Ecological application of biotic resistance to control the invasion of an invasive plant, *Ageratina altissima*

Chaeho Byun\(^1\) | Eun Ju Lee\(^2\)

\(^{1}\)School of Civil and Environmental Engineering, Yonsei University, Seoul, Korea
\(^{2}\)School of Biological Sciences, Seoul National University, Seoul, Korea

**Correspondence**
Eun Ju Lee, School of Biological Sciences, Seoul National University, Seoul, Korea. Email: ejlee@snu.ac.kr

**Funding information**
National Research Foundation of Korea; Ministry of Education, Grant/Award Number: NRF-2015R1A6A3A01058185; DIVERSITAS/Future Earth and the German Centre for Integrative Biodiversity Research (iDiv) Halle-Jena-Leipzig.

**Abstract**

Biotic resistance is the ability of species in a community to limit the invasion of other species. However, biotic resistance is not widely used to control invasive plants. Experimental, functional, and modeling approaches were combined to investigate the processes of invasion by *Ageratina altissima* (white snakeroot), a model invasive species in South Korea. We hypothesized that (1) functional group identity would be a good predictor of biotic resistance to *A. altissima*, whereas a species identity effect would be redundant within a functional group, and (2) mixtures of species would be more resistant to invasion than monocultures. We classified 37 species of native plants into three functional groups based on seven functional traits. The classification of functional groups was based primarily on differences in life longevity and woodiness. A competition experiment was conducted based on an additive competition design with *A. altissima* and monocultures or mixtures of resident plants. As an indicator of biotic resistance, we calculated a relative competition index (RCI\(_{\text{avg}}\)) based on the average performance of *A. altissima* in a competition treatment compared with that of the control where only seeds of *A. altissima* were sown. To further explain the effect of diversity, we tested several diversity–interaction models. In monoculture treatments, RCI\(_{\text{avg}}\) of resident plants was significantly different among functional groups but not within each functional group. Fast-growing annuals (FG1) had the highest RCI\(_{\text{avg}}\), suggesting priority effects (niche pre-emption). RCI\(_{\text{avg}}\) of resident plants was significantly greater in a mixture than in a monoculture. According to the diversity–interaction models, species interaction patterns in mixtures were best described by interactions between functional groups, which implied niche partitioning. Functional group identity and diversity of resident plant communities were good indicators of biotic resistance to invasion by introduced *A. altissima*, with the underlying mechanisms likely niche pre-emption and niche partitioning. This method has the most potential in assisted restoration contexts, where there is a desire to reintroduce natives or boost their population size due to some previous level of degradation.

**KEYWORDS**

*Ageratina altissima*, diversity–interaction model, *Eupatorium rugosum*, functional group, invasive plant management, priority effect
INTRODUCTION

Plant species are often transported outside of their native range, and some of these plants will naturalize without creating major problems (Laviole, Saint-Louis, Guay, Groeneveld, & Villeneuve, 2012; Thomas & Palmer, 2015). However, others are invasive species that can replace natives, alter habitat structure, and interfere with biogeochemical processes (Blossey, 1999; Mack et al., 2000). We often attempt to manage these species to minimize consequences to native species and ecosystems because invasive plants damage ecosystem functions and services (Castro-Diez, Pauchard, Traveset, & Vil, 2016; Mack et al., 2000; Parker et al., 1999; Simberloff, 2005). Invasive plants also negatively affect the biodiversity of native communities (Lambert, Dudley, & Saltonstall, 2010; Matsuzaki, Sasaki, & Akasaka, 2016).

*Ageratina altissima*, white snakeroot (also known as *Eupatorium rugosum*), is an invasive plant in South Korea (Kil et al., 2004). White snakeroot is a perennial herb native to the eastern United States and Canada that is currently receiving much attention for its rapid invasion of Korean forests (Chun, Lee, & Lee, 2001; Lee, Han, Hong, & Choi, 2005). Populations of *A. altissima* are distributed in forest edges disturbed by the development of roads and human settlements from which the plant extends to inner forest patches, although individuals are scattered (Song, Hong, Kim, Byun, & Gin, 2005). Poisoning (milk sickness) in humans usually occurs following the consumption of milk or milk products from cows that consumed *A. altissima* (Davis et al., 2015).

Invasive plants, including *A. altissima*, are commonly controlled by mowing, burning, or applying herbicide (Derr, 2008; Ketenring & Adams, 2011). Controlling invasive plants requires repeated application of herbicide (Derr, 2008) or covering with black plastic for solarization (Marushka & Allen, 2011). Herbicide application is expensive and contributes to other environmental problems such as bioaccumulation in food web systems. After establishment, management costs for invasive species increase dramatically, and, when an invasive plant creates a dense mat of rhizomes and is ready to spread, complete eradication becomes almost impossible. Furthermore, eradication of an invasive plant does not guarantee natural recovery of native plants (Reid, Morin, Downey, French, & Virtue, 2009; but see also Thomsen, Brownell, Grossek, & Kirsch, 2012; Case, Harrison, & Cornell, 2016). Moreover, methods of eradication can create a disturbance on bare ground, which facilitates re-invasion (Buckley, Bolker, & Rees, 2007; Iannone & Galatowitsch, 2008).

Therefore, management strategies should prioritize methods of prevention over those of eradication. Prevention is the most cost-effective method. For example, sowing seeds of native species to reintroduce propagules can increase biotic resistance to invasion (Bakker & Wilson, 2004), and the evidence is increasing that sowing seeds of native species prevents or slows the invasion of invasive plants (Byun, De Blois, & Brison, 2013, 2015; Ketenring & Adams, 2011; Middleton, Bever, & Schultz, 2010). Although no case study has examined the effect of biotic resistance on *A. altissima*, some studies examined the effects of restoration of native plants on the control of other invasive plant species, such as *Phragmites australis* (Byun et al., 2013, 2015; Peter & Burdick, 2010) and *Phalaris arundinacea* (Iannone & Galatowitsch, 2008; Perry, Galatowitsch, & Rosen, 2004; Reinhardt Adams & Galatowitsch, 2008).

Ecological theory provides an opportunity to develop restoration strategies based on how species assemble and regulate invasions (Funk, Cleland, Suding, & Zavaleta, 2008; Laughlin, 2014; Shea & Chesson, 2002; Zedler, 2005). A variety of theories and mechanisms are proposed, but two mechanisms are particularly relevant: competition-based biotic resistance and diversity effect.

First, the mechanism of competition-based biotic resistance is a function of which species are the most resistant to invasive plants. Based on niche difference, native species repel invasive plants through competitive exclusion (MacDougall, Gilbert, & Levine, 2009). A theory of limiting similarity originated from classical competition theories (Macarthur & Levins, 1967; Weldtzin, Muth, Von Holle, & Cole, 2003), and the theory proposes that there is a limit to niche overlap or similarity in resource use between native species and invading species. Based on mechanisms of competition, invading species cannot establish in a niche similar to that of a native species (Funk et al., 2008). When niches overlap, the species with superior fitness (competitive ability) will prevail (MacDougall et al., 2009).

Second, the diversity effect is an indication of how combinations of species resist invasion. This effect is related to niche partitioning, which leads to coexistence among native species and the diversity effect on invasive plants. According to the diversity–resistance hypothesis (Elton, 1958), the uptake of available resources and the occupation of niches are more complete in a species-rich community, which prevents invasion. Niche partitioning is observed when resources are partitioned as the species of neighboring plants and the canopy complexity increase (Ashton, Miller, Bowman, & Suding, 2010; Booth, Caldwell, & Stark, 2003; Frankow-Lindberg, 2012). Summarizing the research to date, compared with one particular alternative species, developing a seed mixture that contains three or four species will lead to a diverse plant community that can maintain biotic resistance in a changing environment and prevent re-invasion by invasive plants.

Functional traits are defined as morpho-physio-phenological traits (Cornelissen, 2003; Violle et al., 2007) that are linked with the niche and fitness of a species (Drenovsky et al., 2012; Eisenhauer, Schulz, Scheu, & Jousset, 2013; Funk et al., 2008). Functional groups are group of species whose traits are similar to each other. According to Fox’s assembly rule, when a native community lacks a particular functional group, the community is easily invaded by an invader that belongs to that functional group based on limiting similarity (Fox, 1987; Von Holle & Simberloff, 2004). In several studies, a predefined functional group, such as one defined by growth form, was used to test the effect of functional groups on invasion (Booth et al., 2003; Gooden & French, 2015; Pokorny et al., 2005; Prieur-Richard, Lavorel, Grigulis, & Dos Santos, 2000; Shelley & James, 2010; Symstad, 2000; Tilman, 1997b; Von Holle & Simberloff, 2004), but these particular groups often ignored functional traits that might be relevant to biotic resistance. For example, some invasive species...
explore temporal niches when these are not occupied by other species (Wilsey, Daneshgar, & Polley, 2011; Wolkovich & Cleland, 2010); therefore, functional traits related to life-history strategies, such as life span, can determine the timing of species establishment and possible competitive interactions. Species that establish early and grow rapidly may preempt niches, leading to inhibition of the slow-growing species in a community assemblage (Mwangi et al., 2007). Therefore, the classification of species into functional groups based on several relevant traits is essential to relate functional group identity with biotic resistance.

Diversity–interaction models (Kirwan et al., 2009) permit predictions of the relationship between diversity and biotic resistance across communities of different compositions by comparing different models based on different ecological assumptions concerning species interactions. When combined with a functional group approach, diversity–interaction models promise to reveal new insights into mechanisms of resistance to invasion (Frankow-Lindberg, 2012; Frankow-Lindberg, Brophy, Collins, & Connolly, 2009).

The focus of this research was on the processes that influence the outcome of community assembly when a site is disturbed, with the goal to limit establishment of an invasive species such as A. altissima. Successful establishment of A. altissima depends on the level of biotic resistance, which is the ability of other plant species to limit the success of invasions. Therefore, the primary objective was to understand the determinants of biotic resistance to invasion in a plant community assembly using A. altissima as a model. Based on the assumption that some species, or combination of species, are more resistant to invasion than others, we hypothesized that certain functional groups will be most resistant to invasion, whereas the species effect will be redundant within each functional group. Based on the hypothesis of limiting similarity, we hypothesized that the functional group of which A. altissima was a member would be more resistant than other groups. Additionally, we hypothesized that a mixture of species will be more resistant to invasion than a monoculture of a species (a diversity effect), and we asked how species interact to produce such a diversity effect.

2 MATERIALS AND METHODS

2.1 Species selection and functional classification

Twenty-two species were selected based on expert opinion of the invaded system and availability of seed. To address the hypotheses, existing functional trait information for the study species was sourced. The TRY trait database (Kattge et al., 2011) was used to obtain the functional traits of species, and specific leaf area, canopy height, life span, growth form, woodiness, relative growth rate, and leaf dry matter content were selected. These functional traits are relevant to the list of common core plant traits related to dispersal, establishment, and persistence (Weiher et al., 1999) and were also related to competitive ability and growth (Funk et al., 2008). To build a species-trait matrix, the median value of a measured trait per species was used for data to be consistent. Species were classified into functional groups based on trait similarity. Based on these functional traits, Gower’s similarity coefficient among species was calculated using the gowdis function in the R statistical software package (Gower, 1971; Podani, 1999). All traits were standardized and equally weighted in the calculation of the similarity coefficient.

Including the 22 species, 37 total plant species for broad interpretation, which included four typical invasive plants (Ambrosia trifida, Ageratina altissima, Sicyos angulatus, and Aster pilosus), in the capital area of Seoul, South Korea, were classified into three functional groups with the cluster analysis with ward option using the hclust function in the R program (Figure 1). Functional groups

FIGURE 1 Functional classification of species. "¶" refers to testing alternative resident plants in the experiment. "φ" refers to major invasive plants in the area of the capital Seoul, South Korea. Among the invasives, the target invasive plant in this experiment was Ageratina altissima.
differed from one another primarily by life span, growth form, and woodiness traits. The three functional groups were FG1 for annual plants, FG2 for perennial herbaceous plants, and FG3 for perennial woody plants. Details of the characteristics of each functional group are shown in Table 1. Species nomenclature and status (native or introduced) in this study followed the Flora of North America (Flora of North America Editorial, 1993) and the database of Vascular Plants of Canada (VASCAN), respectively.

### 2.2 | Experimental setup and seed preparation

A pot experiment was set up in a greenhouse facility in the School of Biological Sciences at Seoul National University. The experiment was designed to simulate a situation in which seeds of *A. altissima* reach bare soil after a biological disturbance. Pots were 22 cm in diameter and 30 cm in height, and the soil used in the experiments was a fertile agricultural soil. Seeds of *A. altissima* were collected on the campus of Seoul National University in November 2015. Most seeds of native plants were purchased from seed suppliers. Seed viability among native plants was standardized by applying the identical number of viable seeds per species to experimental units. To determine pure live seeds, a germination test was conducted. All seeds were cold-stratified at 3°C before the germination test, following standard methods (Lindig-Cisneros & Zedler, 2001). Before the experiment, 100 seeds per species were placed in each of three Petri dishes with filter paper (Whatman® No. 1) moistened with 6 ml of distilled water under fluorescent light. The species with a germination rate below 3% were excluded. Among 22 species, the germination rate was above 3% for only 12 species. Viable seeds per species, not seedlings, were applied in the pot experiments.

### 2.3 | Design of competition test

An additive competition design was applied to test the competitive effect of resident species on *A. altissima* (Connolly, Wayne, & Bazzaz, 2001; Keddy, Twolan-Strutt, & Wisheu, 1994; Snaydon, 1991). Each treatment pot received the seeds of *A. altissima* and those of native plants. For the 12 monoculture treatments, one native species per pot was used. For the seven mixture treatments, four randomly chosen native species per pot were used. Control pots received only seeds of *A. altissima*. All species in monocultures or mixtures were sown in early March 2016 with the seeds of *A. altissima* in treatments or the control. Each seeding density of native plant(s) and *A. altissima* was total 300 viable seeds per each pot. Control pot received 300 viable seeds of *A. altissima* only. The sowing density was approximately 8,000 live seeds/m². Treatments were applied in a randomized complete block design, with three replicates per treatment.

### 2.4 | Data measurement and analyses

At the end of July 2016, the number of shoots, aboveground biomass, plant height, and plant cover of *A. altissima* in each treatment and control pot were measured to calculate the primary response variable (see below). Additionally, plant cover, plant height, and aboveground biomass of all native plants were measured to correlate these variables with the response variables. For aboveground biomass, the aboveground portion of plants was harvested at the end of July and then weighed following drying at 80°C for 48 hr. Plant height was estimated for each species to the closest 0.5 cm. The RCI (relative competition index) was calculated to estimate the competitive effect of native plant(s) on *A. altissima* using the following equation (Weigelt & Jolliffe, 2003):

\[
\text{RCI}_{Y} = \frac{Y_{control} - Y_{treatment}}{Y_{control}}
\]  

(1)

where RCI is the relative competition index of a native plant on *A. altissima* in either monoculture or mixture for a given variable Y (i.e., number of shoots, aboveground biomass, plant height, or plant cover of *A. altissima*). \(Y_{control}\) is the performance of *A. altissima* in the control, and \(Y_{treatment}\) is the performance of *A. altissima* in a treatment. Because \(\text{RCI}_{\text{number of shoots}}\), \(\text{RCI}_{\text{biomass}}\), \(\text{RCI}_{\text{height}}\) and \(\text{RCI}_{\text{plant cover}}\), were highly correlated with one another, \(\text{RCI}_{\text{avg}}\) was calculated, which is the arithmetic mean of \(\text{RCI}_{\text{number of shoots}}\), \(\text{RCI}_{\text{biomass}}\), \(\text{RCI}_{\text{height}}\) and \(\text{RCI}_{\text{plant cover}}\) as the primary response variable for all analyses. A value of 0 for \(\text{RCI}_{\text{avg}}\) indicated no competitive effect on *A. altissima*, a value of 1 indicated complete competitive exclusion of *A. altissima*, and a negative RCI indicated facilitation of the establishment and growth of *A. altissima* by native plants.

For the monoculture treatments in the experiment, ANOVA was used to test for functional group identity effect and species

| Trait          | FG1       | FG2                                      | FG3       |
|----------------|-----------|------------------------------------------|-----------|
| Life longevity | Annual    | Perennial, biennial                      | Perennial |
| Growth form    | Herb, grass, forb | Herb, forb, sedge, grass                | Shrub, tree |
| Woodiness      | Non-woody | Non-woody                                | Woody     |
| SLA            | 25.13 ± 4.10 | 26.95 ± 19.23                           | 25.90 ± 11.12 m²/kg |
| RGR            | 0.22 ± 0.05  | 0.17 ± 0.12                              | 0.17 ± 0.12 g g⁻¹ day⁻¹ |
| LDMC           | 3.57 ± 6.88  | 6.30 ± 10.31                            | 8.23 ± 15.59 g/g |
| Height         | 140.3 ± 135.9 | 70.36 ± 55.16                           | 156.5 ± 56.3 cm |

### Table 1 | Functional group trait characteristics

| Trait    | FG1 | FG2                                      | FG3 | Units  |
|----------|-----|------------------------------------------|-----|--------|
| Life longevity | Annual | Perennial, biennial | Perennial |
| Growth form | Herb, grass, forb | Herb, forb, sedge, grass | Shrub, tree |
| Woodiness | Non-woody | Non-woody | Woody |
| SLA       | 25.13 ± 4.10 | 26.95 ± 19.23 | 25.90 ± 11.12 m²/kg |
| RGR       | 0.22 ± 0.05  | 0.17 ± 0.12 | 0.17 ± 0.12 g g⁻¹ day⁻¹ |
| LDMC      | 3.57 ± 6.88  | 6.30 ± 10.31 | 8.23 ± 15.59 g/g |
| Height    | 140.3 ± 135.9 | 70.36 ± 55.16 | 156.5 ± 56.3 cm |
different ecological assumptions were used to test alternative hypotheses about the relative role of functional groups and functional redundancy in biotic resistance (Kirwan et al., 2009).

Model 1 describes the species identity effect alone without species interaction:

$$y = \sum_{i=1}^{S} \beta_i P_i + \varepsilon$$  \hspace{1cm} (2)

The response variable ($y$) represents RCI_{avg} as an indicator of biotic resistance to invasion by A. altissima. $\beta_i$ is the estimated performance of species $i$ as a contribution to biotic resistance, and $P_i$ is the initial proportion of species $i$ in a seed mixture. For monoculture treatments of species $i$, $P_i$ is equal to 1.

Model 2 describes the functional group identity effect alone without species interaction:

$$y = \beta_{FG1} P_{FG1} + \beta_{FG2} P_{FG2} + \beta_{FG3} P_{FG3} + \varepsilon$$  \hspace{1cm} (3)

where $\beta_{FG1}$ is the estimated functional group identity effect of FG1 and $P_{FG1}$ is the sum of all species proportions within that FG1.

Model 3 describes the functional group identity effect and average species interaction:

$$y = \beta_{FG1} P_{FG1} + \beta_{FG2} P_{FG2} + \beta_{FG3} P_{FG3} + \delta_{av} \sum_{i<j} P_i P_j + \varepsilon$$  \hspace{1cm} (4)

where $\delta_{av}$ is the single interaction coefficient assuming that a pair of species interacts equally to contribute to such a diversity effect.

Model 4 describes the functional group identity effect and species interactions within and between functional groups:

$$y = \beta_{FG1} P_{FG1} + \beta_{FG2} P_{FG2} + \beta_{FG3} P_{FG3} +$$

$$\delta_{wFG1} \sum_{i<j} P_i P_j + \delta_{wFG2} \sum_{i<j} P_i P_j + \delta_{wFG3} \sum_{i<j} P_i P_j +$$

$$\delta_{wFG1FG2} P_{FG1} P_{FG2} + \delta_{wFG1FG3} P_{FG1} P_{FG3} +$$

$$\delta_{wFG2FG3} P_{FG2} P_{FG3} + \varepsilon$$  \hspace{1cm} (5)

where $\delta_{wFG1}$ is the coefficient of pairwise species interaction within FG1 and $\delta_{wFG1FG2}$ is the coefficient of pairwise species interactions between FG1 and FG2.

Model 5 describes the functional group identity effect and separate pairwise species interactions:

$$y = \beta_{FG1} P_{FG1} + \beta_{FG2} P_{FG2} + \beta_{FG3} P_{FG3} + \beta_{FG4} P_{FG4} +$$

$$\sum_{i<j} \delta_{ij} P_i P_j + \varepsilon$$  \hspace{1cm} (6)

where $\delta_{ij}$ is the coefficient of separate pairwise interaction between species $i$ and species $j$.

Model 6 describes the functional group identity effect and species interactions between functional groups without species interactions within each functional group:

$$y = \beta_{FG1} P_{FG1} + \beta_{FG2} P_{FG2} + \beta_{FG3} P_{FG3} + \delta_{FG1FG2} P_{FG1} P_{FG2} +$$

$$\delta_{FG1FG3} P_{FG1} P_{FG3} + \delta_{FG2FG3} P_{FG2} P_{FG3} + \varepsilon$$  \hspace{1cm} (7)
Each model was tested using the glm function in the R statistical software package. Pairs of models were compared for a significant difference in model predictions for RCI$_{avg}$ using the ANOVA function in the R software. Akaike’s information criterion (AIC) was used to compare and select models (Burnham, Anderson, & Burnham, 2002).

All ANOVA tests and correlation analyses were performed using JMP software (© SAS Institute Inc., Cary, NC, USA). Cluster analysis and diversity–interaction modeling, which are based on multiple regressions, were conducted using the R program (R Development Core Team, 2015).

Data are available from the Figshare Digital Repository: https://dx.doi.org/10.6084/m9.figshare.3593049.v1.

3 | RESULTS

3.1 | Monoculture treatments

In monoculture treatments, the relative competitive effect of resident plants on A. altissima was primarily related to their functional group identity, whereas the species identity effect remained redundant within each functional group (Figure 2). The relative competitive index (RCI$_{avg}$) of the 12 resident plants on A. altissima was significantly different among the three FGs ($F_{2,31} = 22.84, p < .001$), but was not significantly different within each FG [FG1: $F_{3,6} = 1.00, p = .4547$; FG2: $F_{3,6} = 4.07, p = .067$; and FG3: $F_{3,6} = 1.17, p = .3937$]. The highest RCI$_{avg}$ was for FG1 (annual plants), followed by FG2 and FG3 (mean RCI$_{avg}$ = 0.975, 0.710, and 0.196, respectively; Figure 2).

The performance traits of resident plants were significantly negatively correlated with the biomass of A. altissima (Pearson coefficients: $r = −0.536$), plant cover ($r = −0.792$), and height ($r = −0.383$; Figure 3).

Among the plant functional traits used to classify functional group, relative growth rate ($r = 0.923$), seed and LDMC ($r = −0.5535$) were significantly correlated with RCI$_{avg}$, and annual plants with grass and herb in growth form and non-woody plant species showed relatively high RCI$_{avg}$ (Appendix S1).

3.2 | Mixture treatments

Mixtures of resident plants were more resistant to invasion than monocultures, and this diversity effect on biotic resistance was the result of positive interactions between FG1 and FG3 (Figures 4 and 5). RCI$_{avg}$ was significantly greater in mixtures than in monocultures ($F_{1,53} = 4.08; p = .048$; Figure 4). Aboveground biomass of resident species was also significantly greater in mixture treatments than in monoculture treatments ($F_{1,53} = 7.33; p < .009$).

Comparisons between pairs of diversity–interaction models fitted to the experimental data set revealed distinctive species interaction patterns by functional group that contributed to biotic resistance. The functional group identity effect terms fitted as well as species identity effect terms (Model 1 vs. Model 2; F-test; $p = .171$, AIC: 30.99 vs.
The evidence was strong for an average interaction term effect (diversity effect) (Model 2 vs. Model 3; F-test; \( p = .003 \), AIC: 27.26 vs. 20.82). The species interaction by functional group (species interaction within and between functional groups) terms fitted much better than the single average interaction term (Model 3 vs. Model 4, F-test; \( p = .001 \), AIC: 20.82 vs. 11.55). However, the separate pairwise species interactions terms did not fit better than the species interaction by functional group term (Model 4 vs. Model 5; F-test; \( p = .579 \), AIC: 11.55 vs. 13.18). No evidence of significant species interaction within each functional group was detected (Model 4 vs. Model 6, F-test; \( p = .725 \), AIC: 11.55 vs. 7.09). Thus, Model 6 (functional group identity effect and species interaction between functional groups) was chosen for the final model prediction because it fitted as well as the complex models with separate pairwise species interactions. Figure 5a shows Model 6 predictions on the effect of functional group composition in seed mixtures on biotic resistance to invasion by A. altissima. Figure 5b shows the identical model prediction when the model was fitted to aboveground biomass instead of \( RIC_{avg} \) of resident plants. In either case, a positive interaction was found between FG1 and FG3 in their contribution to biotic resistance. The highest \( RIC_{avg} \) and aboveground biomass were estimated for a mixture of FG1 and FG3 at a ratio of 2 to 1, approximately.

4 | DISCUSSION

4.1 | Functional groups and biotic resistance

In this study, functional group identity determined biotic resistance to invasion by A. altissima, but the species identity effect was redundant within each functional group. The most resistant functional group was FG1 (fast-growing annuals), which was a different functional group from A. altissima (FG2). Thus, this result did not support the role of limiting similarity in biotic resistance. However, a significant role of functional groups in biotic resistance was found, with some exceptions (Von Holle & Simberloff, 2004), in other studies that tested functional groups based on various plant traits such as life longevity, growth form, root structure, plant height, or phytosynthetic pathways (Byun et al., 2013; Prieur-Richard, Lavorel, Dos Santos, & Grigulis, 2002b; Prieur-Richard, Lavorel, Linhart, & Dos Santos, 2002a; Shelly & James, 2010; Wang, Ge, Zhang, Bai, & Du, 2013). The functional group that most resisted invasion was not always consistent among those studies. In some cases, the functional group most similar to the invasive plant offers the most resistance (Bakker & Wilson, 2004; Dukes, 2002; Fargione, Brown, & Tilman, 2003; Hooper & Dukes, 2010; Mwanti et al., 2007; Pokorny et al., 2005; Turnbull et al., 2005), indicating limiting similarity, whereas, in other cases, different functional groups offer the most resistance to invasion (Byun et al., 2013; Lulow, 2006; Shelly & James, 2010), suggesting fitness inequality as one of the key mechanisms of resistance. Invasion success may depend on both fitness and niche differences with resident species (MacDougall et al., 2009). We demonstrated the important role of a pre-emptive effect (first come, first served) in the control of invasive plants which is consistent with another study (Stuble & Souza, 2016), and early emergence increased components of plant fitness, such as seedling growth, in a controlled experiment (Verd & Traveset, 2005).

In the present study, biomass, coverage, height, and relative growth rate were important to control the invasion by A. altissima. The indicators of fitness and biotic resistance are plant height (Gaudet & Keddy, 1988), biomass (Gaudet & Keddy, 1988; Lulow, 2006; Rinella, Pokorny, & Rekaya, 2007), plant cover (Bakker & Wilson, 2004; Gerhardt & Collinge, 2003), and plant size (Schamp & Aarsen, 2010). In particular, biomass is an indicator of plant competitive ability (Gaudet & Keddy, 1988) and biotic resistance (Lulow, 2006; Rinella et al., 2007).
4.2 | Diversity effect on biotic resistance

In this study, we observed a diversity–resistance relationship, which is consistent with previous community-scale experimental studies on multiple invaders (Abernathy, Graham, Sherrard, & Smith, 2015; Byun et al., 2013; Frankow-Lindberg et al., 2009; Henriksson, Yu, Wardle, Trygg, & Englund, 2016; Stachowicz & Byrnes, 2006), but see also other studies (Henriksson, Yu, Wardle, & Englund, 2015; Schamp & Aarssen, 2010). Similar patterns at a community scale are reported from field observations (Brown & Peet, 2003; Levine, 2000), but opposite patterns are observed at larger scales (Brown & Peet, 2003; Levine, 2000; Stohlgren, Barnett, & Kartesz, 2003; Stohlgren et al., 1999). Spatially covarying environmental factors such as resource availability can affect both diversity and invasibility (Byers & Noonburg, 2003; Davies, Harrison, Safford, & Viers, 2007a; Levine & D’Antonio, 1999). Furthermore, different ecological processes such as dispersal and species recruitment can predominate at a larger scale (Fridley et al., 2007; Pauchard & Shea, 2006; Tilman, 1997a). Notably, the diversity effect was best described by positive species interactions between functional groups in this study, which implied niche partitioning among species in a mixture. This diversity effect implies complementarity rather than selection effects for the control of invasions by biotic resistance (Loreau, 1998; Loreau & Hector, 2001). Functionally diverse resident communities use resources more completely than a simple community (Davies, Pokorny, Shely, & James, 2007b; Pokorny et al., 2005; Prieur-Richard et al., 2000; Rinella et al., 2007). Furthermore, in functionally diverse communities with a complex canopy, less light penetrates through the canopy (Frankow-Lindberg, 2012; Lindig-Cisneros & Zedler, 2002).

4.3 | Case studies to restore resistant plants to control invasion

Several restoration experiments have been conducted to test biotic resistance in an invasion context. Unfortunately, a case study for the control A. altissima has not yet been conducted. Based on this study, restoration of native plant cover controlled up to 100% of A. altissima establishment. Phragmites australis is an exotic invasive plant in the wetlands of North America, and, in an experiment in a salt marsh, the transport of a halophyte into the marsh reduced rhizome growth of Phragmites australis by 60% (Peter & Burdick, 2010). A diversity effect (mixtures are more resistant than monocultures of a species) was also found with the selection effect of Spartina alterniflora, and, in a freshwater mesocosm experiment, biotic resistance was significantly different among functional groups (Byun et al., 2013). In the present study, the strongest biotic resistance was found in rapidly growing annual plants that showed a priority effect. In another experiment that examined environmental effects, flooding always reduced invasion success, and flooding assisted or inhibited biotic resistance depending on the adaption of species to the environment (Byun et al., 2015). Biotic resistance is particularly effective with low propagule pressure (Byun et al., 2015). Other studies also examined the restoration of native plants to control invasive plants, including Centaurea diffusa (Meiman, Redente, & Paschke, 2009), Centaurea solstitialis (Dukes, 2001, 2002), Rapistrum rugosum (Cutting & Hough-Goldstein, 2013; Simmons, 2005), Cardaria draba, Cirsium arvense, Bromus tectorum and B. japonicas (Perry, Cronin, & Paschke, 2009), Arundo donax (Quinn & Holt, 2009), Agropyron cristatum (Bakker & Wilson, 2004), and Persicaria perfoliata (Cutting & Hough-Goldstein, 2013).

Based on empirical evidence, restoring plant species increases biotic resistance. Depending on seed configuration, environment, and invasive plant, plant restoration results in an approximate reduction in invasion ability of 50–100%. In most experiments, invasive plants survived regardless of plant restoration, with the exception of those in the present experiment. In conclusion, biotic resistance alone may not prevent invasive plants completely (Levine, Adler, & Yelenik, 2004); however, biotic resistance contributes to constraining the abundance of invasive plants and determines the identity of an invasive plant at regional scales (Davies, Cavender-Bares, & Deacon, 2011; Fargione et al., 2003).

4.4 | Implications for management

Restoration has many advantages over methods of eradication; restoration is self-regenerative (not requiring repeated application), is less of a threat to native, desirable species, and prevents disturbance that stimulates re-invasion by invasive plants (Simmons, 2005). Therefore, restoration of native plant cover is an alternative, innovative method to protect native species from invasive plants. Practical designs for restoration include some technical questions that must be answered such as how to select and how to combine species for restoration and how to identify appropriate environmental conditions for restoration. However, information on the use of native plant restoration as an alternative to control invasions continues to be lacking (Hazelton, Mozdzer, Burdick, Ketenring, & Whigham, 2014).

Ageratina altissima is a noxious weed and an invasive plant that is very difficult to control (Chun et al., 2001; Kim, Jang, & Park, 2014; Lee, Yoo, & Lee, 2003; Lee et al., 2005). In the field, invasion success is determined by the interplay among environmental conditions, propagule pressure, and biotic resistance (Catford, Jansson, & Nilsson, 2009; D’Antonio, 1993; Dethier & Hacker, 2005; Perelman, Chaneton, Batista, Burkart, & León, 2007). Although this experiment did not test all these factors affecting invasion, the approach generally revealed the importance of biotic resistance. The forest edge, disturbed by human activities such as trampling and creation of paths, is the site for much of the invasion by this invasive plant (Chun et al., 2001; Kim et al., 2014; Lee et al., 2003, 2005), and A. altissima was identified as an indicator species of edge effect following recent silvicultural clearcutting in a mixed mesophytic forest (Landenberger & Ostergren, 2002). Trampling has a role in the invasion window of A. altissima, and sites in which they grow vigorously show low species diversity due to their dense cover (Lee et al., 2003). Human activities that result in disturbance increase the susceptibility of most ecosystems, which highlights the requirement, when applicable, to minimize damage to the matrix of vegetation cover and/or facilitate
the rapid establishment of competitive cover with the goal to restore disturbed habitat. In these cases, the results of this study showed that functional group identity and diversity of resident or restored plant communities were good indicators of potential biotic resistance to seed-mediated invasion by A. altissima. We suggest the use of FG1 species, such as *Hordeum vulgare* and *Secale cereal*, primarily, to restore native plant cover to suppress invasion by *A. altissima* and also mixing FG1 with FG3 species for niche partitioning and potential long-term effects. Concerning propagule pressure, most field situations are expected to have much lower seed pressure than the level tested in this experiment; however, even then, complete competitive exclusion may not be achieved. Follow-up monitoring and selective control of *A. altissima* establishment could be necessary. The distribution of *A. altissima* is closely correlated with the soil contents of total nitrogen and available phosphorus (Suh, Kil, Kim, & Lee, 1997), and *A. altissima* is adaptable to a broad range of soil conditions (Kim et al., 2014); therefore, controlling for these elements will help to further suppress the growth of *A. altissima*. Growth of *A. altissima* is highest at a light intensity of 7,500 lux (Suh et al., 1997) and is correlated with decreasing litter depth (Kim et al., 2014); thus, increased cover of native plants will decrease light intensity and increase litter depth to contribute to the suppression of this plant.

The present study indicates that the guiding ecological principles to understand and/or manage, if desired, biological invasions could emerge from advances in community theory and the use of a functional framework. To facilitate generalization, widely distributed invasive plants should be targeted in different contexts and the results should be scaled-up to field conditions.

**ACKNOWLEDGEMENTS**

We thank Mr. Jeonghwan Bang and Ms. Shinyeong Park for laboratory assistance. This research was supported by Basic Science Research Program through the National Research Foundation of Korea (NRF) funded by the Ministry of Education (NRF-2015R1A6A3A01058185). The study was also supported by the TRY initiative on plant traits (http://www.try-db.org). The TRY initiative and database is hosted, developed, and maintained by J. Kattge and G. Bönisch (Max Planck Institute for Biogeochemistry, Jena, Germany). TRY was currently supported by DIVERSITAS/Future Earth and the German Centre for Integrative Biodiversity Research (iDiv) Halle-Jena-Leipzig.

**AUTHORS’ CONTRIBUTION**

CB and EL conceived the research. CB designed the research, performed the experiment, analyzed data, and wrote the manuscript. CB and EL edited the manuscript. All authors contributed critically to the drafts and gave final approval for publication.

**CONFLICT OF INTEREST**

None declared.

**REFERENCES**

Abernathy, J. E., Graham, D. R., Sherrard, M. E., & Smith, D. D. (2015). Productivity and resistance to weed invasion in four prairie biomass feedstock with different diversity. GCB Bioenergy, 8, 1082–1092.

Ashton, I. W., Miller, A. E., Bowman, W. D., & Suding, K. N. (2010). Niche complementarity due to plasticity in resource use: Plant partitioning of chemical N forms. Ecology, 91, 3252–3260.

Bakker, J. D., & Wilson, S. D. (2004). Using ecological restoration to constrain biological invasion. *Journal of Applied Ecology*, 41, 1058–1064.

Blossey, B. (1999). Before, during and after: The need for long-term monitoring in invasive plant species management. *Biological Invasions*, 1, 301–311.

Bolker, B. M., Brooks, M. E., Clark, C. J., Geange, S. W., Poulson, J. R., Stevens, M. H., & White, J. S. (2009). Generalized linear mixed models: A practical guide for ecology and evolution. *Trends in Ecology & Evolution*, 24, 127–135.

Booth, M. S., Caldwell, M. M., & Stark, J. M. (2003). Overlapping resource use in three great basin species: Implications for community invasibility and vegetation dynamics. *Journal of Ecology*, 91, 36–48.

Brown, R. L., & Peet, R. K. (2003). Diversity and invasibility of Southern Appalachian plant communities. *Ecology*, 84, 32–39.

Buckley, Y. M., Bolker, B. M., & Rees, M. (2007). Disturbance, invasion and re-invasion: Managing the weed-shaped hole in disturbed ecosystems. *Ecology Letters*, 10, 809–817.

Burnham, K. P., Anderson, D. R., & Burnham, K. P. (2002). Model selection and multimodel inference: A practical information-theoretic approach. New York: Springer.

Byers, J. E., & Noonnburg, E. G. (2003). Scale dependent effects of biotic resistance to biological invasion. *Ecology*, 84, 1428–1433.

Byun, C., De Blois, S., & Brisson, J. (2013). Plant functional group identity and diversity determine biotic resistance to invasion by an exotic grass. *Journal of Ecology*, 101, 128–139.

Byun, C., De Blois, S., & Brisson, J. (2015). Interactions between abiotic constraint, propagule pressure, and biotic resistance regulate plant invasion. *Oecologia*, 178, 285–296.

Case, E. J., Harrison, S., & Cornell, H. V. (2016). After an invasion: Understanding variation in grassland community recovery following removal of a high-impact invader. *Biological Invasions*, 18, 371–380.

Castro-Diez, P., Pauchard, A., Traveset, A., & Vill, M. (2016). Linking the impacts of plant invasion on community functional structure and ecosystem properties. *Journal of Vegetation Science*, 27, 1233–1242.

Catford, J. A., Janssens, R., & Nilsson, C. (2009). Reducing redundancy in invasion ecology by integrating hypotheses into a single theoretical framework. *Diversity and Distributions*, 15, 22–40.

Chu, Y. J., Lee, H. W., & Lee, E. J. (2001). Allozyme variation and population genetic structure of an invasive plant, *Ageratina altissima* (white snake root), in Seoul. *Korean Journal of Biological Sciences*, 5, 309–312.

Connolly, J. L., Wayne, P., & Bazza, F. A. (2001). Interspecific competition in plants: How well do current methods answer fundamental questions? *The American Naturalist*, 157, 107–125.

Cornelissen, J. H. C. (2003). A handbook of protocols for standardised and easy measurement of plant functional traits worldwide. *Australian Journal of Botany*, 51, 335.

Cutting, K. J., & Hough-Goldstein, J. (2013). Integration of biological control and native seeding to restore invaded plant communities. *Restoration Ecology*, 21, 648–655.

D’Antonio, C. M. (1993). Mechanisms controlling invasion of coastal plant communities by the alien succulent Carpobrotus Edulis. *Ecology*, 74, 83.

Davies, K. F., Cavender-Bares, J., & Deacon, N. (2011). Native communities determine the identity of exotic invaders even at scales at which communities are unsaturated. *Diversity and Distributions*, 17, 35–42.

Davies, K. F., Harrison, S., Safford, H. D., & Viers, J. H. (2007a). Productivity alters the scale dependence of the diversity-invasibility relationship. *Ecology*, 88, 1940–1947.
Davies, K. W., Pokorny, M. L., Sheley, R. L., & James, J. J. (2007b). Influence of plant functional group removal on inorganic soil nitrogen concentrations in native grasslands. Rangeland Ecology & Management, 60, 304–310.

Davis, T. Z., Lee, S. T., Collett, M. G., Stegelmeyer, B. L., Green, B. T., Buck, S. R., & Pfister, J. A. (2015). Toxicity of white snakeroot (Ageratina altissima) and chemical extracts of white snakeroot in goats. Journal of Agricultural and Food Chemistry, 63, 2092–2097.

Derr, J. F. (2008). Common reed (Phragmites Australis) response to mowing and herbicide application. Invasive Plant Science and Management, 1, 12–16.

Dethier, M. N., & Hacker, S. D. (2005). Physical factors vs. biotic resistance in controlling the invasion of an estuarine marsh grass. Ecological Applications, 15, 1273–1283.

Drenovsky, R. E., Grewell, B. J., D’Antonio, C. M., Funk, J. L., James, J. J., Molinari, N., ..., Richards, C. L. (2012). A functional trait perspective on plant invasion. Annals of Botany, 110, 141–153.

Dukes, J. S. (2001). Biodiversity and invasibility in grassland microcosms. Oecologia, 126, 563–568.

Dukes, J. S. (2002). Species composition and diversity affect grassland susceptibility and response to invasion. Ecological Applications, 12, 602–617.

Eisenhauer, N., Schulz, W., Scheu, S., & Jousset, A. (2013). Niche dimensionality links biodiversity and invasibility of microbial communities. Functional Ecology, 27, 282–288.

Elton, C. S. (1958). The ecology of invasions by animals and plants. London: The University of Chicago Press.

Fargione, J., Brown, C. S., & Tilman, D. (2003). Community assembly and invasion: An experimental test of neutral versus niche processes. Proceedings of the National Academy of Sciences of the United States of America, 100, 8916–8920.

Flora of North America Editorial, C. (1993). Flora of North America: North of Mexico. New York: Oxford University Press.

Fox, B. J. (1987). Species assembly and the evolution of community structure. Evolutionary Ecology, 1, 201–213.

Frankow-Lindberg, B. (2012). Grassland plant species diversity decreases invasion by increasing resource use. Oecologia, 169, 793–802.

Frankow-Lindberg, B. E., Brophy, C., Collins, R. P., & Connolly, J. (2009). Biodiversity effects on yield and unsown species invasion in a temperate forage ecosystem. Annals of Botany, 103, 913–921.

Fridley, J. D., Stachowicz, J. J., Naeem, S., Sax, D. F., Seabloom, E. W., Smith, M. D., ..., Holle, B. V. (2007). The invasion paradox: Reconciling pattern and process in species invasions. Ecology, 88, 3–17.

Funk, J. L., Cleland, E. E., Suding, K. N., & Zavaleta, E. S. (2008). Restoration through reassembly: Plant traits and invasion resistance. Trends in Ecology & Evolution, 23, 695–703.

Gaudet, C. L., & Keddy, P. A. (1988). A comparative approach to predicting competitive ability from plant traits. Nature, 334, 242–243.

Gerhardt, F., & Collinge, S. K. (2003). Exotic plant invasions of vernal pools in the Central Valley of California, USA. Journal of Biogeography, 30, 1043–1052.

Gooden, B., & French, K. (2015). Impacts of alien plant invasion on native plant communities are mediated by functional identity of resident species, not resource availability. Oikos, 124, 298–306.

Gower, J. C. (1971). A general coefficient of similarity and some of its properties. Biometrics, 27, 857–871.

Hazelton, E. L., Mozdzer, T. J., Burdick, D. M., Kettenring, K. M., & Whigham, D. F. (2014). Phragmites australis management in the United States: 40 years of methods and outcomes. AoA Plants, 6, plu001.

Henriksson, A., Yu, J., Wardle, D. A., & Englund, G. (2015). Biotic resistance in freshwater fish communities: Species richness, saturation or species identity? Oikos, 124, 1058–1064.

Henriksson, A., Yu, J., Wardle, D. A., Trygg, J., & Englund, G. (2016). Weighted species richness outperforms species richness as predictor of biotic resistance. Ecology, 97, 262–271.

Hooper, D. U., & Dukes, J. S. (2010). Functional composition controls invasion success in a California serpentine grassland. Journal of Ecology, 98, 764–777.

Iannone, B. V. III., & Galatowitsch, S. M. (2008). Altering light and soil N to limit Phalaris arundinacea reinvasion in sedge meadow restoration. Restoration Ecology, 16, 689–701.

Katta, J., Díaz, S., Lavorel, S., Prentice, I. C., Leadley, P., Bönisch, G., ..., Wirth, C. (2011). TRY – a global database of plant traits. Global Change Biology, 17, 2905–2935.

Keddy, P. A., Twolan-Strutt, L., & Wisheu, I. C. (1994). Competitive effect and response rankings in 20 wetland plants: Are they consistent across three environments? The Journal of Ecology, 82, 635–643.

Kettenring, K. M., & Adams, C. R. (2011). Lessons learned from invasive plant control experiments: A systematic review and meta-analysis. Journal of Applied Ecology, 48, 970–979.

Kil, J. H., Shim, K. C., Park, S. H., Koh, K. S., Suh, M. H., Ku, Y. B., ..., Kong, H. Y. (2004). Distributions of naturalized alien plants in South Korea. Weed Technology, 18, 1493–1495.

Kim, H., Jang, Y. L., & Park, P. S. (2014). Distribution pattern of Ageratina altissima along trails at Mt. Myeong in Seoul, Korea. Korean Journal of Agricultural and Forest Meteorology, 16, 227–232.

Kirwan, L., Connolly, J., Finn, J. A., Brophy, C., Lüscher, A., Nyfeler, D., & Sebasti, M. T. (2009). Diversity–interaction modeling: Estimating contributions of species identities and interactions to ecosystem function. Ecology, 90, 2032–2038.

Lambert, A. M., Dudley, T. L., & Saltonstall, K. (2010). Ecology and impacts of the large-statured invasive grasses Arundo donax and Phragmites australis in North America. Invasive Plant Science and Management, 3, 489–494.

Landenberg, R. E., & Ostergren, D. A. (2002). Eupatorium rugosum (Asteraceae) flowering as an indicator of edge effect from clearingcut in mixed-mesophytic forest. Forest Ecology and Management, 155, 55–68.

Laughlin, D. C. (2014). Applying trait-based models to achieve functional targets for theory-driven ecological restoration. Ecology Letters, 17, 771–784.

Lavoie, C., Saint-Louis, A., Guay, G., Groeneve, E., & Villeneuve, P. (2012). Naturalization of exotic plant species in north-eastern North America: Trends and detection capacity. Diversity and Distributions, 18, 180–190.

Lee, K.-J., Han, B.-H., Hong, S.-H., & Choi, J.-W. (2005). A study on the characteristics of urban ecosystems and plans for the environment and ecosystem in Gangnam-gu, Seoul, Korea. Landscape and Ecological Engineering, 1, 207–219.

Lee, H. S., Yoo, H. M., & Lee, C. S. (2003). Distribution pattern of white snakeroot as an invasive alien plant and restoration strategy to inhibit its expansion in Soriripool park, Seoul. Korean Journal of Biological Sciences, 7, 197–205.

Levine, J. M. (2000). Species diversity and biological invasions: Relating local process to community pattern. Science, 288, 852–854.

Levine, J. M., Adler, P. B., & Yelenik, S. G. (2004). A meta-analysis of biotic resistance to exotic plant invasions. Ecology Letters, 7, 975–989.

Levine, J. M., & D’Antonio, C. M. (1999). Elton revisited: A review of evidence linking diversity and invasibility. Oikos, 87, 15–26.

Lindig-Cisneros, R., & Zedler, J. (2001). Effect of light on seed germination in Phalaris arundinacea L. (reed canary grass). Plant Ecology, 155, 75–78.

Lindig-Cisneros, R., & Zedler, J. B. (2002). Relationships between canopy complexity and germination microsites for Phalaris arundinacea L. Oecologia, 133, 159–167.

Loreau, M. (1998). Separating sampling and other effects in biodiversity experiments. Oikos, 82, 600–602.

Loreau, M., & Hector, A. (2001). Partitioning selection and complementarity in biodiversity experiments. Nature, 412, 72–76.

Lulow, M. E. (2006). Invasion by non-native annual grasses: The importance of species biomass, composition, and time among California native grasses of the central valley. Restoration Ecology, 14, 616–626.
MacArthur, R., & Levins, R. (1967). The limiting similarity, convergence, and divergence of coexisting species. The American Naturalist, 101, 377–385.

MacDougall, A. S., Gilbert, B., & Levine, J. M. (2009). Plant invasions and the niche. Journal of Ecology, 97, 609–615.

Mack, R. N., Simberloff, D., Lonsdale, W. M., Evans, H., Clout, M., & Bazzaz, F. A. (2000). Biotic invasions: Causes, epidemiology, global consequences, and control. Ecological Applications, 10, 689–710.

Marushia, R. G., & Allen, E. B. (2011). Control of exotic annual grasses to restore native forbs in abandoned agricultural land. Restoration Ecology, 19, 45–54.

Matsuzaki, S.-I., Sasaki, T., & Akasaka, M. (2016). Invasion of exotic piscivores causes losses of functional diversity and functionally unique species in Japanese lakes. Freshwater Biology, 61, 1128–1142.

Meiman, P., Redente, E., & Paschke, M. (2009). Diffuse knapweed (Centaurea diffusa Lam.) seedling emergence and establishment in a Colorado grassland. Plant Ecology, 201, 631–638.

Middleton, E. L., Bever, J. D., & Schultz, P. A. (2010). The effect of restoration methods on the quality of the restoration and resistance to invasion by exotics. Restoration Ecology, 18, 181–187.

Mwangi, P. N., Schmitz, M., Scherer, C., Roscher, C., Schumacher, J., Scherer-Lorenzen, M., --- Schmid, B. (2007). Niche pre-emption increases with species richness in experimental plant communities. Journal of Ecology, 95, 65–78.

Parker, I. M., Simberloff, D., Lonsdale, W. M., Goodell, K., Wonham, M., Kareiva, P. M., --- Goldwasser, L. (1999). Impact: Toward a framework for understanding the ecological effects of invaders. Biological Invasions, 1, 3–19.

Pauchard, A., & Shea, K. (2006). Integrating the study of non-native plant invasions across spatial scales. Biological Invasions, 8, 399–413.

Perelman, S. B., Chaneton, E. J., Batista, W. B., Burkart, S. E., & León, R. J. C. (2007). Habitat stress, species pool size and biotic resistance influence exotic plant richness in the Flooding Pampa grasslands. Journal of Ecology, 95, 662–673.

Perry, L., Cronin, S., & Paschke, M. (2009). Native cover crops suppress exotic annuals and favor native perennials in a greenhouse competition experiment. Plant Ecology, 204, 247–259.

Perry, L. G., Galatowitsch, S. M., & Rosen, C. J. (2004). Competitive control of invasive vegetation: A native wetland sedge suppresses Phalaris arundinacea in Carbon-Enriched Soil. Journal of Applied Ecology, 41, 151–162.

Peter, C. R., & Burdick, D. M. (2010). Can plant competition and diversity reduce the growth and survival of exotic Phragmites australis invading a tidal marsh? Estuaries and Coasts, 33, 1225–1236.

Podani, J. (1999). Extending grower’s general coefficient of similarity to ordinal characters. Taxon, 48, 331–340.

Pokorny, M., L., Sheley, R. L., Zabiński, C. A., Engel, R. E., Svejcar, T. J., & Borkowski, J. J. (2005). Plant functional group diversity as a mechanism for invasion resistance. Restoration Ecology, 13, 448–459.

Prieur-Richard, A. H., Lavorel, S., Dos Santos, A., & Grigulis, K. (2002b). Mechanisms of resistance of Mediterranean annual communities to invasion by Conyza bonariensis: Effects of native functional composition. Oikos, 99, 338–346.

Prieur-Richard, A. H., Lavorel, S., Grigulis, K., & Dos Santos, A. (2000). Plant community diversity and invasibility by exotics: Invasion of Mediterranean old fields by Conyza bonariensis and Conyza canadensis. Ecology Letters, 3, 412–422.

Prieur-Richard, A.-H., Lavorel, S., Linhart, Y., & Dos Santos, A. (2002a). Plant diversity, herbivory and resistance of a plant community to invasion in Mediterranean annual communities. Oecologia, 130, 96–104.

Quinn, L. D., & Holt, J. S. (2009). Restoration for resistance to invasion by giant reed (Arundo donax). Invasive Plant Science and Management, 2, 279–291.

R Development Core Team (2015). R: A language and environment for statistical computing. Vienna, Austria: R Foundation for Statistical Computing.
Von Holle, B., & Simberloff, D. (2004). Testing Fox’s assembly rule: Does plant invasion depend on recipient community structure? Oikos, 105, 551–563.

Wang, J., Ge, Y., Zhang, C. B., Bai, Y., & Du, Z. K. (2013). Dominant functional group effects on the invasion resistance at different resource levels. PLoS ONE, 8, e77220.

Weigelt, A., & Jolliffe, P. (2003). Indices of plant competition. Journal of Ecology, 91, 707–720.

Welker, E., Van Der Werf, A., Thompson, K., Roderick, M., Garnier, E., & Eriksson, O. (1999). Challenging theophrastus: A common core list of plant traits for functional ecology. Journal of Vegetation Science, 10, 609–620.

Weltzin, J. F., Muth, N. Z., Von Holle, B., & Cole, P. G. (2003). Genetic diversity and invasibility: A test using a model system with a novel experimental design. Oikos, 103, 505–518.

Wilsey, B. J., Daneshgar, P. P., & Polley, H. W. (2011). Biodiversity, phenology and temporal niche differences between native- and novel exotic-dominated grasslands. Perspectives in Plant Ecology, Evolution and Systematics, 13, 265–276.

Wolkovich, E. M., & Cleland, E. E. (2010). The phenology of plant invasions: A community ecology perspective. Frontiers in Ecology and the Environment, 9, 287–294.

Zedler, J. (2005). Ecological restoration: Guidance from theory. San Francisco Estuary and Watershed Science, 3, 1–31.

SUPPORTING INFORMATION

Additional Supporting Information may be found online in the supporting information tab for this article.

How to cite this article: Byun C, Lee EJ. Ecological application of biotic resistance to control the invasion of an invasive plant, Ageratina altissima. Ecol Evol. 2017;7:2181–2192. https://doi.org/10.1002/ece3.2799