The role of diversity and functional traits of species in community invasibility

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Abstract. The invasion of exotic species into assemblages of native plants is a pervasive and widespread phenomenon. Many theoretical and observational studies suggest that diverse communities are more resistant to invasion by exotic species than less diverse ones. However, experimental results do not always support such a relationship. Therefore, the hypothesis of diversity-community invasibility is still a focus of controversy in the field of invasion ecology. In this study, we established and manipulated communities with different species diversity and different species functional groups (16 species belong to C_3, C_4, forbs and legumes, respectively) to test Elton's hypothesis and other relevant hypotheses by studying the process of invasion. Alligator weed (*Alternanthera philoxeroides*) was chosen as the invader. We found that the correlation between the decrement of extractable soil nitrogen and biomass of alligator weed was not significant, and that species diversity, independent of functional groups diversity, did not show a significant correlation with invasibility. However, the communities with higher functional groups diversity significantly reduced the biomass of alligator weed by decreasing its resource opportunity. Functional traits of species also influenced the success of the invasion. *Alternanthera sessilis*, in the same morphological and functional group as alligator weed, was significantly resistant to alligator weed invasion. Because community invasibility is influenced by many factors and interactions among them, the pattern and mechanisms of community invasibility are likely to be far subtler than we found in this study. More careful manipulated experiments coupled with theoretical modeling studies are essential steps to a more profound understanding of community invasibility.

Keywords: Alligator weed; Community; Diversity; Functional groups; Invasibility; Invasion.

Introduction

Biological invasions are important components of human-caused global environmental change (Vitousek et al., 1997; Evans et al., 2001). They profoundly affect biodiversity, ecosystem function, resource availability, human health, and economic sustainability (Mack et al., 2000; Alvarez and Cushman, 2002; Dukes, 2002; Stachowicz et al., 2002) and have become pervasive and costly environmental problems (Vitousek et al., 1996). Individual nations and international organizations have responded to this threat with various workshops, conferences, and research initiatives designed to further our understanding of what the properties of certain species and communities are that allow them to resist invasion (Reichard and Hamilton, 1997; Tilman, 1997; Miller et al., 2002).

The relationship between species diversity and community invasibility has been discussed intensively in recent years. Traditional theory suggests that more diverse communities are less susceptible to invasion than species-poor communities (Elton, 1958; Lodge, 1993). It is commonly hypothesized that diverse communities use resources more completely and have more intense competition than simple communities, and they are thus more resistant to invasion (Levine and D' Antonio, 1999; Dukes, 2001; Brown and Peet, 2003). However, recent studies do not consistently support this hypothesis. Positive or neutral (Wiser et al., 1998; Lonsdale, 1999; Stohlgren et al., 1999; Levine, 2000) and negative (Tilman, 1997; Knops et al., 1999; Naeem et al., 2000; Prieur-Richard et al., 2000) relationships between diversity and invasibility have been reported on different spatial scales.

Resource availability has been suggested to be a key determinant of invasion success (Burke and Grime, 1996; Tilman, 1999). Recent experiments have shown negative relationships between species or functional group richness and resource availability (Tilman et al., 1997; Hooper and Vitousek, 1998; Shea and Chesson, 2002). There are two hypothetical mechanisms for these relationships: diverse communities have greater variety of means of capturing resources than do simple communities, and they use these resources more efficiently, leaving fewer available for invading species and thus reducing invasibility, i.e., resource use complementarity (Knops et al., 1999; Symstad, 2000). Another possible mechanism is that diverse communities have a higher probability of including species most highly competitive for limited resources or have a key role in driving the resistance to invasion increases, i. e., sampling effect (Huston, 1997; Wardle, 2001). In this case, the species composition of a community plays an important role in its invasibility because of the influence of

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individual species on resources. On the basis of the diversity-invasibility hypothesis, Lodge (1993) has suggested that communities are prone to invasions partly for lacking species which are ecologically similar to the invader. A relevant explanation is the niche limitation of community assembly theory, i.e., two species' ecological characteristics are too similar, and one may competitively exclude the other.

Community invasibility is influenced by many factors, including disturbance, herbivory, habitat traits, community structure, species composition, and the invasiveness of the invasive species (such as life history, physiological and morphological traits). Meanwhile, the inconsistency in the scale of observation or manipulated experiment also commonly results in the discrepancy of relationship between diversity and invasibility (Levine, 2000). In addition, the following questions need to be considered: which types of functional groups in manipulated communities should be selected, and should the effects of diversity and other co-varying extrinsic factors be isolated? A lot of studies have been conducted to resolve the debate, including computer modeling, correlation analyses, microcosm studies, or field studies, but few direct experimental tests concern the properties of communities that determine their resistance to invasion. To better understand how diversity influences community invasibility, researchers still have a long way to go to clarify the mechanisms involved.

Biological invasions have happened on a large scale in so many regions of the globe. With this background, there is a need to study the process of invasion and the response of communities on a small scale. In this paper, we report an experimental test on the effects of diversity and the role of functional groups' traits of the species on invasion. We examined the performance of the invasive alligator weed (*Alternanthera philoxeroides*) in experimental plant assemblages in which resident species richness and functional groups richness were directly manipulated. Through integrating and separating species diversity and functional groups diversity in the established plant communities, we analyze the effects of diversity on community invasibility. Functional groups diversity includes two aspects: the number of functional groups (richness) and the types of functional groups (composition). The following questions are explored: (1) Are communities with more species more resistant to invasion? (2) Are communities with more functional groups more resistant to invasion? (3) Is it more difficult for invasive species to invade communities with species functionally similar to them? (4) Are there negative relationships between species or functional group richness and resource availability?

Alligator weed is an invasive weedy species in the Amaranthaceae family native to South America. This species has now invaded South America, North America, Oceania, and Asia. Its potential geographical distribution is perhaps even larger than its current distribution. In China, alligator weed has burst out in the Yangtze River Valley and in South China. This perennial species usually roots on shore or in shallow water or floats on the water surface. Furthermore, the aquatic and terrestrial habitat ecotypes of alligator weed are both common. Observations indicate that alligator weed only flowers and seldom bears. Populations multiply and spread through vegetative propagation. The fragmented roots or stems from parental plants can rapidly develop into complete plants and establish new populations easily, especially through human-mediated dispersal.

Materials and Methods

In our study, we used controlled experiments during the 2001-2002 growing season at our field station (23°8´N, 113°17´E, 8 m elevation) in Guangzhou, Guangdong Province, PRC, where the climate is lower subtropical. Ten circular cement pools were constructed in the field with a diameter of 3 m and height of 40 cm. Between pools, 1 m spaces were maintained. PVC boards, 1.2 m long and 50 cm wide, were used to divide each pool into six equal sectors, and thus each circular cement pool was separated into six equal sectors and one central circular site with a diameter of 60 cm. Each pool (including six sectors and the central circular site) was filled with soil, 30 cm in depth. The soil was made up of organic fertilizer, mud in the pond, and yellow clay in the proportion of 1:1.5:1.5. Sixty sectors were used to allocate sixty resident communities, respectively, and ten central circular sites were used to allocate alligator weed.

Sixteen resident species (Table 1) for constructing communities were selected from alligator weed habitats. They

Table 1. Species and seedling densities in monocultures*.

Species	Functional groups**	Seeding or seedling density (No. seedling or seeds/plot)
Leptochloa chinensis	C_3	96
Axonopus compressus	C_3	48
Erigeron crispus	C_4	48
Zea mays	C_4	32
Arachis hypogaea	L.	48
Phaseolus radiatus	L.	48
Alternanthera sessilis	F.	48
Jussiaea crispus	F.	32
Arthraxon hispidus	C_3	48
Oplismenus undulatifolius	C_3	48
Cyperus rotundus	C_4	48
Cynodon dactylon	C_4	48
Glycine max	L.	48
Mimosa pudica	L.	32
Solanum photeinocarpum	F.	32
Lactuca indica	F.	48

*Not all species were grown monoculture. The seedling densities presented here formed the basis for calculating seedling densities in the poly-cultures. For instance, 8-species communities received seedling of all of the species listed at 1/8 the densities listed here.

** C_3: C_3 graminoids; C_4: C_4 plants; F: forbs; L: legumes.

belonged to four functional groups: C_3 graminoids, C_4 plants, forbs and legumes. These functional groups differ in their morphology, physiology, and spatial-temporal resource use. C_4 plants generally perform better in hot, dry growing conditions while C_3 graminoids grow relatively better under cooler, wetter conditions. Legumes can fix atmospheric nitrogen, and they are more likely to be limited by soil moisture and nutrients other than nitrogen, such as phosphate. Many forbs access resources from greater depths than grasses. These characteristics are also related to temporal and spatial patterns in nutrient utilization. We used these four functional groups to construct different communities designated by the numbers 0, 1, 2, 4. Zero functional group (bare soil) was the control. The details follow.

In this study, we created six treatments : zero species (bare soil), monocultures, three 2-species, one 4-species, one 8-species, and one 16-species combination. Species were chosen at random from the four functional groups for monocultures and species combinations. Eight species (the first 8 in Table 1) were used for monocultures, and two species were drawn from each of the four functional groups. The three 2-species combinations were *Erigeron crispus-Axonopus compressus*, *Alternanthera sessilis-Axonopus compressus*, *Jussiaea crispus-Leptochloa chinensis*. The 4-species combination consisted of *Alternanthera sessilis*, *Arachis hypogaea*, *Erigeron crispus*, and *Axonopus compressus*, which were drawn from the four functional groups at random. The 8-species combination consisted of the first eight species in Table 1, i. e., two species drawn from each of the four functional groups . The 16-species combination contained all 16 species (Table 1). Thus, 4-species, 8-species and 16-species combinations all had the same functional groups diversity (four functional groups). These communities differed in species diversity and functional groups diversity. Each of the six treatments was replicated four times, resulting in a total of 60 treatment replicates.

A species pool, containing all 16 species belonging to the four functional groups, was established beforehand. All seedlings were grown from seeds we collected. Monocultures were established by transplanting the seedlings at densities estimated to allow maximum biomass production for each species (Table 1). In poly-cultures, seedling densities were reduced according to the total number of species in the monocultures. For instance, in eight-species communities, the density of each species was reduced to one-eighth its density in monoculture. The resident species were planted on 20 March, 2002. At the same time, we cultured lots of alligator weed propagula in Hogland nutrient solution in an incubator (KXG-350A, in China) from stems with stipites. One month later, we transplanted twelve alligator weed propagula (with roots 2-2.5 cm) with the same size and performance into the central sites of ten cement pools and covered them with thin layer of soil.

Soil analyses were carried out prior to the experiments to confirm that each community had a homogenous nutrient content. In addition, on 12 March, 14 May, 15 July,

and 15 September, extractable soil N (NO_3^- and NH_4^+) in the surface soil (0~20 cm) was measured, with three samplings from each of the 60 sectors extracted with 0.01 M KCl and analyzed. From the beginning of the experiment to the end of harvest, water content of the soil surface (5-15 cm) was maintained at a level of 16%~21%. Pesticide and rat poison were applied periodically to control the disturbance and damage of herbivores and rodents. Herbicide was applied before transplanting. Non-targeted weeds were removed by hand once a month. By controlling these experimental conditions, the effects of extrinsic factors that might affect biodiversity and invasion were relatively isolated from the effects of species diversity, functional groups diversity, and functional traits of species on community invasibility.

During the growing season, we sampled eight alligator weed seedlings in the 1 and 2-species communities and six alligator weed seedlings in the zero, 4, 8, 16-species communities, respectively, and monitored and measured periodically their demographic (survival to reproduction), vegetative performance (distance of invading, number of the new nodes on the stem with roots once per two days. The observation lasted from 21 April to 21 May). Percent cover of alligator weed was visually estimated before harvesting. The final total biomass (aboveground and underground) was harvested in each community. To study the invasion success of alligator weed, we measured the following indices: distance of dispersion from the border of the central sites to resident communities; number of new nodes on the stems with roots; the final total dry biomass of alligator weed; and the percent cover of alligator weed that invaded the resident communities.

Results

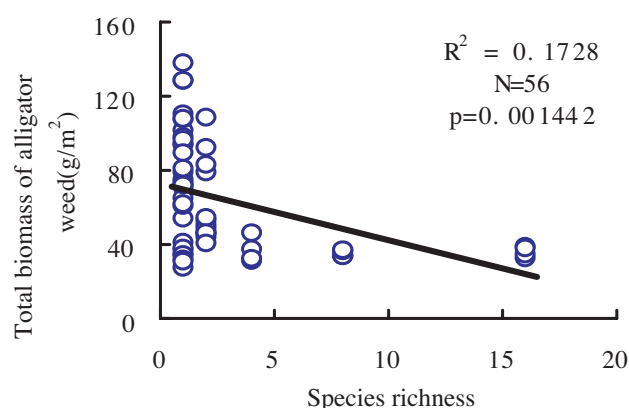### Invasion Process of Alligator Weed in Different Communities

From 21 April to 21 May, we monitored the growth of alligator weed in bare soil, monocultures, and polycultures. Because this growth varies in different communities, we focused on the data from 29 April to 11 May to analyze the distance of dispersion to resident communities and number of the new nodes on the stem with roots. Invasive speed and the number of the new nodes on the stem with roots of the alligator weed were higher in bare soil than in the other communities. There was no significant difference in the dynamic invasion process between monocultures and 2-species communities. The invasion distance of alligator weed in 4-species communities was smaller than those in the control treatment, 1-species or 2-species communities. The invasion distance in 4-, 8-, 16-species treatments showed no significant difference (Figure 1).

A determining factor in whether alligator weed can establish its population in a new habitat is the ability of its regenerating nodes on the stems to sprout new roots to capture or compete for nutrients in the soil. Alligator weed is sensitive to intensity of illumination, and it will grow
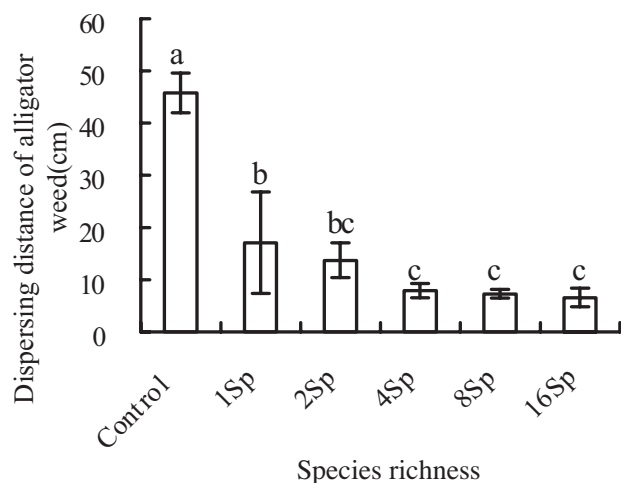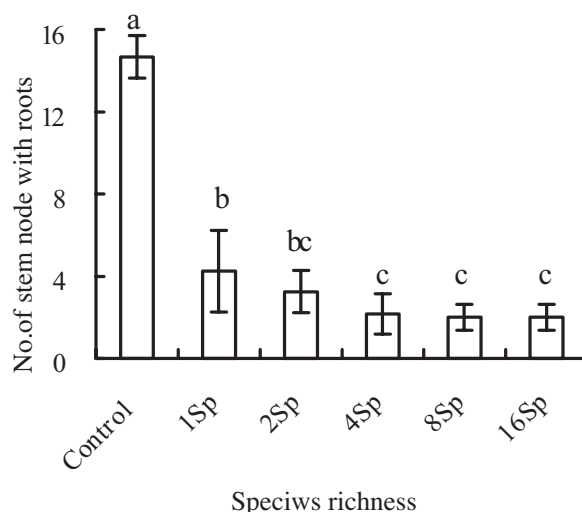
Figure 1. Dispersing distance of alligator weed in different species richness communities (mean±SE, n=6 for control, 4-species, 8-species, and 16-species; n=8 for 1-species and 2-species). Each bar represents the mean ± SE from six observations. Bars that do not share letters are significantly different (p<0.05, ANOVA followed by Turkey's-b post hoc test).

Figure 2. Number of new nodes on the stem with roots of alligator weed across the diversity gradient. (mean±SE, n= for control, 4-species, 8-species, and 16-species; n=8 for 1-species and 2-species). Bars that do not share letters are significantly different (p<0.05, ANOVA followed by Turkey's-b post hoc test).

upwards without illumination. Thus, the number of nodes on the stem with sprouting roots can be taken as a measure of invasion processes and patterns. In Figure 2, the mean number of nodes with sprouting roots in control treatment is 14.67 in 12 days, and the other communities significantly reduced the weed roots sprouting. The number of nodes with sprouting roots in monocultures and 2-species communities showed no difference, but it was a little higher than those of 4-, 8-, and 16-species. In the communities of 4-, 8-, 16-species, the number of nodes with sprouting roots were 2.16, 2.00, and 2.00, respectively, within 12 days. Values were not significantly different (p> 0.05 ANOVA).

Species Diversity and Community Invasibility

At harvest, communities with greater plant species richness had significantly lower total biomass of alligator weed. With the increase of species diversity from zero to 16 species per community, biomass of the alligator weed decreased significantly (Figure 3). This effect of species diversity on community invasibility is confounded with the functional groups diversity. To avoid such confounding effects, we analyzed the effects of species diversity groups with 4, 8, and 16 species that have the same number of functional groups. The results indicate that total biomass of alligator weed was not significantly correlated with the richness of resident species (Figure 4) and ANOVA
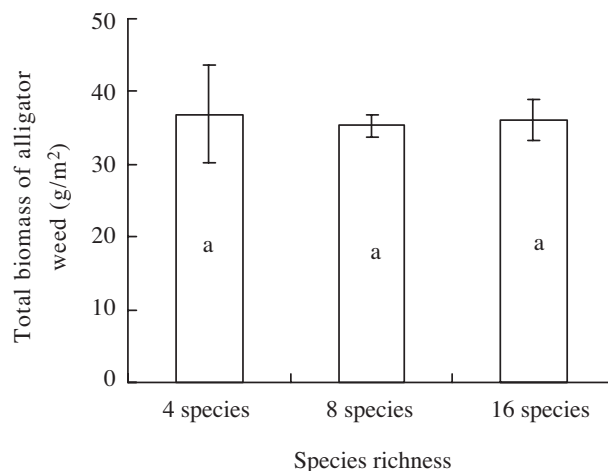

Figure 3. Linear regression of total biomass of alligator weed on community species diversity. Control treatment was not indicated because of the significant difference with the other treatments. Linear equation: y=-3.0505x+72.783.
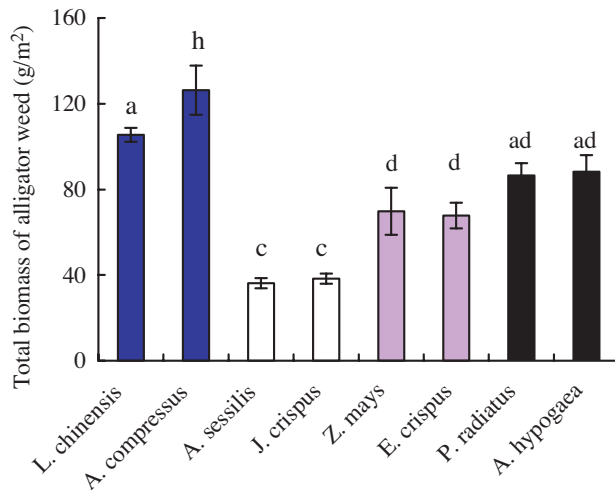

Figure 4. Invasion success across the 4-species, 8-species, and 16-species communities. The number and type of functional groups were consistant in these communities. Bars with the letter are not significantly different (p>0.05).

Figure 5. Invasibility in different types of functional groups. Invasibility is displayed as total biomass of alligator weed in monocultures. Each bar represents the mean of four observations ± SE. Bars that do not share letters are significantly different (p<0.05, ANOVA followed by Turkey's-b post hoc test).
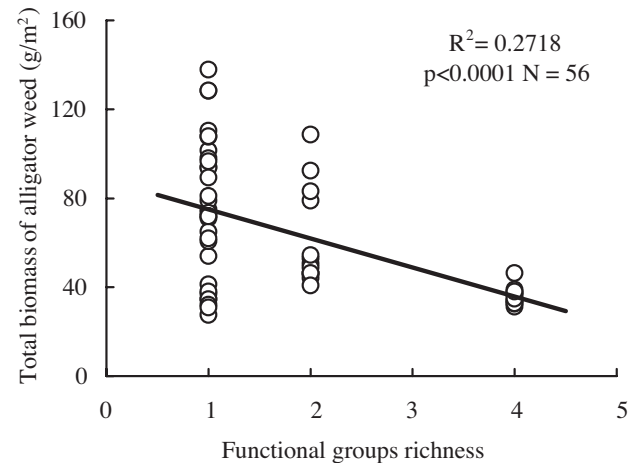
Figure 6. Linear regression of total biomass of alligator weed on community functional groups diversity. Control treatment was not indicated because of the significant difference from the other treatments. Linear equation: y=-13.107x+88.152.

indicates that there was no significant difference among the three levels of species richness (p>0.05).

Identity and Diversity of Functional Groups and Community Invasibility

Functional groups identity (the types of functional groups or composition) influences community invasibility significantly (Table 2 and Figure 5). In the monoculture treatments, communities with C_3 graminoids are significantly more invaded than the other three kinds of communities (Figure 5). Legumes are also subjected to easy invasion, and forbs show the strongest invasion resistance. *Alternanthera sessilis,* which belongs to the same morphological group as alligator weed and has similar requirements for ecological niche, decreases the establishment of alligator weed intensively and shows the strongest resistance to invasion.

Both the total biomass and percent cover of alligator weed are significantly negatively related to functional group diversity in the communities (Table 2, Figure 6 and

Figure 7). Because the monoculture treatment with *A. sessilis* had considerably higher invasion resistance than other monoculture treatments (Figure 5), it may have driven the significant relationship between functional group diversity and invasion resistance. To investigate this possibility, we redesigned a set of experimental treatments using the same method in the same site from September to December 2002, i.e., a treatment that had the same species diversity, but a different functional groups diversity, and *A. sessilis* was not in the species list. The results still indicated a significant, negative relationship between functional groups diversity and community invasibility (Figure 8). A more direct test of whether the effect of diversity on invasion success is due to the strong effects of one species (i.e., the sampling effect) or true species complementarity is provided by the metrics of Loreau (Stachowicz et al., 2002). Loreau's D_{max} compares whether the poly-culture treatments significantly enhance ecosystem function (in this case, invasion resistance) relative to the monoculture that is most able to resist invasion. Our results indicate the lower the alligator weed biomass, the

Table 2. Dependence of invasion success extractable soil N (NO_3^- and NH_4^+) on functional group richness and composition.

Response variable	F values			Overall r^2
	Functional group richness (df=2,55)	Functional group composition (df=14, 55)	Overall model (df=16, 55)	
Biomass of alligator weed	5.800**	30.896***	37.782***	0.934
Cover of alligator weed*	6.348**	29.051***	37.100***	0.936
Decrement of extractable soil N	26.000***	25.606***	46.582***	0.926

*Cover of alligator weed was evaluated by natural logarithem.

Notes: The combined effect of functional group richness and on community invasibility was tested by two-way ANOVAs in which functional group richness and functional composition were the independent variables. **p<0.01; ***p<0.001.
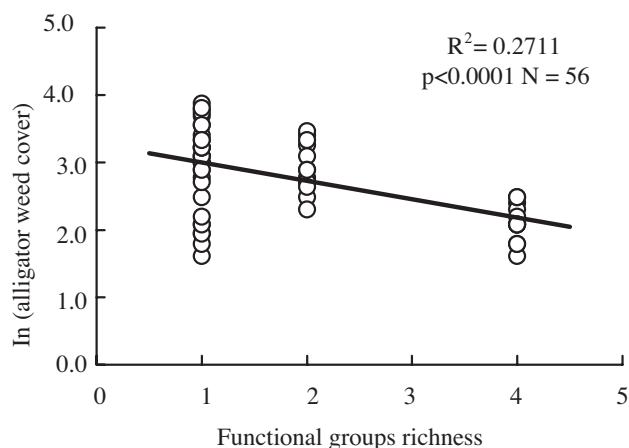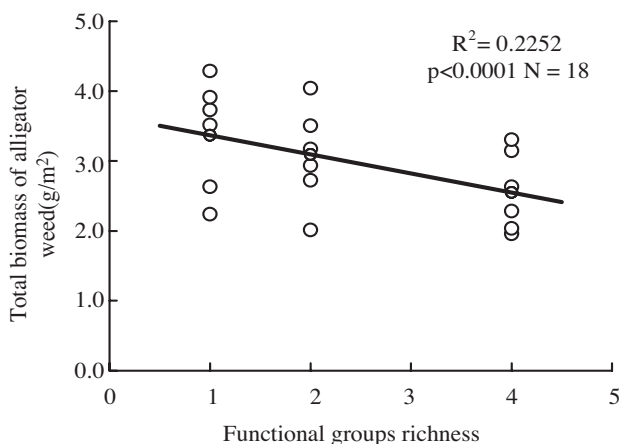
Figure 7. Linear regression of cover of alligator weed on community functional groups diversity. Data of percent cover of alligator weed were log-transformed. Linear equation: y=-0.2724x +3.2733.

Figure 8. Linear regression of total biomass of alligator weed on community functional groups diversity. *Alternanthera sessilis* was not used in this experiment. Linear equation: y=-5.4357x+ 72.75.

stronger the community's invasion resistance. So we calculated D_{min} as the deviation of alligator weed's biomass in the poly-culture treatments from the minimum observed in monoculture (*A. sessilis*). The following is Loreau's (1998) formula: $D_{min} =[O_t -min (M_i)]/min (M_i)$, where O_t is the observed invader biomass cover in poly-culture and min (M_i) is the minimum invader biomass in eight monoculture treatments. For all four-functional groups communities (4-, 8- and 16-species treatments), and some two-functional groups communities, we found that the biomass of alligator weed was less than that of the most resistant monoculture treatment (*A. sessilis*), i.e., D_{min} <0. The results also suggest that species complementarity, and not the sampling effect, is responsible for the invasion resistance of more diverse functional groups communities.

Resource (N) Availability and Community Invasibility

High diversity communities had, on average, greater cover and biomass of resident species and lower levels of extractable soil nitrogen, light at the soil surface, and less bare ground, and our results are in agreement with Tilman et al. (1997) and Naeem et al. (2000). By harvest time, average biomass increased from 1081.5 g to 1860.5 g (monocultures versus 4 functional groups poly-cultures) per sector across 1, 2, and 4 functional groups (including all 4, 8, and 16-species poly-cultures), while the decrement of average extractable soil nitrogen across the functional diversity gradient varied from 13.962 to 26.327 mg/kg soil. With the increase of functional group richness, the biomass of resident species increased, and consequently led to a decrease in resource availability (extractable nitrogen). Functional group richness and functional group composition affected the decrement of extractable nitrogen significantly (Table 2). The biomass of resident species and the decrement of soil N were in significant positive correlation (r= 0.702, p<0.0001). When the effect of the invader on the

decrement of soil N was accounted for, the partial correlation was still significant (r=0.6539, p<0.001). The decrement of soil N and the biomass of the invader significantly negatively correlated (r=-0.349, p=0.0084). However, when the effect of biomass of resident species on soil N was accounted for, the partial correlation was no longer significant (r=-0.0942, p=0.494).

Discussion

This experiment tested the hypothesis of species diversity-invasibility and the hypothesis of functional groups diversity-invasibility. The effects of community species richness, functional groups richness, and functional groups composition on community invasibility were studied as well as the relationship between the functional groups identity of the resident species and alligator weed. Our results indicate that community functional groups richness is correlated with community invasibility on the base of characteristics of species rather than species diversity, and that functional groups composition is also related to community invasibility. However, species diversity independent of the functional groups diversity has no significant relationship with community invasibility. Functional groups diversity's effects on community invasibility may have driven some of these relationships, or by resident species' repelling functionally similar invaders.

Recent studies have described positive, negative, or no relationships between diversity and invasibility. The most likely explanation for these conflicting results may be the co-variation of the extrinsic factors, e.g., disturbance, soil fertility, or water conditions. Lack of control of these extrinsic factors makes it difficult to determine whether or not the non-positive relationships result from the independent effect of biodiversity on invasibility. Naeem et al. (2000) have found that co-varying extrinsic factors may obscure the impact of diversity on invader success. Thus, it is im-

portant to control the extrinsic factors in studying the relationships. In our experiment, soil water supply was controlled, and soil resources availability was remained constant. Disturbances from herbivores and human beings were also excluded. Therefore, our results indicate the independent effect of biodiversity on community invasibility.

It is commonly believed that more diverse communities are less susceptible to invasion by exotic species because they have fewer resources available for the invaders (Lodge, 1993). Our results based on functional groups diversity support this hypothesis, but our results based on species diversity independent of functional groups diversity do not. The reason may be related to resource availability and species redundancy in the communities. With the increase of resident species or functional group richness, the resident species biomass increased in our study. However, the extractable soil nitrogen decreased from low to high functional groups diversity, which was not influenced by the invader in partial correlation analyses. The negative correlation between the decrement of extractable soil nitrogen and biomass of alligator weed was not significant when biomass of resident species was considered by partial correlation analyses. This suggests that the increase in functional groups diversity may have resulted in the decrement of extractable soil nitrogen, which would have reduced the N availability or made N limited. Thus, competition for the limited resources by all plants is greater in the communities with diverse functional groups than in the communities with fewer functional groups. Consequently, niche opportunity left for the invaders is limited as well as the population establishment of the invaders in these communities. Therefore, these communities will be more resistant to invasion than the communities with fewer functional groups. The biomass and cover of alligator weed and the decrement of extractable soil nitrogen were not significantly different among 4-, 8- and 16-species communities in our study, which might be due to species redundancy. Based on this, the hypothesis of functional groups diversity-invasibilty seems more convincing, and our results do not support the hypothesis of species diversity-invasibility.

Resident functional groups identity also influenced the community invasibility in our study. Forbs, especially *A. sessilis*, caused the most decrease in establishment of alligator weed. *Alternanthera sessilis* belongs to the same morphological group and the same genus as alligator weed. This suggests that competition for resources and spaces within functional groups is more intensive than competition among functional groups. Symstad (2000) and Lavorel et al. (1999) found that the communities with more coverage were less susceptible to invasion by exotic species. In our study, legumes had relatively higher coverage but did not show stronger resistance to invasion. The possible explanation for this is that due to biological nitrogen fixation by legumes, their community N availability was not reduced enough to limit invasion.

We also found that high densities of *L. chinensis* (annual grass) monoculture limited alligator weed's estab-lishment during the vegetative period and flowering season of *L. chinensis*, but after bearing in August, the vegetative body gradually withered away, and invasion resistance decreased significantly. This suggests that resource availability may vary with life history traits and then influence its community invasibility. This mechanism in monoculture might also work in diverse communities. In these communities, different species may have different history traits and use the same resources at different times. Thus, these communities would provide fewer windows of opportunity for invaders to establish a population. Furthermore, sampling effects could also operate, i.e., the probability of including the more competitive species or functional groups for a given resource in a community may increase as community diversity increases. In this regard, a plant community may become more susceptible to invasion whenever the amount of unused resources increases, as reported by Davis et al. (2000)

Resource availability is influenced by many factors, and it can decline or increase depending on the variation of community structure and function, as shown by the results in the *L. chinensi* monoculture in our study. This suggests that community invasibilty is not a static or permanent attribute, but is dynamic and can fluctuate over time with variations in resource availability. In natural communities, resource variability is related to the dynamic changes of communities, disturbance, and fluctuating environmental conditions. These physical-biological interactions may explain some of the reported site-to-site variability in invasion success as reported by Byers (2002).

It is well known that the factors influencing community invasibility do not operate independently. Biodiversity varies widely with physical extrinsic factors, such as latitude, climate, disturbance, soil, and the supply rates of physical resources to a system. This can help to explain the discrepancy between different studies: a positive relationship between species diversity and invasibility on a broad spatial scale or in observational studies (Stohlgren et al., 1999; Stohlgren and Chong, 2002), and a negative relationship on a small scale or in many experimental studies (Levine, 2000; Dukes, 2002; Kennedy et al., 2002). A discrepancy also arises in experimental studies in which functional groups diversity is experimentally manipulated. This suggests that if a niche limitation does occur, it may only happen when the definitions of functional groups or guilds are more refined. Functional groups' definitions of plants had better be based on the methods by which species utilize and compete for resources. Based on this, research on relationships between species functional groups diversity and community invasibility will make sense. In our study, the selected resident species can all be found in the habitats in which alligator weed establishes its population. In these manipulated communities, interactions between the species within the communities could be maintained in some degree.

Community invasibility in natural ecosystems is influenced by many factors, some of which cannot be manipulated by human beings, so the patterns and mechanisms determining community invasibilty in relation to its diver-

sity are likely to be far subtler than we have discussed so far. Although we can manipulate the experiments in a uniform condition, further research is still needed into the effects of functional groups composition and functional groups types on community invasibility, such as the interactions between ecological diversity and environmental variability and interactions among functional groups. All of these need to be considered through carefully designed experiments coupled with theoretical modeling studies.

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物種多樣性及功能群特徵性對群落可入侵性的作用研究

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　　生物入侵已經成為一個普遍性的環境問題，但人們對之仍瞭解甚少。儘管一些理論分析和觀察研究表明生物多樣性豐富的群落不容易受到外來種的入侵，但後來有些實驗研究並沒能證實兩者的負相關性，多樣性–可入侵性假說仍然是入侵生態學領域爭論比較多的一個焦點。本實驗以喜旱蓮子草（*Alternanthera philoxeroides* (Mart.) Griseb.）為入侵種，人為構建不同物種多樣性和物種功能群多樣性（16 個物種分別屬於 C_3 禾本科植物、C_4 植物、禾本科植物和豆科植物 4 個不同的功能群）梯度的小尺度草地群落，同時盡可能把其他影響可入侵性的外在因素和多樣性效應隔離開來，研究喜旱蓮子草在不通群落裏的入侵過程，驗證多樣性與可入侵性及其相關假說。研究結果顯示，物種功能群愈豐富的群落很可能通過降低資源可利用率從而表現出對入侵較強的抵抗力，而基於功能群數目的不同物種多樣性的群落可入侵性沒有顯著差異。物種功能群特特徵不同的群落也表現出可入侵性的差異，生活史周期短的單一物種群落和有著生物固氮功能的豆科植物對入侵抵抗力較弱，和喜旱蓮子草屬於同一功能群且有著相似生態位的土著種蓮子草（*Alternanthera sessilis*）對入侵的抵抗力最強。實驗結果暗示，群落可入侵性和物種多樣性並沒有很顯著的負相關，而是和物種特徵性基礎上的物種功能群多樣性呈負相關，群落中留給入侵種的生態位機會的多少很可能是決定群落可入侵性的一個關鍵因素。因為可入侵性受到的影響因素太多，還需通過更為細緻的試驗設計和理論模型來進一步論證。

關鍵詞：喜旱蓮子草；群落；多樣性；功能群；可入侵性；入侵。