). Petiole length was determined using a ruler to an accuracy of 0.1 cm (Xiao et al., 2015; Wang et al., 2016c). Leaf shape index was calculated as the ratio of the leaf length to the corresponding leaf width (Jeong et al., 2011; Wang and Zhang, 2012). Leaf length was defined as the maximum value along the midrib, and leaf width was the maximum value perpendicular to the midrib (Wang and Zhang, 2012). Leaf length and leaf width were measured using a ruler to an accuracy of 0.1 cm (Wang et al., 2016a, 2016b, 2016c, 2017b, 2017c, 2017d). Relative chlorophyll and nitrogen (N) concentrations in the leaves were estimated with a hand-held plant nutrient meter (TYS-3N; TOP Instrument Co., Ltd., Hangzhou, China) and chlorophyll concentrations were calculated in SPAD units based on absorbance at 650 nm and 940 nm (Wang et al., 2016a, 2016b, 2017c, 2017d). Leaf thickness was determined from the combined thickness of five leaves using a Vernier caliper to an accuracy of 0.01 mm (Wang et al., 2016a, 2016b, 2016c, 2017c, 2017d).

The functional differences index (FD_j) of functional traits between *S. canadensis* and coexisting NPS in the same quadrat was assessed. Specifically, it was calculated as the ratio of the absolute difference between the community-weighted trait values of *S. canadensis* and those of coexisting NPS within the same quadrat relative to the mean difference across all quadrats (Gross et al., 2013). The community-weighted trait values estimate the mean trait value of the community, weighted by the relative abundance of each plant species (Violle et al., 2007; Gross et al., 2013).

2.3. Determination of taxonomic and functional diversity of plant communities

The taxonomic diversity of plant communities was calculated using the basis of Shannon–Wiener diversity index (H') and Margalef's richness index (F). H' was calculated as $H' = -\sum p_i \ln p_i$ (Shannon and

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