Dominant Functional Group Effects on the Invasion Resistance at Different Resource Levels

Jiang Wang1, Yuan Ge2*, Chong B. Zhang1, Yi Bai1, Zhao K. Du1

1 School of Life Science, Taizhou University, Linhai, China, 2 Bren School of Environmental Science and Management/Earth Research Institute, University of California Santa Barbara, Santa Barbara, California, United States of America

Abstract

Background: Functional group composition may affect invasion in two ways the effect of abundance, i.e. dominance of functional group; and the effect of traits, i.e. identity of functional groups. However, few studies have focused on the role of abundance of functional group on invasion resistance. Moreover, how resource availability influences the role of the dominant functional group in invasion resistance is even less understood.

Methodology/Principal Findings: In this experiment, we established experimental pots using four different functional groups (annual grass, perennial grass, deciduous shrub or arbor and evergreen shrub or arbor), and the dominant functional group was manipulated. These experimental pots were respectively constructed at different soil nitrogen levels (control and fertilized). After one year of growth, we added seeds of 20 different species (five species per functional group) to the experimental pots. Fertilization significantly increased the overall invasion success, while dominant functional group had little effect on overall invasion success. When invaders were grouped into functional groups, invaders generally had lower success in pots dominated by the same functional group in the control pots. However, individual invaders of the same functional group exhibited different invasion patterns. Fertilization generally increased success of invaders in pots dominated by the same than by another functional group. However, fertilization led to great differences for individual invaders.

Conclusions/Significance: The results showed that the dominant functional group, independent of functional group identity, had a significant effect on the composition of invaders. We suggest that the limiting similarity hypothesis may be applicable at the functional group level, and limiting similarity may have a limited role for individual invaders as shown by the inconsistent effects of dominant functional group and fertilization.

Introduction

Determining the factors that control the invasion of exotic species is important in invasion biology [1,2]. Recent studies suggest that invasibility of plant communities can be influenced by a number of factors, including traits of invaders [1,3–5], traits of dominant species [6–8] and resource availability [9,10]. However, few studies have considered the interactions of these factors in determining effects on invasion [11,12].

Functional group composition of the resident community has been proved critical to community resistance to invasion [13–16]. The limiting similarity hypothesis predicts that resident species most functionally similar to the invader should provide greater invasion resistance because of a greater overlap in resource use [14,17]. Consequently, functional group composition should be a good predictor of invasion resistance [18]. However, prior studies have either supported [19–23] or contradicted [8,24,25] the limiting similarity hypothesis.

Functional group composition most likely affects invasion in two major ways: the effect of abundance, i.e. dominance of functional group; and the effect of traits, i.e. identity of functional groups [26]. Many previous studies focused on the effect of functional group identity on invasion [8,14,18,27]. However, dominant functional groups in communities are known to strongly regulate community structure and ecosystem function [13,15,16]. Consequently, it is most likely that relative abundance, rather than presence, of certain functional groups may be a more powerful predictor of invasibility [8,14]. At present, the relative roles of dominance and identity of functional group in invasion resistance remain little understood [26].

Evidence in support of limiting similarity is mainly from artificially established not natural communities [28]. Abiotic factors, such as variations in nutrient availability, disturbance and propagule pressure, which were controlled in these artificially established communities, were postulated as the reason for the mixed results [28]. However, how abiotic factors influence the role of limiting similarity remains little known. Davis and Pelsor [29]
found increased resource availability tended to reduce competition intensity between resident species and invaders. Consistent with their result, many prior studies showed that high nutrient availability promoted community invasibility [29–31]. Consequently, we postulate that competitive exclusion of invaders by functionally similar resident species may be affected by resource availability.

Life form is the long-term adaptation performance of plants to environment, and plants of the same life form should have similar ways and methods of adapting to the environment [32]. In eastern China, many early successional communities established from disturbed plant communities and abandoned agricultural fields are hotspots of invasions in the area. Plants of these communities mainly belong to four life forms: annual grass, perennial grass, deciduous shrub or arbor and evergreen shrub or arbor. The resource use efficiency of these life forms differ significantly [33]. Moreover, the amounts of soil nitrogen in eastern China are consistently increasing due to atmospheric nitrogen deposition [34]. Here we consider how invasibility is influenced by the interactive effects of dominant functional group and fertilization (nitrogen addition). We created experimental communities that differed in dominant functional groups with two soil nitrogen levels, and controlled for functional group richness (four functional groups) and functional group identity. We used a total of 20 invader species: five species from each of four different functional groups (annual grass, perennial grass, deciduous shrub or arbor and evergreen shrub or arbor). We tested whether invading species had lower success in pots dominated by a functionally similar group, independent of functional group identity. We also tested whether the effects of the dominant functional group on invaders changed with resource availability and what mechanisms led to such change.

Materials and Methods

Ethics Statement

No specific permissions were required for this research. The pot experiment was conducted in the campus of Taizhou University, where some of the authors are staff members. The site of Taizhou University used for conducting the study is the experimental center for the authors. Consequently, use of this site did not require permission. The exotic species used in this study were either natives or common exotics with established local populations in the mountain area around Linhaim city where Taizhou University is located. Consequently, all plant species used in this study are not endangered or protected.

Experiment Design

We conducted an outdoor pot experiment at the campus of Taizhou University (28°35′12″N, 120°47′91″E) from June 2008 to May 2011. The region has a subtropical climate with an annual rainfall of 1800 mm, occurring mostly during spring and summer. The annual average temperature is 19.5°C. Photosynthetically active radiation (PAR, 9:00–15:00) was in the range of 600–1000 μmol m–2 s–1 at the experimental site. We established experimental pots using four different functional groups, each with a different number of transplanted seedlings of different species. To test whether the resident and invader species, the seedlings of other spontaneously colonizing species were removed monthly. However, there were still seedlings of other species that spontaneously colonized the control and fertilized pots when the success of invasion was measured, which may be due to germination between hand-weeding operations (Table S1 in File S1). However, the coverage of these species only represented a very small proportion of total coverage of invader species (10.4 and 6.2% in the control and fertilized pots of 2010, respectively, and correspondingly 11.8 and 8.9% in 2011), and were not included in the data analysis. In May of 2010 and 2011, we measured the coverage and seedling numbers of invader species in each pot. To measure coverage, we overlaid a 100-cell grid (1 cm² per cell in a 10×10 grid) over each pot and tallied the number of grid cells occupied by invader species.

A PAR ceptometer (GLZ-C, Zhejiang Top Instrument Co., Ltd) was used to measure light availability in the control and fertilized pots. Two months after the seed addition of invader species, four points of each pot were randomly determined to
measure the light transmittance percentage every month from August 2009 to May 2011 at midday on cloud-free days (Figure S1 in File S1). The PAR above the community canopy and the PAR at ground level were measured at the same point. The average

| Resident species | Dominant functional group treatment | AG | PG | D | E |
|------------------|------------------------------------|----|----|---|---|
| AG | Perilla frutescens (Linn.) | 10 | 2 | 2 | 2 |
| | Britt and Mazus pumilus (Burm.f.) Van Steenis | 10 | 2 | 2 | 2 |
| PG | Inula japonica Thunb | 2 | 10 | 2 | 2 |
| | Plantago asiatica Linn | 2 | 10 | 2 | 2 |
| D | Grewia biloba G. Don var. parviflora (Bunge) H.-M | 2 | 2 | 10 | 2 |
| | Koelreuteria integrifoliola Merr | 2 | 2 | 10 | 2 |
| E | Cinnamomum camphora (L.) Presl | 2 | 2 | 2 | 10 |
| | Urena procumbens Linn | 2 | 2 | 2 | 10 |

Footnotes: AG: annual grass; PG: perennial grass; D: deciduous shrub or arbor; E: evergreen shrub or arbor.

doi:10.1371/journal.pone.0077220.t001

| Life form | Invader species | Abbreviation | Family |
|-----------|-----------------|--------------|--------|
| Annual grass (AG) | Celosia argentea Linn | CA | Amaranthaceae |
| | Corchoropsis tomentosa (Thunb.) Makino | CT | Tiliaceae |
| | Cerastium glomeratum Thuill | CG | Caryophyllaceae |
| | Bidens bipinnata Linn | BB | Compositae |
| | Triumfetta annua Linn | TA | Tiliaceae |
| Perennial grass (PG) | Tubocapsicum anomalum (Franch. et Sav.) Makino | TAM | Solanaceae |
| | Oxalis corniculata Linn | OC | Oxalidaceae |
| | Reynoutria japonica Houtt | RJ | Polygonaceae |
| | Polygonum perfoliatum Linn | PP | Polygonaceae |
| | Gahnia tristis Nees | GT | Cyperaceae |
| Deciduous shrub or arbor (D) | Rhus chinensis Mill | RC | Anacardiaceae |
| | Vitex negundo var. cannabifolia (Sieb.et Zucc.) Hand-Mazz | VN | Verbenaceae |
| | Litsea cubeba (Lour.) Pers | LC | Lauraceae |
| | Hibiscus mutabilis Linn | HM | Malvaceae |
| | Euscaphis japonica (Thunb.) Kanitz | EJ | Staphyleaceae |
| Evergreen shrub or arbor (E) | Pittosporum tobira (Thunb.) Ait | PT | Pittosporaceae |
| | Syzygium buxifolium Hook. et Am | SB | Myrtaceae |
| | Photinia serrulata Lindl. var. Serrulata | PS | Rosaceae |
| | Elaeagnus obovata Li | EO | Elaeagnaceae |
| | Nandina domestica Thunb | ND | Berberidaceae |

Table 1. The number of transplanted seedlings in different dominant functional group treatments.

Table 2. The sown invader species in the experimental pots.

doi:10.1371/journal.pone.0077220.t002
Statistical Analyses

We used indicator species analysis [8,35,36] to determine which invader species had the highest coverage and seedling numbers in pots dominated by which functional group. Indicator species analysis involved calculating a metric (indicator value, IV) that summarized both the relative abundance and the frequency of each invader species in each dominant functional group treatment. First, the mean abundance of invader species in pots dominated by a certain functional group was calculated:

\[
x_{kj} = \frac{\sum_{i=1}^{n_k} a_{ijk}}{n_k}
\]

where \( a_{ijk} \) = abundance of invader species \( j \) in pot \( i \) dominated by functional group \( k \), and \( n_k \) = number of pots dominated by functional group \( k \).

Then the relative abundance \( RA_{kj} \) of invader species \( j \) in pots dominated by functional group \( k \) was calculated:

\[
RA_{kj} = \frac{x_{kj}}{\sum_{k=1}^{g} x_{kj}}
\]

where \( g \) = total number functional groups.

Then relative frequency \( RF_{kj} \) of invader species \( j \) in pots dominated by functional group \( k \) was calculated:

\[
RF_{kj} = \frac{\sum_{i=1}^{n_k} b_{ijk}}{n_k}
\]

where \( b_{ijk} \) = the presence (1) or absence (0) of invader species \( j \) in pot \( i \) dominated by functional group \( k \).

Then \( IV \) was calculated:

\[
IV_{kj} = RA_{kj} \times RF_{kj} \times 100
\]

\( IV \) ranges from 0 (no presence of an invader species in a given dominant functional group treatment) to 100 (perfect indication). A perfect indication score (100) means that an invader species occurred only in a given dominant functional group treatment, and always in that treatment. Data of control and unfertilized pots were respectively analyzed. The observed \( IV \) was compared with an expected \( IV \) calculated using Monte Carlo randomizations of the data, where species frequency and abundance data from each pot were randomly assigned to a group/treatment 1000 times. The null hypothesis was that the observed \( IV \) was not larger than would be expected by chance (as calculated by the randomization procedure). The indicator species analyses were performed in PCORD 4.25 [37]. The \( IV \) of each invader species were analyzed by one-way ANOVA to determine whether the invader species had the lowest invasion success in pots dominated by the same functional group.

The effect of fertilization on the invader species was explored by calculating the relative effect index (REI):

\[
REI = (value_{fertilized} - value_{control}) / value_{control}
\]

where \( value_{fertilized} \) is the coverage (seedling number) of invader species in the corresponding fertilized pots and \( value_{control} \) is the coverage (seedling number) of invader species in the corresponding control pots. All values for the control pots were plused 1 in order to guarantee computation.

Effects of fertilization and dominant functional group on the total coverage and seedling number of invaders, and on the coverage and seedling number of individual invaders, were evaluated using two-way ANOVA for years 2010 and 2011 separately. Effects of fertilization and dominant functional group on the coverage and seedling number of invaders of the same functional group were also evaluated using two-way ANOVA for 2010 and 2011 separately, and LSD tests detected differences in dominant functional group treatment means. The differences of \( IV \) and REI of invader species between pots dominated by the same functional group and pots dominated by another functional group were evaluated using independent-sample t-tests for the control and fertilized pots separately. We used ANCOVA to determine how dominant functional group, light availability, other invaders of the same functional group and invaders of other functional group influenced the coverage and seedling number of individual invader species.

Results

Experimental fertilization significantly increased the total coverage and seedling number of invaders in 2010, with these increases persisted in 2011 (Table 3, Figure 1). However, for pots dominated by D and E, fertilization did not significantly increase the total coverage and seedling number of invaders in 2011. Dominant functional group had no significant effect on the total coverage and seedling number of invaders in 2010. However, invaders had more coverage and seedling numbers in pots dominated by AG and PG than those dominated by D and E in 2011. Moreover, the interaction of fertilization and dominant functional group also had a significant effect on total coverage and seedling number of invaders in 2011.

When invaders were grouped into functional groups there was a significant association between invaders and dominant functional group in control pots (Figure 2). Consistent with the hypothesis of limiting similarity, invaders had the lowest coverage and seedling number in control pots dominated by the same functional group. However, the limiting similarity disappeared in fertilized pots. Moreover, all four functional groups of invaders had lower coverage and seedling numbers in pots dominated by D and E than those dominated by AG and PG in 2011.

Although limiting similarity applied at functional group level in control pots, individual invaders of the same functional group did not always match this pattern in control pots (Table 4). For example, CG had the highest coverage in control pots dominated by PG but did not have the lowest coverage in control pots dominated by the same functional group. However, compared with fertilized pots, there were still more individual invaders with the least coverage and seedling numbers in control pots dominated by the same functional group. In general, invaders had lower indicator values in control pots dominated by the same than by another functional group (Figure 3, coverage: \( t_{2010} = -3.369,\)
df = 78, P = 0.001; \( t_{2011} = -4.234, \ df = 78, \ P < 0.001 \); seedling number: \( t_{2010} = -4.918, \ df = 78, \ P < 0.001 \); \( t_{2011} = -4.259, \ df = 78, \ P < 0.001 \). Similar to the functional group level, most individual invader species had the highest coverage in fertilized pots dominated by AG or PG in 2011, while nearly all species showed no differences in seedling numbers among pots dominated by a different functional group.

Two-way ANOVA showed that the effects of fertilization on coverage and seedling number exhibited great differences among individual invader species, and had a stronger influence than the dominant functional group (Tables S2 and S3 in File S1). However, invaders generally had higher REI in pots dominated by the same than by another functional group (Figure 4, coverage: \( t_{2010} = 4.729, \ df = 478, \ P < 0.001 \); \( t_{2011} = 3.190, \ df = 478, \ P = 0.002 \); seedling number: \( t_{2010} = 6.601, \ df = 478, \ P < 0.001 \); \( t_{2011} = 5.288, \ df = 478, \ P < 0.001 \). ANCOVA showed that the REI for coverage of many individual invader species was also affected by light availability and other invaders of the same functional group (Table S4 in File S1), while they nearly had no significant effect on REI for seedling numbers of all invader species (Table S5 in File S1).

### Discussion

The results showed that fertilization significantly reduced the invasion resistance of experimental plant communities to total invaders. However, in contrast to expectations, the dominant functional group had little influence on the invasion resistance of...
Figure 2. The coverage and seedling number of different functional groups of invaders in the pots dominated by different dominant functional groups in 2010 and 2011. Dominant functional group treatments: AG – annual grass dominated pots, PG – perennial grass dominated pots, D – deciduous shrub or arbor dominated pots and E – evergreen shrub or arbor dominated pots. AG_{invasive species} – the invader belong to annual grass. PG_{invasive species} – the invader belong to perennial grass. D_{invasive species} – the invader belong to deciduous shrub or arbor. E_{invasive species} – the invader belong to evergreen shrub or arbor. The legends are as given in Figure 1. Arrows (↓) indicate that the coverage and seedling number of invaders had lower values in the pots dominated by same functional group than those dominated by other functional group. doi:10.1371/journal.pone.0077220.g002

Figure 3. The indicator value (IV) of invaders for coverage (A) and seedling number (B) in the pots dominated by same functional group and the pots dominated by other functional group in 2010 and 2011. Higher indicator values represent higher colonization success. *indicate significant difference between the pots dominated by same functional group and the pots dominated by other functional group. doi:10.1371/journal.pone.0077220.g003
total invaders in 2010. In 2011, mostly likely owing to lower light transmittance in pots dominated by D and E (F<sub>1,20</sub> = 137.64, P<0.001, data not shown), they had higher invasion resistance than pots dominated by AG and PG. Prior studies have shown that abiotic factors (e.g. light, nitrogen availability and soil moisture) regulated invasion success at the seedling establishment stage [38–

| Coverage     | 2010       | 2011       | Number of seedling | 2010       | 2011       |
|--------------|------------|------------|--------------------|------------|------------|
| Control      | Fertilized | Control    | Fertilized         | Control    | Fertilized |
| CA           | D(34.5**)  | ns         | D(30.3*)           | PG(29.9**) | ns         |
| CT           | E(31.8*)   | ns         | ns                 | AG(27.6*)  | ns         |
| CG           | PG(27.2*)  | ns         | PG(26.9*)          | AG(27.1*)  | ns         |
| BB           | E(90.3**)  | ns         | D(34.4**)          | PG(28.1**) | D(37.9**)  |
| TA           | AG(28.4*)  | ns         | AG(28.7**)         | AG(30.8**) | ns         |
| TAM          | PG(50.5**) | ns         | PG(47.6**)         | ns         | PG(54.1**) |
| OC           | AG(27.7*)  | ns         | PG(27.6*)          | ns         | ns         |
| RU           | AG(31.5*)  | ns         | ns                 | ns         | ns         |
| PP           | E(31.4**)  | ns         | AG(30.6*)          | ns         | ns         |
| GT           | D(34.2*)   | E(26.4**)  | D(33.7**)          | AG(32**)   | D(35.9*)   |
| RC           | E(32.6*)   | ns         | AG(33.8**)         | AG(32.2**) | AG(34.6*)  |
| VN           | D(26.8*)   | ns         | PG(27*)            | PG(33.8*)  | ns         |
| LC           | E(29.6*)   | AG(26.4**) | PG(31.4**)         | AG(38.1**) | ns         |
| HM           | D(27.6**)  | ns         | ns                 | AG(47.9**) | ns         |
| EJ           | AG(37.7**) | ns         | AG(36.3**)         | AG(40.3**) | ns         |
| PT           | ns         | D(29.1*)   | AG(28.2*)          | ns         | D(31.6*)   |
| SB           | D(28.8*)   | ns         | AG(30.3**)         | ns         | ns         |
| PS           | ns         | ns         | AG(28.1*)          | D(31.3*)   | ns         |
| EO           | ns         | ns         | ns                 | ns         | ns         |
| ND           | ns         | AG(32.9**) | ns                 | AG(50.2**) | ns         |

Significant relationships between the coverage and seedling number of each invader and certain dominant functional group treatment are shown for having the highest coverage and seedling number in the treatment. Numbers in parentheses are the indicator values (IV). Significance values are calculated based on 1000 randomizations in a Monte Carlo simulation, with *P<0.05, **P<0.01 and ns not significant (P>0.05). Species abbreviations are as given in Table 2. Arrows (↓) indicate that the coverage and seedling number of invaders had lower values in the pots dominated by the same than by another functional group, which indicates limiting similarity.
Studies of invasion usually concern non-native invaders colonizing communities with which they have had no previous interactions [27]; however, native species were used as invaders in the present study. Despite somewhat different focuses, the ecological principles (e.g. niche limitation and competition for resources) underlying both types of studies are the same [27]. Thus, experiments using either native or non-native species as invader species are both pertinent to explaining which traits characterize the invasibility of communities. Although we only examined two years of establishment of invader species, seedling establishment is a key life-stage for invaders [43–45]. Understanding the effect of initial environmental ‘filters’, the resident dominant functional group and resource availability on invasion may aid in the control of natural or human-induced invasions.

**Supporting Information**

**File S1** Contains: Table S1 The spontaneously colonized species in experimental pots. **Table S2** Results of two-way ANOVA for the effects of fertilization and dominant functional group on the coverage of each invader. Significant variables ($P<0.05$) are in bold. Arrows indicate significant increase (↑) or decrease (↓) of coverage of invader with fertilization. The values out of and in the bracket is the results of 2010 and 2011 respectively. **Table S3** Results of two-way ANOVA for the effects of fertilization and dominant functional group on the seedling number of each invader. Significant variables ($P<0.05$) are in bold. Arrows indicate significant increase (↑) or decrease (↓) of seedling number of invader with fertilization. The values out of and in the bracket is the results of 2010 and 2011 respectively. **Table S4** Results for ANCOVA of effects of dominant functional group on the relative effect index (REI) of invader coverage with the change of light availability, the coverage change of invaders of same functional group and the coverage change of invaders of other functional group as covariate. Significant variables ($P<0.05$) are in bold. The values out of and in the bracket is the results of 2010 and 2011 respectively. **Table S5** Results for ANCOVA of effects of dominant functional group on the relative effect index (REI) of invader seedling number with the change of light availability, the seedling number change of invaders of same functional group and the seedling number change of invaders of other functional group as covariate. Significant variables ($P<0.05$) are in bold. The values out of and in the bracket is the results of 2010 and 2011 respectively. **Figure S1** The changes of light transmittance percentage in different dominant functional group treatments. Dominant functional group treatments: A) annual grass dominated pots, B) perennial grass dominated pots, C) deciduous shrub or arbor dominated pots and D) evergreen shrub or arbor dominated pots. The average value of six replicated pots was used. Light transmittance percentage was measured every month at midday on cloud free days, and was measured 20 times in total (2009-Aug to 2010-May and 2010-Aug to 2011-May).

**Acknowledgments**

We thank Mark Nachison, Esq., for English assistance and two anonymous referees for their helpful comments.

**Author Contributions**

Conceived and designed the experiments: JW YG. Performed the experiments: CBZ YB ZKD. Analyzed the data: JW. Wrote the paper: JW YG.
References

1. Milbau A, Nips J (2004) The role of species traits (invasiveness) and ecosystem characteristics (invasibility) in grassland invasions: a framework. Weed Technol 18: 1301–1304.

2. Emery SM, Gross KL (2007) Dominant species identity, not community evenness, regulates invasion in experimental grassland plant communities. Ecology 88: 854–964.

3. Hamilton MA, Murray BR, Cadotte MW, How GC, Baker AC, et al. (2005) Life-history correlates of plant invasiveness at regional and continental scales. Ecol Lett 8: 1066–1074.

4. Roscher C, Beller H, Oelmann Y, Engels C, Wilcke W, et al. (2009) Resources, recruitment limitation and invader species identity determine pattern of spontaneous invasion in experimental grasslands. J Ecol 97: 32–47.

5. Drenovský RE, Khasanova A, James JJ (2012) Trait convergence and plasticity among native and invasive species in resource-poor environments. Am J Bot 99: 629–639.

6. Smith MD, Wilcox JC, Kelly T, Knapp AK (2004) Beyond species: functional diversity in riparian and upland plant communities. Ecol Monogr 64: 241–249.

7. Hooper DU, Dukes JS (2006) Dominant species identity regulates invasibility of old-field plant communities. Oikos 115: 549–558.

8. Emery SM (2007) Limiting similarity between invaders and dominant species in herbaceous plant communities? J Ecol 95: 1027–1035.

9. Incera M, Olabarria C, Troncoso JS, López J (2009) Response of the invader Senecio inaequidens and Conyza bonariensis to 7 years of plant functional group removals. J Veg Sci 20: 503–515.

10. Li W, Henry M, Stevens H (2012) Fluctuating resource availability increases invasibility in microbial microcosms. Oikos 121: 435–441.

11. Maron JL, Marler M (2007) Native plant diversity resists invasion at both low and high resource levels. Ecology 88: 2651–2661.

12. Maron JL, Marler M (2008) Field-based competitive impacts between invaders and natives at varying resource supply. J Ecol 96: 1187–1197.

13. Hooper DU, Dukes JS (2004) Overyielding among plant functional groups in a long-term experiment. Ecol Lett 7: 95–105.

14. Hooper DU, Dukes JS (2010) Functional composition controls invasion success in a California serpentine grassland. J Ecol 98: 764–772.

15. Cadotte MW, Casrückla K, Nisbet N (2011) Beyond species: functional diversity and the maintenance of ecological processes and services. J Appl Ecol 48: 1079–1087.

16. McLaren JB, Turkington R (2011) Biomass compensation and plant responses to 7 years of plant functional group removals. J Veg Sci 22: 565–575.

17. Funk JL, Cleland EE, Suding KN, Zavaleta ES (2008) Restoration through reassembly: plant traits and invasion resistance. Trends Ecol Evol 23: 695–703.

18. Byun C, de Bois S, Brison J (2013) Plant functional group identity and diversity determine biotic resistance to invasion by an exotic grass. J Ecol 101: 129–139.

19. Dukes JS (2001) Biodiversity and invasibility in grassland microcosms. Oecologia 126: 563–568.

20. Dukes JS (2002) Species composition and diversity affect grassland susceptibility and response to invasion. Ecol Appl 12: 602–617.

21. Priœur-Richard AH, Lavorel S, Dos Santos A, Grégois K (2002) Mechanisms of resistance of Mediterranean annual communities to invasion by Cynara cardunculus: effects of native functional composition. Oikos 99: 339–346.

22. Fargione JE, Brown CS, Tilman D (2003) Community assembly and invasion: an experimental test of neutral versus niche processes. PNAS 100: 8916–8920.

23. Fargione JE, Tilman D (2005) Diversity decreases invasion via both sampling and complementarity effects. Ecol Lett 8: 604–611.

24. Von Holle B (2003) Biotic resistance to invader establishment of a southern Appalachian plant community is determined by environmental conditions. J Ecol 91: 16–26.

25. Thompson K, Petchey OL, Askew AP, Dunnett NP, Beckerman AP, et al. (2010) Little evidence for limiting similarity in a long-term study of a roadside plant community. J Ecol 98: 480–487.

26. Longo G, Szüller TG, Garbaldi LA, Tognetti PM, Chaanon EJ (2013) Functional group dominance and identity effects influence the magnitude of grassland invasion. J Ecol (In press).

27. Symstad AJ (2006) A test of the effects of functional group richness and composition on grassland invasibility. Ecology 81: 99–109.

28. Price JN, Paërl M (2013) Can limiting similarity increase invasion resistance? A meta-analysis of experimental studies. Oikos 122: 649–656.

29. Davis MA, Peloš M (2001) Experimental support for a resource-based mechanistic model of invasibility. Ecol Lett 4: 421–428.

30. Gross KL, Mittelbach GG, Reynolds HL (2003) Grassland invasibility and diversity: responses to nutrients, seed input, and disturbance. Ecology 84: 476–486.

31. Leininger MR, Thomson VP (2005) Experimental evidence for the effects of additional water, nutrients and physical disturbance on invasive plants in low fertility Hawkesbury Sandstone soils, Sydney. Aust J Ecol 39: 38–49.

32. Shekhar RB, Mallik AU (2010) Disturbance effects on species diversity and functional diversity in riparian and upland plant communities. Ecology 91: 28–35.

33. Tan WB, Wang GA, Han JM, Liu M, Zhou LP, et al. (2009) δ13C and water-use efficiency indicated by δ13C of different plant functional groups on Changbai Mountains, Northeast China. Chinese Sci Bull 54: 1759–1764.

34. Yang R, Hayashi K, Zhu B, Li F, Yan X (2010) Atmospheric NH3 and NO2 concentration and nitrogen deposition in an agricultural catchment of Eastern China. Science of the Total Environment 408: 4624–4632.

35. Dufrène M, Legendre P (1997) Species assemblages and indicator species: the need for a flexible asymmetrical approach. Ecol Monogr 67: 345–366.

36. McCune B, Grace JB, Urban DL (2002) Analysis of Ecological Communities. MJM Software Design, Gleneden Beach, OR.

37. McCune B, Mefford MJ (1999) PC-ORD: Multivariate Analysis of Ecological Data. MJM Software, Gleneden Beach, OR.

38. Foster BL, Smith VH, Dickson L, Hilderbrand T (2002) Invasion and compositional stability in a grassland community: relationships to diversity and extrinsic factors. Oikos 99: 300–307.

39. Priœur-Richard AH, Lavorel S, Linhart YB, Dos Santos A (2002) Plant diversity, herbivory and resistance of a plant community to invasion in Mediterranean annual communities. Oecologia 130: 96–104.

40. Garcia-Serrano H, Escarre J, Sans FX (2004) Factors that limit the emergence of woody and herbaceous perennials. J Ecol 93: 38–49.

41. Petchey OL, Gaston KJ (2006) Functional diversity: back to basics and looking forward. Ecol Lett 9: 741–758.

42. Bruno JF, Stachowicz JJ, Bertness MD (2003) Inclusion of facilitation into ecological theory. Trends Ecol Evol 18: 119–125.

43. Silvertown J, Franco M, Pisanty I (1993) Comparative plant demography-relative importance of life-cycle components to the finite range of increase in woody and herbaceous perennials. J Ecol 81: 463–476.

44. Shea K, Kelly D (1998) Estimating biocontrol agent impact with matrix models: Cardus marianus in New Zealand. Ecol Appl 8: 824–832.

45. Parker IM (2000) Invasion dynamics of Cytisus scoparius and Senecio inaequidens and Senecio peregrinus and the native Senecio malacophytes in Mediterranean climate. Can J Bot 82: 1346–1355.

46. Petchey OL, Gaston KJ (2006) Functional diversity: back to basics and looking forward. Ecol Lett 9: 741–758.

47. Bruno JF, Stachowicz JJ, Bertness MD (2003) Inclusion of facilitation into ecological theory. Trends Ecol Evol 18: 119–125.

48. Silvertown J, Franco M, Pisanty I (1993) Comparative plant demography-relative importance of life-cycle components to the finite range of increase in woody and herbaceous perennials. J Ecol 81: 463–476.

49. Shea K, Kelly D (1998) Estimating biocontrol agent impact with matrix models: Cardus marianus in New Zealand. Ecol Appl 8: 824–832.