

Research Article

The relative importance of multiple invasion mechanisms

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Received: 24 July, 2019

Accepted: 01 December, 2020

Published: 02 December, 2020

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Keywords: Biological invasions; Invasion mechanism; Multimodel inference; Nature-sieve hypothesis; Relative importance

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Abstract

Aim: Plant invasions are driven by suites of factors in nature. To better understand the success of invasive plants, it is crucial to quantify the relative importance of multiple invasion mechanisms during plant invasions.

Location: Eastern China.

Methods: We surveyed 300 pairs of uninvaded and invaded quadrats by *Solidago canadensis* across its entire invaded range, quantified its invasion intensities, and identified the relative importance of 19 causal factors and 11 invasion hypotheses using the multimodel inference approach.

Results: The relative contributions of all the 19 factors to *S. canadensis* invasion varied depending on different invasion intensities, so did the relative importance of 11 different hypotheses vary with invasion intensities. At the low invasion intensity, abiotic factors dominated over biotic factors; in contrast, biotic factors dominated over abiotic factors at the high invasion intensity. The role of *S. canadensis*-recipient community interactions was highly important.

Main conclusions: These findings suggest that the relative importance of multiple invasion mechanisms may be staged in a real invasion. Based on our results, we propose a novel nature-sieve hypothesis, which provides a universal framework for an understanding of successful invasion.

Introduction

The publication of the book *The ecology of invasions by animals and plants* by Charles Elton [1] is commonly viewed as the beginning of modern invasion ecology [2]. Ever since, the studies on biological invasions have grown exponentially [3], and, in particular, what determines invasion success has fascinated ecologists so that dozens of influential hypotheses have been proposed [4]. Numerous studies have advanced our understanding of successful invasion, but we yet fail to get a complete picture because researchers usually study different pieces of the same invasion puzzle [5]. According to the traditional paradigm, plant invasions are influenced by three aspects: propagule pressure, invader traits, and ecosystem characteristics ([3,6–8]. As such, it is valuable to holistically understand the mechanisms underlying invasion success under different circumstances [3,9].

Plant invasion is conceptualized as a staged process [7,10–12]. This process is controlled by a series of causal factors that

can be different depending on invasion stages [7,12,13]. These factors constitute a basis for different invasion hypotheses. Thus, we can explain invasion success using suites of factors or hypotheses, both of which shape invasion mechanisms; [2,4,9,14]. Although some ecologists have recognized that the processes driving plant invasions are likely to change over time (Dietz & Edwards, 2006), no studies have explicitly addressed how invasion mechanisms are staged, thereby raising several important questions in a real invasion.

First, what is the relative importance of a suite of factors influencing plant invasions? It is clear that propagule pressure, invader traits, and ecosystem characteristics determine plant invasions [3,6–8]. However, little is known about the role of these three sets of factors and about the role of interactions between invaders and ecosystems in invasion success. For a given invader, its success strongly depends on its traits, ecosystem properties, and their interactions, because propagule pressure can be seen as constant [15]. Studies with



the same species across a larger range of sites would help to reveal the full suite of factors that affect invasion [9], and their relative contributions under different circumstances should be quantified to predict or manage plant invasions [3,16].

Second, what is the relative importance of multiple invasion hypotheses? It has become increasingly clear that no one individual hypothesis is sufficient to explain the invasion success of exotic plants [3,4,17,18]. Individual hypotheses partially overlap in mechanism and may contribute synergistically or interactively to invasions; different hypotheses are non-mutually exclusive and may also act simultaneously [3,14,18]. Different hypotheses usually encompass different determinants so that the importance of hypotheses should be strongly linked with the net effect of the corresponding determinants.

Finally, how might the factors driving plant invasions and the associated hypotheses vary with invasion stages? Plant invasion is a staged process, in which drivers can be different depending on the stage of invasion ([7,10-12,20]. For a successful invader, it must experience different stages due to the spatiotemporal dynamics of determining factors. Accordingly, different invasion stages might be closely linked with different sets of filtering sieves, which shape invasion mechanisms.

To answer these questions, we quantified the extent of *Solidago canadensis* invasion and determined 19 causal factors across its entire range. The purpose of the current study was to quantify the relative importance of multiple mechanisms at different invasion intensities and to propose an invasion hypothesis. Specifically, we could determine what explanatory variables dominate over others in driving invasion, identify whether different hypotheses explain the success of *S. canadensis* invasions equally or differentially, and assess how the relative importance of causal factors and invasion hypotheses varies with invasion stages.

Methods

Study species and region

Solidago canadensis L. is among the most serious invasive plants in China, which was introduced from North America as an ornamental plant in 1935 [21]. This invader has now invaded large areas of southern China, such as Jiangsu, Shanghai, Zhejiang, Jiangxi, and Anhui; it occurs along roadsides or in abandoned agricultural fields and other disturbed habitats [22]. The entire invaded range belongs to a subtropical climate. Our study region roughly covered an area of 800 × 800 km, and the elevation ranged from 3 m to 79 m.

Field survey and soil analyses

To quantify the extent of successful invasion and the relative importance of multiple invasion mechanisms, we surveyed 300 pairs of uninvaded and invaded quadrats by *S. canadensis* across its entire invaded range from July to September 2014 [22]. *Solidago canadensis* was the only one invader in the sampling sites. During the investigation, species cover, population density, and plant height in a quadrat were recorded; specific

fine root area (SRA) and leaf traits (leaf area, Specific Leaf Area [SLA], Leaf Dry Matter Content [LDMC], chlorophyll, leaf C, leaf N, and leaf C:N) of *S. canadensis* in 300 invaded quadrats were determined. To measure these traits, we sampled five roots and 30 leaves per quadrat. See Cornelissen, et al. [23] for the details about determining these traits. We sampled soils from each quadrat for measurements of their biotic and biotic properties.

For soil microbes, we employed the Phospholipid Fatty Acid (PLFA) analysis [22]. Previous studies have suggested that the fatty acid 18:2 ω 6,9c can indicate soil saprotrophic pathogens and that 16:1 ω 5, cy17:0, and cy19:0 can indicate soil beneficial microbes [24-27]. Accordingly, we chose 18:2 ω 6,9c as pathogens, and 16:1 ω 5, cy17:0, and cy19:0 as beneficial microbes. Additionally, the fatty acid 18:2 ω 6,9c is dominant in fungi [28]. We calculated the fungi:bacteria ratio using the ratio of 18:2 ω 6,9c to bacterial PLFAs [22].

For soil abiotic properties, we measured pH in a soil solution rate of 1:2.5 (soil:distilled water) using a pH meter (Sartorius PB-10 meter), soil texture using a laser particle size analyzer (Mastersizer 2000), Available Phosphorus (AP) using a UV-2550 ultraviolet spectrophotometer, and ammonia (NH₄-N) and nitrate (NO₃-N) using a continuous flow analyzer.

Data analyses

To quantify the success of *S. canadensis* invasion, we coined a relative invasion index (RII) as follows:

$$RII = \left\{ \frac{Ci}{\text{Max}(Ci)} + \frac{Di}{\text{Max}(Di)} + \frac{Hi}{\text{Max}(Hi)} \right\} / 3 \quad (1)$$

where C_i , D_i , and H_i represent cover, density, and height of *S. canadensis* in invaded quadrats, respectively. We ranked RII values in the ascending order, and then categorized 300 invaded quadrats into three groups, representing three invasion intensities/stages. The quadrats from 1 to 100 were treated as intensity I, quadrats from 101 to 200 as intensity II, and quadrats from 201 to 300 as intensity III. We calculated the mean and standard error of RII values for each invasion intensity, and tested whether there were differences in RII among three intensities using a one-way analysis of variance. RII values were treated as a response variable in the following data analyses.

To quantify the relative contribution of determinants to invasion success (i.e. RII), we categorized these determinants into five different sets: invader traits, climate, native plant communities, soil abiotic and biotic properties, and invader-community interactions. We calculated a phenotypic variation index (PVI) and leaf tradeoff index (LTI) as follows:

$$PVI = \sum_{j=1}^8 \frac{\text{Max}(T_i) - T_i}{\text{Max}(T_i) - \text{Min}(T_i)} / 8 \quad (2)$$

$$LTI = \text{LDMC} / \text{SLA} \quad (3)$$



where T_i represents a given trait of the i^{th} quadrat ($i = 1, 2, \dots, 300$), and $Max(T_i)$ and $Min(T_i)$ represent the maximum and minimum values of a specific trait among 300 quadrats. j represents SRA, leaf area, SLA, LDMC, chlorophyll, leaf C, leaf N, and leaf C:N, respectively. We used the average PVI of eight traits to indicate the phenotypic variation of *S. canadensis*. In general, SLA is related to the growth potential of a leaf and LDMC is related to its stress potential [23]. Thus, we used the ratio of LDMC to SLA to indicate a leaf tradeoff. Climatic data (*i.e.* mean annual temperature [MAT] and mean annual precipitation [MAP]) were collected from the nearest sampling sites. Native plant diversity (*i.e.* native species richness, Pielou evenness index, and dominance index) was calculated as described by Dong, et al. [22]. Soil microbes included beneficial microbes, pathogens, and fungi/bacteria ratio. Soil abiotic properties included soil pH, soil texture (*i.e.* clay%:silt%:sand%), and soil nutrients (*i.e.* the sum of AP, $\text{NH}_4\text{-N}$, and $\text{NO}_3\text{-N}$). To quantify *S. canadensis*-recipient community interactions, we calculated the relative changes in native plant diversity (*i.e.* Δ richness), soil abiotic properties (*i.e.* Δ pH and Δ nutrients), and soil microbes (*i.e.* Δ beneficial microbes, Δ pathogens, and Δ fungi/bacteria ratio). All the relative changes were calculated as follows:

$$\Delta = \frac{V_i - V_u}{V_i + V_u} \quad (4)$$

where V_i and V_u represent a given trait in the pairwise invaded and uninvaded quadrats, respectively.

To evaluate the relative contributions of different determinants to the invasion success of *S. canadensis*, we selected the Multimodel Inference (MMI) approach, which is based on all the models in *a priori* set, not just the one estimated to be best, and therefore can provide more stable and reliable inference results than traditional statistical inference [29]. Additionally, this approach does not explicitly determine whether individual variables are statistically significant but ranks parameters based on their ability to explain variation [30].

We used separate models for intensities I, II, III, and across all three intensities to quantify the relative contribution of 19 determinants to *S. canadensis* invasion along the invasion intensity. Specifically, the global models included one dependent variable (*i.e.* RII) and 19 explanatory variables (*i.e.* PVI, LTI, MAT, MAP, richness, evenness, dominance, pH, texture, nutrients, beneficial microbes, pathogens, F/B ratio, Δ richness, Δ pH, Δ nutrients, Δ beneficial microbes, Δ pathogens, and Δ F/B ratio). We used the model selection method to generate all possible candidate models from the global models. All the candidate models were then ranked according to the second-order Akaike's information criterion. The effect size of each determinant was expressed by the averaged model parameters deriving from accumulated model probability exceeded 95%. The importance of each determinant was estimated by summing the Akaike's weights of each model. The relative contribution of a given factor was estimated through dividing its importance by the total importance of 19

factors.

To contrast the relative importance of different invasion hypotheses, we standardized the contribution of factors that are involved in each invasion hypothesis. Specifically, we quantified the per capita contribution of a set of factors, thereby allowing us to compare the relative importance of different invasion hypotheses. See the figure legends of Figure 3 for more details.

All statistical analyses were performed using R version 3.3.1 [31]. The MMI approach was performed using *dredge* function in the package MuMIn [32].

Results

The RII values ranged from 29.8% to 57.3% at the invasion intensity I, ranged from 57.4% to 65.7% at the intensity II, and ranged from 65.8% to 86.3% at the intensity III; the grand mean of RII was $61.9 \pm 0.7\%$ [1 SE] (Figure 1a). There were significant differences in RII among three intensities (Figure 1b: $46.5 \pm 0.8\%$ at intensity I; $61.8 \pm 0.4\%$ at intensity II; $77.2 \pm 0.7\%$ at intensity III).

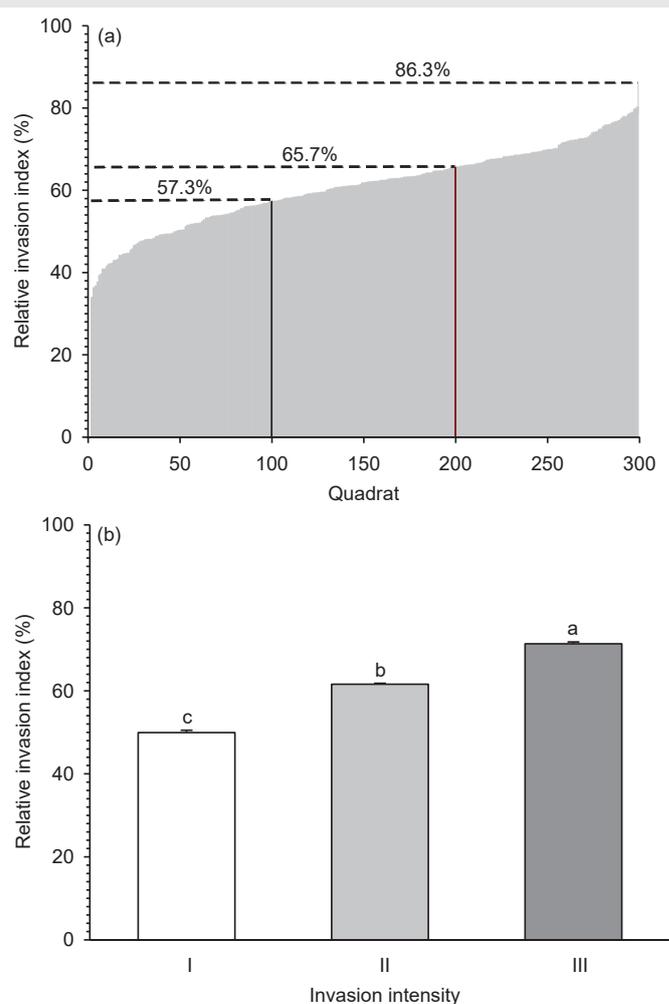


Figure 1: Relative invasion index (RII) of *Solidago canadensis* from 300 quadrats (a), and comparisons of RII among three invasion intensities (b). All the quadrats were ranked in the ascending RII order in the upper panel. Data are means + 1 SE ($n = 100$) and different letters indicate significant differences at $P = 0.05$ in the lower panel.

There were three patterns for the relative contributions of 19 factors to RII along the invasion intensity. First, the relative contributions fluctuated slightly; four factors followed this pattern, that is, phenotypic variation (Figure 2a), soil texture (Figure 2i), and the changes in soil pathogens (Figure 2r) and fungi/bacteria (Figure 2s). Second, the relative contributions fluctuated modestly; five factors followed this pattern, that is, leaf tradeoff (Figure 2b), soil pH (Figure 2h), soil-borne pathogens (Figure 2l), fungi/bacteria (Figure 2m), and the change in soil nutrients (Figure 2p). Third, the relative contributions of the remaining ten factors increased or decreased with invasion intensity dramatically.

At the intensity I, the predominant factors contributing to RII were MAT (Figure 2c), MAP (Figure 2d), and the change in soil pH (Figure 2h); they accounted for 35.3% of the total contribution. At the intensity II, the predominant drivers included native species richness (Figure 2e), species evenness (Figure 2f), and species dominance (Figure 2g); they accounted for 29.7% of the total contribution. At the intensity III, the predominant factors covered native species evenness (Figure 2f), species dominance (Figure 2g), and the change in native species richness (Figure 2n); they accounted for 36.7% of the total contribution. Across all three intensities, the dominant factors were leaf tradeoff (Figure 2b), MAT (Figure 2c), soil nutrients (Figure 2j), and the change in species richness (Figure 2n); their contributions were extremely similar (ca. 8.7%). The overall contribution of *S. canadensis* traits, climate, native plant communities, soils, and *S. canadensis*-recipient community interactions to RII was 15.4%, 15.9%, 16.3%, 27.0%, and 25.4%, respectively.

The relative importance of different invasion hypotheses was assessed on a per capita contribution basis. Overall, no hypothesis maintained the same ranking among three invasion intensities, and the relative importance of each hypothesis always differed depending on invasion intensities (Figure 3). At the intensity I, the temperature constraint hypothesis (14.9%) was overwhelming, and the importance of other hypotheses ranged from 6.0% for invader–community interactions to 3.0% for soil pH (Figure 3a). At the intensity II, the biotic resistance hypothesis (9.9%) was predominant, and the importance of other hypotheses ranged from 5.4% for temperature to 3.3% for soil texture (Figure 3b). At the intensity III, the biotic resistance hypothesis (9.5%) was also predominant, and the importance of other hypotheses ranged from 6.8% for temperature to 2.7% for belowground mutualism (Figure 3c). Across all three intensities, the predominant hypotheses were: temperature constraint (8.8%) and reckless invader (8.8%), and the importance of other hypotheses ranged from 7.9% for increased resource availability to 3.0% for soil texture (Figure 3d).

Discussion

The most novel contribution of our results is that 19 determining factors contributed differentially to the invasion success of *S. canadensis* and their contributions varied with invasion intensities. These findings suggest that all the driving forces, particularly dominants, vary with invasion stages, because invasion intensities and invasion stages are strongly

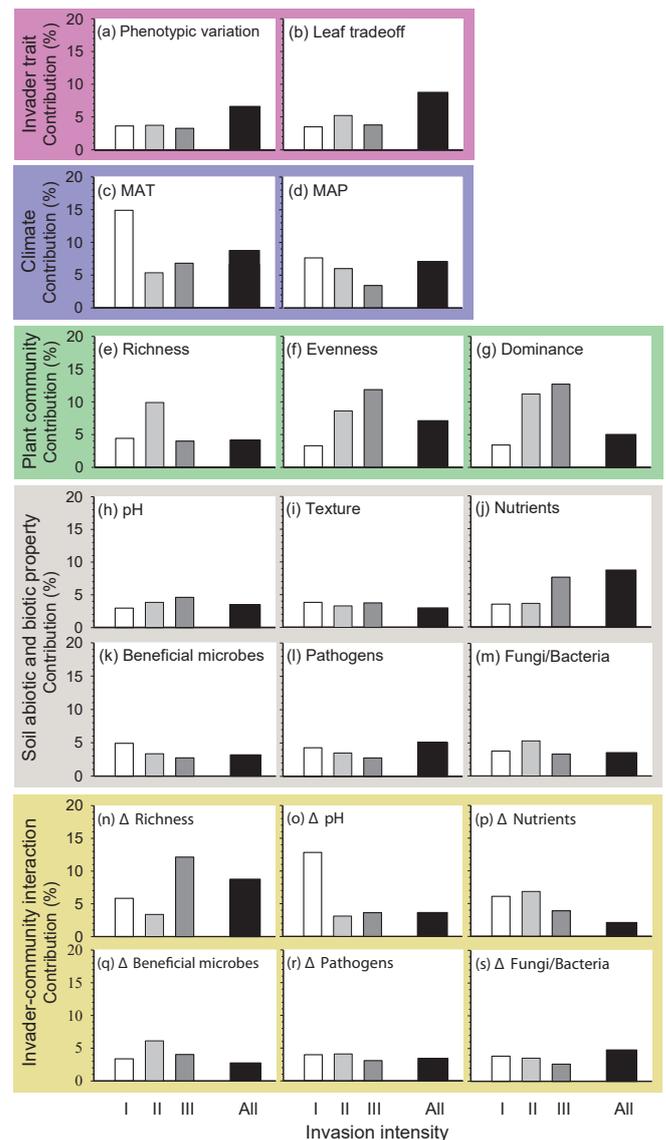


Figure 2: The relative contributions of 19 factors to the success of *Solidago canadensis* invasion. MAT: mean annual temperature; MAP: mean annual precipitation.

correlated [3,7]. For example, at the earlier invasion stage, abiotic factors (e.g. climate) dominated over other factors; at the later stage, biotic factors (e.g. plant diversity) dominated over other factors. We also observed that many non-dominant factors exhibited modest contributions to *S. canadensis* invasion. This finding is in agreement with a previous meta-analysis that multiple factors lead to the success of invasive trees [9]. Additionally, the relative contribution of causal factors may depend on the scale of the investigation [5].

A second key result of our study was that the relative importance of multiple hypotheses varied with invasion stages and multiple hypotheses explained invasion success. We quantified the relative importance of 11 hypotheses based on the per capita contribution of the factors reflecting a given invasion hypothesis. The temperature constraint hypothesis was overwhelming at the first stage, and biotic resistance was predominant at the second and third stages. These results support the viewpoints that the relative importance of various

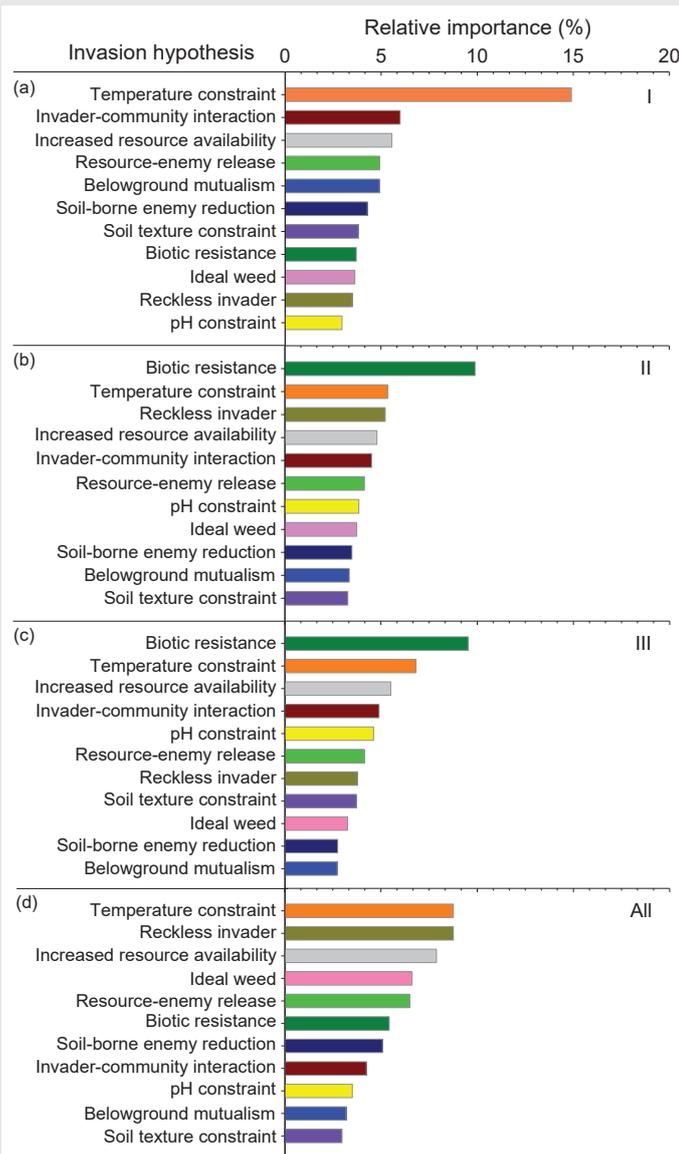


Figure 3: The relative importance of 11 invasion hypotheses during *Solidago canadensis* invasion. The ideal weed hypothesis is based on the contribution of phenotypic variation; reckless invader hypothesis based on the contribution of leaf tradeoff; temperature constraint hypothesis based on the contribution of MAT; biotic resistance hypothesis based on the mean contribution of native plant diversity; pH constraint hypothesis based on the contribution of soil pH; soil texture constraint hypothesis based on the contribution of soil texture; increased resource availability hypothesis based on the mean contribution of MAP and soil nutrients; belowground mutualism hypothesis based on the contribution of beneficial microbes; soil-borne enemy reduction based on the contribution of soil pathogens; resource-enemy release hypothesis based on the mean contribution of MAP, nutrients, and pathogens; invader-community interaction hypothesis based on the mean contribution of the relative changes in native plant richness and soil properties.

We observed that the *S. canadensis*-recipient community interactions played a key role in driving its invasion. Specifically, the contribution of this interaction accounted for about 25% of the total contribution of all factors, regardless of at intensities I, II, and III or across three intensities. This role was tightly correlated with the changes in native species and soil abiotic properties. Although soil microbes commonly play an important role in plant invasions [33-35], we found that the contribution of changing soil microbes was relatively low. Our results are exceptionally valuable because previous studies have overlooked the key role of this interaction.

We propose several possibilities that might explain our results. First, environmental factors constitute suites of filtering sieves; at a given phase, there are a set of factors that dominate over others and are most influential [36]. For example, at the earlier invasion stage, suitable climate is predominant; suitable biological environments are predominant at the later stage. Thus, there exist a series of filtering sieves, which vary with invasion stages. Second, multiple factors/processes contribute to invasion success. This is beneficial to decrease the dependence of invasion success on the predominant determinants and to spread the potential risks of failure. In other words, multiple mechanisms facilitate successful invasion jointly. Lastly, if the invasion is processing into more closed communities, environmental pressures may favor invasive species [7].

Our findings have three implications. One important corollary of our results is that plant invasion may be a stochastic but not deterministic process and invasion trajectories may be unpredictable. As some ecologists point out: invasions are intrinsically unpredictable because every case is unique [7]. The processes driving plant invasion are variable so that the knowledge of the mechanisms operating at the primary phase may be little use in predicting what happens later [7]. Thus, predicting invasion remains a challenge, and invasion history matters [37]. The second implication is that our findings provide evidence for those apparent conflicting results. For example, in some cases abiotic constraints overwhelmingly determine invasion success [38], and biotic factors predominate in other cases [39]; inconsistent results may come from different invasion stages, although the same factors/hypotheses are addressed. Finally, one promising way of investigating how species' responses change from one stage to another is to study the ecology of invasive species along strong environmental gradients, particularly at a regional scale [7].

It is obvious that 19 factors are just a small proportion of determinants shaping invasion success. These factors can indicate multiple hypotheses that represent part of existing hypotheses [4]. Our findings cannot exclude other invasion mechanisms because invasion processes are extremely complicated and dynamic. For example, herbivores play a key role in controlling plant invasions [40], allelochemicals from roots can facilitate plant invasions [14,19], disturbance is a key driver for invasion success [41], and clonal growth and propagation may be an advantage for clonal invaders. However, these mechanisms were not considered in our study due to the lack of data.

mechanisms varies depending on invasion stages and the inconsistencies in the results from testing plant invasion hypotheses can potentially be resolved by partitioning of the invasion stages [7]. We found that many hypotheses explained invasion success similarly, suggesting that the success of a given invader can be explained with multiple hypotheses but not one only [13,14,17,19]. Additionally, leading hypotheses did not equally explain plant invasions. This phenomenon has been reported by Lamarque, et al. [9].



Conclusion

Our study provides a first basis for understanding how invader traits, climate, native plant diversity, soil abiotic and biotic properties, and interactions between invasive plants and recipient communities contribute to invasion success at different invasion intensities. Our findings suggest that the relative importance of multiple invasion mechanisms may be staged. Based on our results, we put forward a novel nature-sieve hypothesis. This hypothesis can link the internal attributes of invaders and external environmental sieves together. Invader attributes include suites of intrinsic traits like growth potential, competitive ability, and releasing allelochemicals. Environmental sieves are basically characterized by hierarchy. For example, environmental sieves encompass biotic and abiotic ones, which contain multiple components/subcomponents. The nature-sieve hypothesis is likely to provide a universal framework for complete understanding of invasion success in a real invasion.

Acknowledgements

This study was financially supported by grants from National Natural Science Foundation of China (31700476).

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Citation: Zhao YF, Zhou SQ, Wei ZF, Zhao BS, Dong LJ (2020) The relative importance of multiple invasion mechanisms. *Glob J Ecol* 5(1): 139-145. DOI: <https://dx.doi.org/10.17352/gje.000033>