

Plant functional group identity and diversity determine biotic resistance to invasion by an exotic grass

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Summary

1. Biotic resistance, the ability of species in a community to limit invasion, is central to our understanding of how communities at risk of invasion assemble after disturbances, but it has yet to translate into guiding principles for the restoration of invasion-resistant plant communities. We combined experimental, functional, and modelling approaches to investigate processes of community assembly contributing to biotic resistance to an introduced lineage of *Phragmites australis*, a model invasive species in North America. We hypothesized that (i) functional group identity would be a good predictor of biotic resistance to *P. australis*, while species identity effect would be redundant within functional group (ii) mixtures of species would be more invasion resistant than monocultures.

2. We classified 36 resident wetland plants into four functional groups based on eight functional traits. We conducted two competition experiments based on the additive competition design with *P. australis* and monocultures or mixtures of wetland plants. As an indicator of biotic resistance, we calculated a relative competition index (RCI_{avg}) based on the average performance of *P. australis* in competition treatment compared with control. To explain diversity effect further, we partitioned it into selection effect and complementarity effect and tested several diversity–interaction models.

3. In monoculture treatments, RCI_{avg} of wetland plants was significantly different among functional groups, but not within each functional group. We found the highest RCI_{avg} for fast-growing annuals, suggesting priority effect.

4. RCI_{avg} of wetland plants was significantly greater in mixture than in monoculture mainly due to complementarity–diversity effect among functional groups. In diversity–interaction models, species interaction patterns in mixtures were described best by interactions between functional groups when fitted to RCI_{avg} or biomass, implying niche partitioning.

5. Synthesis. Functional group identity and diversity of resident plant communities are good indicators of biotic resistance to invasion by introduced *Phragmites australis*, suggesting niche pre-emption (priority effect) and niche partitioning (diversity effect) as underlying mechanisms. Guiding principles to understand and/or manage biological invasion could emerge from advances in community theory and the use of a functional framework. Targeting widely distributed invasive plants in different contexts and scaling up to field situations will facilitate generalization.

Key-words: community assembly, diversity and invasibility, diversity–interaction model, ecological restoration, niche partitioning, invasive plant management, limiting similarity, *Phragmites australis*, priority effect, wetland invasion

Introduction

Biotic resistance refers to the ability of species in a community to limit the recruitment or invasion of other species from the regional pool (Levine, Adler & Yelenik 2004; Catford, Jansson & Nilsson 2009). Biotic resistance has a long history

in community ecology (Elton 1958; Fox 1987; Levine & D'Antonio 1999; Prieur-Richard *et al.* 2000; Pokorny *et al.* 2005; Fridley *et al.* 2007) and has been well documented, particularly against invasive plants (Davis, Grime & Thompson 2000; Lindig-Cisneros & Zedler 2002; de Blois, Brisson & Bouchard 2004; Simmons 2005; Iannone & Galatowitsch 2008; Reinhardt Adams & Galatowitsch 2008; Meiman, Redente & Paschke 2009; Perry, Cronin & Paschke 2009).

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It is central to our understanding of how communities at risk of invasion assemble after disturbances, but it has yet to translate into wide-ranging guiding principles for the ecological restoration of invasion-resistant plant communities (Zedler 2000; Bakker & Wilson 2004; Iannone & Galatowitsch 2008; Hobbs & Richardson 2010; Middleton, Bever & Schultz 2010). Identifying species interactions and processes of community assembly that contribute to biotic resistance (Levine, Adler & Yelenik 2004; MacDougall, Gilbert & Levine 2009) is a promising approach particularly with the most widely distributed invasive plants. The latter provide good models for comparing invasion patterns across communities and regions, allowing generalizations to emerge.

Several concepts from community ecology theory such as limiting similarity, fitness inequality, and the diversity–resistance hypothesis have been proposed to explain biotic resistance (Shea & Chesson 2002; Funk *et al.* 2008; MacDougall, Gilbert & Levine 2009). These are not necessarily mutually exclusive as several processes may work synergistically or in alternation depending on the context. Limiting similarity from classical competition theory (MacArthur & Levins 1967; Waltzin *et al.* 2003) postulates that a resident species whose niche overlaps with that of an invading species will compete most with the invader. When this happens, fitness inequality between resident species and the invader determines which species will be competitively excluded (MacDougall, Gilbert & Levine 2009).

The diversity–resistance hypothesis predicts a positive relationship between species diversity and biotic resistance (Elton 1958). Small-scale experimental studies generally support Elton's hypothesis (Knops *et al.* 1999; Naeem *et al.* 2000; Hector *et al.* 2001; Dukes 2002; Kennedy *et al.* 2002; Rinella, Pokorny & Rekaya 2007; Frankow-Lindberg *et al.* 2009; Frankow-Lindberg 2012) and so do competition-based models (Case 1990). It is assumed that diverse communities with broad niche breadth offer fewer niches for invaders. The so-called empty niche concept remains controversial, however, because non-invaded resident communities can have unsaturated niches (Tilman 1997). On the other hand, large-scale observational studies report opposite patterns (Stohlgren *et al.* 1999; Stohlgren, Barnett & Kartesz 2003). The scale dependence of the diversity–resistance relationship is further confirmed by observational studies that directly investigate the effect of scales (Levine 2000; Brown & Peet 2003) and statistical models that consider both competition and resource availability across communities (Byers & Noonburg 2003) or assumed null species interaction (Fridley, Brown & Bruno 2004). In other words, species-rich communities are more resistant to invasion than species-poor communities, meanwhile species-rich ecosystems and regions are likely to be hotspots not only for native species but also for exotic species (Fridley *et al.* 2007). The latter species may be better adapted to their new environment than the former (Shea & Chesson 2002; Callaway & Maron 2006; Verhoeven *et al.* 2009).

From a functional perspective, species-rich communities often result in high functional diversity when species show different functional traits and thereby strategies to acquire

resources. Functional traits are defined as morpho-physio-phenological traits of species (Cornelissen 2003; Violle *et al.* 2007). Functional trait similarity between resident species and invading species is expected to lead to overlapping resource requirement and therefore competition (Funk *et al.* 2008). When species are grouped on the basis of similarity in functional traits, it is hypothesized that the lack of a certain functional group in a resident community will make that community more susceptible to invasion by a species from that functional group (Fox 1987; Von Holle & Simberloff 2004). Functional group identity and diversity in a resident community should therefore be good predictors of biotic resistance.

Several studies have used pre-defined functional groups such as growth form to test limiting similarity (Tilman 1997; Prieur-Richard *et al.* 2000; Symstad 2000; Booth, Caldwell & Stark 2003; Von Holle & Simberloff 2004; Pokorny *et al.* 2005; Sheley & James 2010), but these groups often ignore functional traits that may be relevant to biotic resistance. For instance, functional traits such as specific leaf area, height at maturity, and seed mass in Westoby's (1998) LHS plant ecology strategy were shown to correlate with plant invasiveness (Hamilton *et al.* 2005). Moreover, some invasive species take advantage of temporal niches when these are not occupied by other species (Wolkovich & Cleland 2010; Wilsey, Daneshgar & Polley 2011), so functional traits related to life-history strategies, such as life longevity, determine the timing of species establishment and possibly competitive outcomes. Species that establish early and grow fast may lead to priority effect by pre-empting resources, leading to an inhibition of the slow-growing species in community assembly (Mwangi *et al.* 2007). It is therefore important to classify species into functional groups based on the several relevant traits to relate functional group identity with biotic resistance.

The diversity effect on biotic resistance can be further partitioned into selection effect and complementarity effect (Loreau 1998; Loreau & Hector 2001). Selection effect refers to the situation where the dominance of species with particular traits will determine the diversity effect, whereas complementarity effect describes a situation where resource partitioning among species or positive species interactions contributes most to the diversity effect. Loreau & Hector (2001) proposed an additive partitioning diversity effect equation to help separate complementarity effect from selection effect, thereby allowing the assessment of their respective contribution to biotic resistance. Furthermore, by comparing different models based on the different ecological assumptions about species interactions, diversity–interaction models (Kirwan *et al.* 2009) permit predictions of the relationship between diversity and function such as biotic resistance across different community composition. Partitioning diversity effect as well as applying diversity–interaction models promises new insights in relation to invasion resistance (Frankow-Lindberg *et al.* 2009; Frankow-Lindberg 2012), especially if combined with a functional group approach.

We combined experimental, functional, and modelling approaches to investigate biotic resistance to *Phragmites*

australis, a model species for large-statured invasive grasses in North America (Lambert, Dudley & Saltonstall 2010). Genotype identity of species can influence their invasiveness (Vellend, Drummond & Tomimatsu 2010; Drummond & Vellend 2012), and currently three distinct lineages of *P. australis* are recognized in North America, including one of Eurasian origin (principally haplotype M, Saltonstall 2002), which is widely distributed and invasive in many regions. Given its cosmopolitan distribution, the characterization of the genetic diversity of *P. australis* is an active area of research (Saltonstall 2002; Hauber *et al.* 2011; Lambertini *et al.* 2012; Meyerson *et al.* 2012). Recent evidence shows that seed dispersal is the main strategy to colonize new sites (Alvarez, Tron & Mauchamp 2005; Féra & Hroudová 2009; Belzile *et al.* 2010), with roadside or ditches offering well-connected habitats (Maheu-Giroux & de Blois 2007; Jodoin *et al.* 2008; Brisson, de Blois & Lavoie 2010). A niche opportunity is provided for seed germination and seedling establishment of *P. australis* when disturbance removes the vegetation cover and exposes bare soil (Minchinton & Bertness 2003). *Phragmites australis* is being controlled often through the use of chemicals with little consideration for fundamental ecological principles or knowledge of species interactions. In areas where biodiversity is considered valuable or where *P. australis* is a major nuisance, for instance within or near protected reserves, restoring invasion-resistant wetland plant communities could be an innovative complementary management strategy to constrain *P. australis* expansion (Wang *et al.* 2006; Carlson, Kowalski & Wilcox 2009). Even in situations where control is not an option, it is fundamental to understand how communities at risk of invasion assemble after disturbances. Few studies have tested the relevance of biotic resistance to the restoration of wetland communities (Wang *et al.* 2006; Carlson, Kowalski & Wilcox 2009; Peter & Burdick 2010).

We investigated the relative competitive effect of resident species (our measure of biotic resistance) on seedling establishment of *P. australis* using pot experiments simulating community assembly. Based on the assumption that some species, or combination of species, would be more resistant to invasion than others, we hypothesized that (i) functional group identity would be a good predictor of biotic resistance to *P. australis*, while species identity effect would be redundant within functional group, (ii) mixtures of species would be more invasion-resistant than monocultures due to either selection effect or complementarity–diversity effect. This study allowed us to identify and evaluate species interaction processes, such as niche overlapping, niche pre-emption, and niche partitioning, contributing to biotic resistance to invasion.

Materials and methods

OVERVIEW OF EXPERIMENTAL DESIGN

We classified wetland plants occurring in our region into four functional groups based on the eight functional traits (life longevity, seed dry mass, specific leaf area, leaf nitrogen content, relative growth rate, growth form, leaf dry matter content, and height at maturity). We

conducted two experiments based on the additive competition design (Connolly, Wayne & Bazzaz 2001) to evaluate the biotic resistance of wetland plant(s) to invasion by *P. australis* seedlings. In the first experiment starting in 2009, 11 wetland plants from three functional groups were tested in either monoculture (one species + *P. australis*) or species mixtures (three or four species + *P. australis*) with controls (only *P. australis*). In 2011, the second experiment tested 25 wetland plants, 8 of which also tested in the first experiment, from four functional groups in monoculture with *P. australis*. In both experiments, biotic resistance of wetland plants was estimated by a relative competition index (RCI) measuring how much *P. australis*' establishment and growth was reduced in competition treatments compared with control (without competition). The monoculture treatments allowed us to test the hypothesis about functional group effect vs. species identity effect within each functional group. The mixture treatments of the first experiment allowed us to test diversity effect by comparing biotic resistance in monoculture vs. mixture and investigating species interaction patterns that contribute to biotic resistance. To explain further this diversity effect, we partitioned diversity effect into selection effect and complementarity effect and we built diversity–interaction models describing biotic resistance as a function of different levels of species interactions.

SPECIES SELECTION AND FUNCTIONAL CLASSIFICATION

We chose 36 wetland herbaceous plants that are found at least 50% of the time in freshwater wetlands (OBL, FACW, or FAC in wetland indicator status in United States Department of Agriculture's PLANTS data base). These plants represent a selection among the regional species pool, constrained by seed availability. Random subsets of these species were used for the experiments reported in this study and for a related field experiment (Byun *et al.* unpublished data). All species tested are native except *Lolium multiflorum*, which is introduced but naturalized in the study region (Lavoie *et al.* 2012). Species nomenclature and status (native or introduced) in this study follow the Flora of North America (Flora of North America Editorial 1993) and the data base of Vascular Plants of Canada (VASCAN), respectively.

We classified the wetland plants into emergent functional groups based on the following functional traits: life longevity, seed dry mass, specific leaf area, leaf nitrogen content, relative growth rate, growth form, leaf dry matter content, and height at maturity. These functional traits are relevant to leaf-height-seed plant ecology strategy scheme (Westoby 1998), the common core list of plant traits related to dispersal, establishment, and persistence (Weiher *et al.* 1999), functional traits related to competitive ability and growth (Funk *et al.* 2008), and functional classification of wetland plants (Boutin & Keddy 1993). Most numerical functional trait information was obtained from TRY global data base of plant traits (Kattge *et al.* 2011). We used the median value of several measurements of functional trait per each species from the TRY data base for data consistency. For life longevity, we allocated annual for therophytes in Raunkiaer life-form and perennial for the others referring to Flora of Canada (Scoggan 1978). For growth form, we referred to the United States Department of Agriculture's PLANTS data base (<http://plants.usda.gov>) and followed their definition (single crown, single stem, bunch, stoloniferous, and rhizomatous). Based on these functional traits, Gower's similarity coefficient among species was calculated using *gowdis* function in R (Gower 1971; Podani 1999). All traits were standardized and equally weighted in the calculation of the similarity coefficient. Average similarity coefficient to *P. australis* was 0.40 in FG 1, 0.58 in FG 2, 0.72

in FG 3a, and 0.76 in FG 3b, respectively (Appendix S6). Similarity coefficient to *P. australis* was significantly different among FG 1, FG 2, and FG 3, but not between FG 3a and FG 3b (Contrast test; $F_{1,31} = 0.96$, $P = 0.332$).

The 36 wetland plants were classified into functional groups using cluster analysis with ward option using *hclust* functions in R packages (Fig. 1). Classification led to the definition of four functional groups differing mostly by life longevity, growth form, height at maturity, and seed mass (see Appendix S1 in Supporting Information). Species in functional group 1 (hereafter, FG 1) were annual plants characterized by the highest seed mass but the lowest height at maturity among species. Species in FG 2 were short perennial plants without rhizome characterized by the lowest seed mass. Species in FG 3 were rhizomatous perennial plants. FG 3 is further subclassified into FG 3a, short rhizomatous perennial plants, and FG 3b, tall rhizomatous perennial plants. *Phragmites australis*, our target invader, belongs to FG 3b.

EXPERIMENT SETTING AND SEED PREPARATION

We constructed outdoor pot experiments at the Montreal Botanical Garden to simulate a situation where seeds of *P. australis* arrive on bare soil after biological disturbance. Soil used in the experiments was fertile clay soil, collected from a wetland basin in Saint-Etienne-de-Beauharnois, Quebec, Canada where *P. australis* is abundant. The soil was first sterilized using a steam pasteurizer at 76 °C for 4 h to kill all viable seeds inside the soil and thus prevent our system from contamination by unwanted species while minimizing the impact on natural soil physical properties. Soil was placed in each pot (diameter 10 and height 12), and six pots were immersed in a large container, with water (see Appendix S2). Water level was maintained at -3 cm (± 1 cm) using an automatic water gauge device throughout the experiment.

Seeds of introduced *P. australis* (haplotype M) were collected in roadside ditches in Dundee in Quebec, Canada (N 45°05', 50.6, W 74°24', 36.4) in 2008. Most seeds of wetland plants were purchased from seed suppliers (© Prairie Moon Nursery; © Shooting Star Native Seeds) in North America at the time of the experiment. Seeds of each

species were from single-seed lot harvested from an identified ecotype in natural habitats across North America. The seeds of *Typha latifolia* and *Typha angustifolia* were collected from a pond at the Botanical Garden of Montreal for the second experiment. Seed viability among wetland plants was standardized by applying the same number of pure live seeds per species to experimental units. Most pure live seed rate information was obtained from seed suppliers. Pure live seed rate is calculated by multiplying seed purity rate (excluding non-seed) and seed viability rate (excluding non-viable seeds) using standard tetrazolium testing procedures. All seeds, including *P. australis* ones, were cold-stratified at 3 °C prior to the germination test, following the standard methods (Lindig-Cisneros & Zedler 2001). Prior to the experiment, 50 seeds per species were placed in each of three Petri dishes with filter papers (Whatman® No. 1; Whatman, Kent, UK), moistened with 3 mL of distilled water, and sealed with Parafilm under fluorescent light (Plant & Aquarium T12®, General Electric, Fairfield, CT, USA). We excluded any species with germination rate below 5%. Pure live seeds per species, not seedlings, were applied for the pot experiments.

COMPETITION DESIGN

Additive competition design (Snaydon 1991; Keddy, Twolan-Strutt & Wisheu 1994; Connolly, Wayne & Bazzaz 2001) was used to test the competitive effect of resident species on *P. australis*. In the first experiment, 11 wetland plants were selected among three functional groups (FG 1, FG 2, and FG 3a). They represent more than 25% of the species pool size of each FG. FG 3b had to be excluded in the first experiment as the seeds of species selected in this group such as *Typha angustifolia* did not germinate well enough in the pre-germination test (< 5%). Because trait similarity to *P. australis* was not significantly different between FG 3a and FG 3b (Appendix S6), we conducted the first experiment without FG 3b, assuming that biotic resistance to invasion by *P. australis* of FG 3a would be similar to that of FG 3b if trait similarity determines biotic resistance. We were, however, able to test this group in the second experiment with new

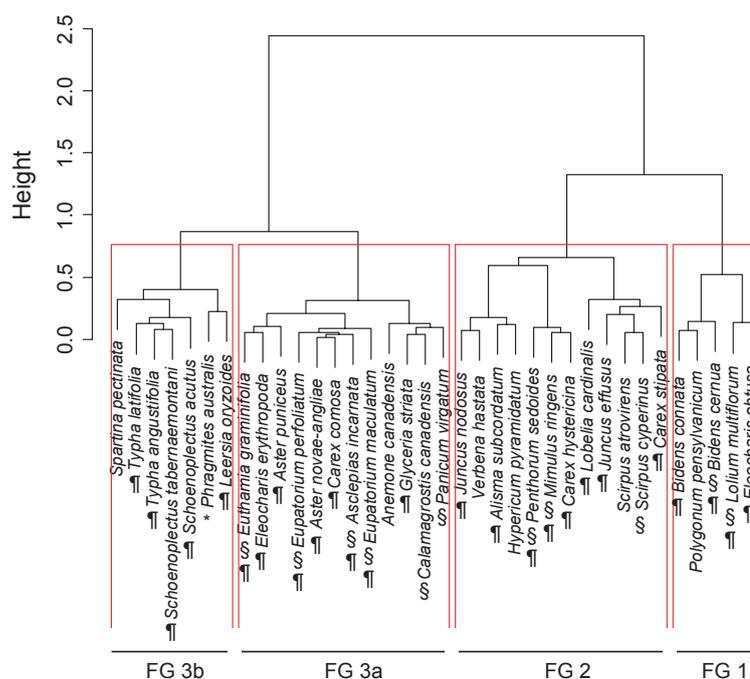


Fig. 1. Classification of 36 wetland plants into four functional groups by functional trait similarity. §Species selected for the first experiment, ¶species selected for the second experiment, *the target invasive species in the experiments.

seed lots. For mixture treatments, 3 or 4 species among the 11 species were randomly assigned to a mixture for a total of 8 mixtures that represent a variety of functional group composition. There were 11 monocultures and 8 mixture treatments plus one control with *P. australis*; a total of 20 experimental units (treatment + control) were replicated three times in a randomized complete block design (RCBD).

All species in monocultures or mixtures were sown at the start of the growing season in 2009 along with seeds of *P. australis* in treatment or control. The seeding density of wetland plant(s) and *P. australis* was 210 and 70 pure live seeds per each pot, respectively. We applied a 3 : 1 ratio of wetland plant to *P. australis* in seeding density to maximize the chances of detecting quantitative differences in biotic resistance among treatments. The total 280 pure live seeds of all species per each pot (surface area = 700 cm²) is equivalent to 4000 seeds m⁻². This seeding density is within the range of the level (from 3000 to 7000 seeds m⁻²) found in soil seedbank of some restored wetlands and natural wetlands (Galatowitsch & van der Valk 1996). To verify whether biotic resistance changes with time, we took measurements in the monocultures at the end of the growing season in 2009 and again in 2010. Only monocultures were followed up for 2 years. While pot experiments can provide an adequate setting for the first year of growth, they were not ideally suited for long-term monitoring of more complex species mixtures. Seeds were not reintroduced in pots for the second year of the monoculture experiment.

In addition, we conducted a second experiment with 25 wetland plants in 2011 to validate some of the findings of the first monoculture experiment. We used the same experimental design for monocultures as before but followed the experiment for the first growing season only and included a new functional group (FG 3b). For seeding density, we kept the same level for *P. australis* (70 pure live seeds per pot), but doubled the number of seeds of resident species (420 pure live seeds per pot) based on the results of the first experiment to be able to compare biotic resistance more clearly among functional groups. It must be noted that we were aiming for experimental conditions that would lead to a quantitative response in terms of biotic resistance, not just a dichotomous one (invaded or not invaded).

DATA MEASUREMENT AND ANALYSES

At the end of the growing season, we measured the number of shoots, above-ground biomass, plant height, and plant cover of *P. australis* in each treatment and control pot to calculate the main response variable (see below). In addition, we also measured plant cover, plant height, and above-ground biomass of all wetland plants to correlate them with the response variables. Plant cover was measured using point intercept method with a 40-cells mesh. For above-ground biomass, above-ground portion of plant was collected at the end of September of each year and stored in stove at 70 °C for 48 h until weighed. Plant canopy height was estimated for each species to the closest 0.5 cm. We calculated the RCI to estimate the competitive effect of wetland plant(s) on *P. australis* using the following equation (Weigelt & Jolliffe 2003):

$$RCI_Y = \frac{Y_{\text{control}} - Y_{\text{treatment}}}{Y_{\text{control}}} \quad \text{eqn 1}$$

where RCI is the relative competition index of wetland plant on *P. australis* in either monoculture or mixture for a given variable *Y* (number of shoots, above-ground biomass, plant height, or plant cover of *P. australis*). Y_{control} is performance of *P. australis* in control, and $Y_{\text{treatment}}$ is performance of *P. australis* in treatment. Because $RCI_{\text{number of shoots}}$, RCI_{biomass} , RCI_{height} , and $RCI_{\text{plant cover}}$ were highly

correlated with each other (Appendix S8), we used RCI_{avg} , the arithmetic mean of $RCI_{\text{number of shoots}}$, RCI_{biomass} , RCI_{height} , and $RCI_{\text{plant cover}}$ as the main response variable for all analyses. A value of 0 for RCI_{avg} suggests no competitive effect on *P. australis*, a value of 1 suggests complete competitive exclusion of *P. australis*, and negative RCI suggests facilitation of *P. australis*' establishment and growth by wetland plants. Finally, we also calculated yearly change of RCI_{avg} between 2009 and 2010 (ΔRCI_{avg}) to assess time effect on biotic resistance.

We used ANOVA to test for functional group identity effect and species identity effect nested within each functional group on RCI_{avg} or ΔRCI_{avg} for monoculture treatment in both experiments. The generalized linear mixed model (REML; *F* test) was used for this test to take into account random block effect (Bolker *et al.* 2009). Normality of residuals and homoscedasticity were checked, and response variables were transformed when necessary. When significant functional group effect was found, we compared the mean of functional groups using contrast test on each pair of functional groups. If we found a significant species identity effect within each functional group, we used Tukey's HSD multiple comparison test to compare means of species identity effect by each functional group.

PARTITIONING DIVERSITY EFFECT

The net diversity effect in mixture treatments of the first experiment was partitioned into selection effect and complementarity effect using the additive partitioning biodiversity effect equation (Loreau & Hector 2001). In the original equation, selection effect is calculated using a covariance function that relates yield of species in a mixture with one in monoculture, and the complementarity effect measures any change in the average relative yield in the mixture. The net diversity effect (the sum of these two effects) represents the deviation of the yield in mixture from its expected yield value in monoculture and the relative abundance of species in the mixtures. Because the original equation was developed for yield, we replaced yield with RCI_{avg} , then we estimated the relative contribution of each species to RCI_{avg} in mixture based on the assumption that it is proportional to the relative plant cover of that species in the mixture (Appendix S3).

DIVERSITY INTERACTION MODEL

As a complement to the additive partitioning biodiversity effect equation, we used diversity–interaction models (Kirwan *et al.* 2009) to investigate species interaction patterns, contributing to biotic resistance in the mixtures from the first experiment. Comparing models based on the different ecological assumptions allowed us to test alternative hypotheses about the relative role of functional groups and functional redundancy in biotic resistance (Kirwan *et al.* 2009).

Model 1 describes species identity effect alone without species interaction:

$$y = \sum_{i=1}^s \beta_i P_i + \varepsilon \quad \text{eqn 2}$$

The response variable (*y*) represents RCI_{avg} as an indicator for biotic resistance to invasion by *P. australis*. β_i is the estimated performance of species *i* in contribution to biotic resistance, and P_i is the initial proportion of species *i* in seed mixture. In the case of monoculture treatment of species *i*, P_i is equal to 1.

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

$$y = \beta_{FG1}P_{FG1} + \beta_{FG2}P_{FG2} + \beta_{FG3}P_{FG3} + \varepsilon \quad \text{eqn 3}$$

β_{FG1} is the estimated functional group identity effect of FG 1, and P_{FG1} is the sum of all species proportions within that FG 1.

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

$$y = \beta_{FG1}P_{FG1} + \beta_{FG2}P_{FG2} + \beta_{FG3}P_{FG3} + \delta_{av} \sum_{i,j=1,i < j}^s P_i P_j + \varepsilon \quad \text{eqn 4}$$

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

Model 4 describes functional group identity effect and species interaction within and between functional group:

$$y = \beta_{FG1}P_{FG1} + \beta_{FG2}P_{FG2} + \beta_{FG3}P_{FG3} + \delta_{wFG1} \sum_{i,j=1,i < j}^t P_i P_j + \delta_{wFG2} \sum_{i,j=t+1,i < j}^{t+h} P_i P_j + \delta_{wFG3} \sum_{i,j=t+h+1,i < j}^s P_i P_j + \delta_{bFG1-FG2}P_{FG1}P_{FG2} + \delta_{bFG1-FG3}P_{FG1}P_{FG3} + \delta_{bFG2-FG3}P_{FG2}P_{FG3} + \varepsilon \quad \text{eqn 5}$$

where δ_{wFG1} is the coefficient of pairwise species interaction within FG 1, and $\delta_{bFG1-FG2}$ is the coefficient of pairwise species interactions between FG 1 and FG 2.

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

$$y = \beta_{FG1}P_{FG1} + \beta_{FG2}P_{FG2} + \beta_{FG3}P_{FG3} + \sum_{i,j=1,i < j}^s \delta_{ij}P_i P_j + \varepsilon \quad \text{eqn 6}$$

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

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

$$y = \beta_{FG1}P_{FG1} + \beta_{FG2}P_{FG2} + \beta_{FG3}P_{FG3} + \delta_{bFG1-FG2}P_{FG1}P_{FG2} + \delta_{bFG1-FG3}P_{FG1}P_{FG3} + \delta_{bFG2-FG3}P_{FG2}P_{FG3} + \varepsilon \quad \text{eqn 7}$$

Each model was tested using *glm* function in R software. Pairs of models were compared for significant difference in model predictions for RCI_{avg} using *anova.lm* function in R software. Using Model 6, we estimated model prediction about the effect of functional group composition (both functional group identity and interaction) on RCI_{avg} using *predict* function in *stats* package in R software. The model prediction on response surface was drawn in ternary plot using *levelplot* function in *lattice* package in R software.

All ANOVA tests and correlation analyses were conducted using the JMP[®] software (© SAS Institute Inc.; Cary, NC, USA). Partitioning diversity effect was calculated using mathematical equations in the Excel software (© Microsoft). Cluster analysis and diversity–interaction modelling, which is based on multiple regressions, were conducted using R (<http://www.r-project.org>).

Results

MONOCULTURE TREATMENTS

In monoculture treatments and for both experiments, relative competitive effect of wetland plants on *P. australis* was mostly related to their functional group identity, while species identity effect remained redundant within each functional

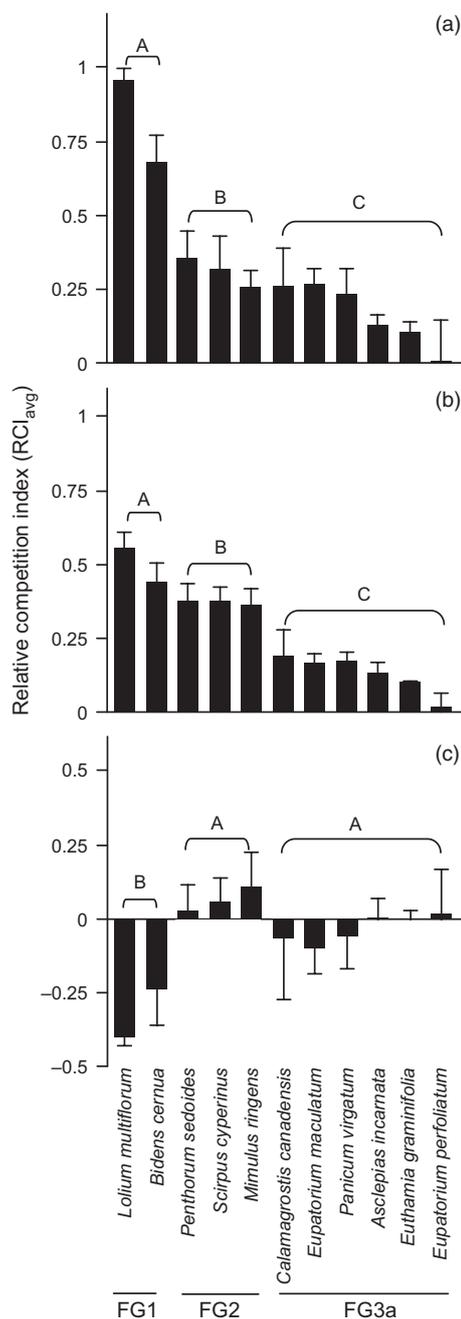


Fig. 2. The relative competition index of monoculture (RCI_{avg}) of a wetland plant (a) in 2009, (b) in 2010, and (c) yearly change in the first experiment. Error bar shows standard error of mean. Functional groups connected by same letter are not significantly different from each other.

group (Figs 2 and 3). In 2009 experiment, relative competitive index (RCI_{avg}) of 11 wetland plants on *P. australis* was significantly different among three FGs ($F_{2,20} = 46.62$, $P < 0.001$), but it was not significantly different within each FG ($F_{8,20} = 1.79$, $P = 0.137$). RCI_{avg} of FG 1 (annual plants) was the highest, followed by FG 2 and FG 3a ($RCI_{avg} = 0.817$, 0.308, and 0.166, respectively; Fig. 2a). In 2010, we found a similar functional redundancy pattern. RCI_{avg} was significantly different among three FGs ($F_{2,20} = 47.43$, $P < 0.001$), but not

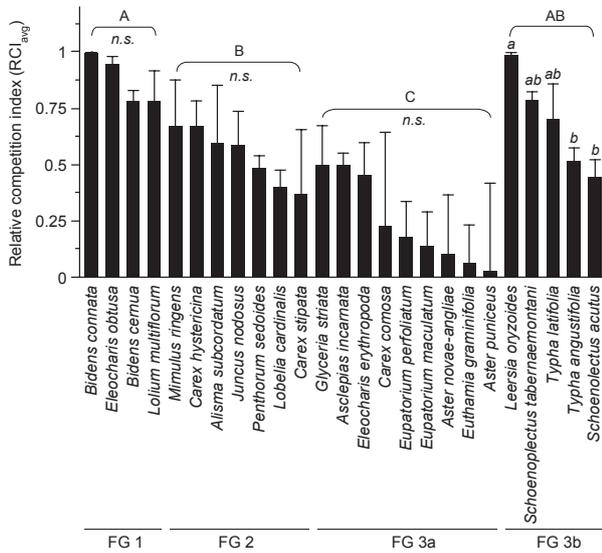


Fig. 3. The relative competition index of monoculture (RCI_{avg}) of a wetland plant in the second experiment in 2011. Error bar shows standard error of mean. Functional groups connected by same capital letters (A, B, C) are not significantly different from each other. Within each functional group, species connected by same lower-case letter (a or b) or 'n.s.' are not significantly different.

within each FG ($F_{8,20} = 1.29$, $P = 0.299$). RCI_{avg} of FG 1 was the highest, followed by FG 2 and FG 3a ($RCI_{avg} = 0.498$, 0.373 , and 0.131 , respectively; Fig. 2b). From 2009 to 2010, RCI_{avg} (hereafter, ΔRCI_{avg}) of FG 1 decreased, but RCI_{avg} of FG 2 and FG 3a did not change much (Fig. 2c). ΔRCI_{avg} was significantly different among three FGs ($F_{2,20} = 8.14$, $P = 0.002$), but not within each FG ($F_{8,20} = 0.30$, $P = 0.957$). RCI_{avg} of FG 1 decreased greatly ($\Delta RCI_{avg} = -0.319$), RCI_{avg} of FG 2 increased slightly ($\Delta RCI_{avg} = +0.064$), and RCI_{avg} of FG 3a decreased slightly ($\Delta RCI_{avg} = -0.035$; Fig. 2c).

When the same analysis was conducted replacing RCI_{avg} with biomass of *P. australis* as the main response variable, a similar functional redundancy pattern was found (Appendix S9).

Plant cover of wetland plants relative to *P. australis* also changed differently depending on the functional group from 2009 to 2010 (see Appendix S4). In 2009, FG 1 became dominant over *P. australis*, but *P. australis* became dominant over FG 2 and FG 3a. In 2010, *P. australis* became dominant over FG 1 and FG 3a, but FG 2 became dominant over *P. australis*. Wetland plants' performance traits were significantly correlated with RCI_{avg} in terms of biomass (Pearson's coefficient, $r = 0.77$), height ($r = 0.61$), and plant cover ($r = 0.79$; Appendix S7 a–c). Among the plant functional traits used to classify functional group, relative growth rate ($r = 0.51$), seed mass ($r = 0.59$), and LDMC ($r = -0.36$) were significantly correlated with RCI_{avg} , and annual plants with single crown or bunch in growth form showed relatively high RCI_{avg} (Appendix S7 d–h).

In the second experiment with 25 wetland plants including one additional FG (FG 3b; tall perennial with rhizome), we found a functional redundancy pattern similar to the first experiment. In the second experiment, RCI_{avg} was arcsine-transformed to meet ANOVA's assumption about equal variance. RCI_{avg} was significantly different among four FGs (arcsine-transformed; $F_{3,48} = 24.74$, $P < 0.001$), and RCI_{avg} was significantly different within each FG ($F_{21,48} = 1.78$, $P = 0.049$). RCI_{avg} of FG 1 was the highest, followed by FG 3b, FG 2, and FG 3a ($RCI_{avg} = 0.877$, 0.687 , 0.540 , and 0.244 , respectively; Fig. 3). When the one-way ANOVA test was conducted on species identity effect alone within each functional group, there was no significant difference in RCI_{avg} among species identity within FG 1 ($F_{3,6} = 3.71$, $P = 0.080$), FG 2 ($F_{6,12} = 0.68$, $P = 0.665$), and FG 3a ($F_{8,16} = 1.33$, $P = 0.294$), but there was one for FG 3b ($F_{4,8} = 10.28$, $P = 0.003$). The significant

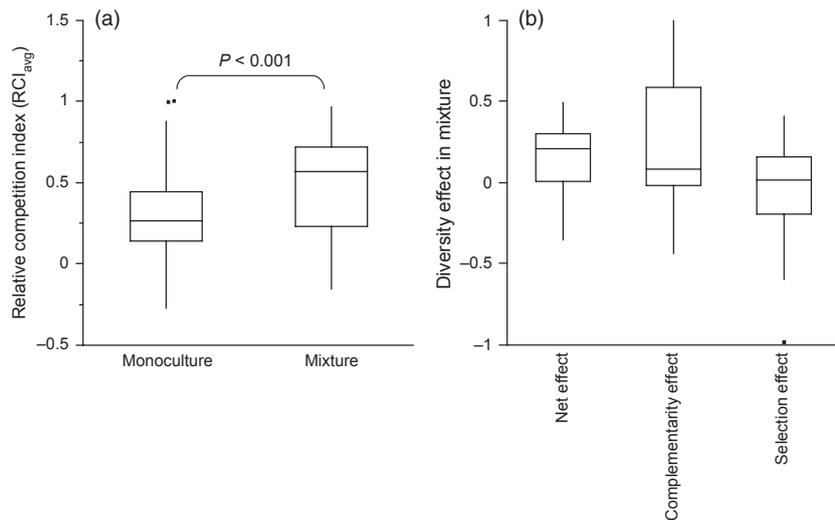


Fig. 4. (a) Relative competition index of monoculture and mixture of wetland plants in the first experiment. P values represent contrast test to compare mean. (b) Partitioning diversity effect into selection effect and complementarity effect by applying additive partitioning diversity effect equation (Loreau & Hector 2001).

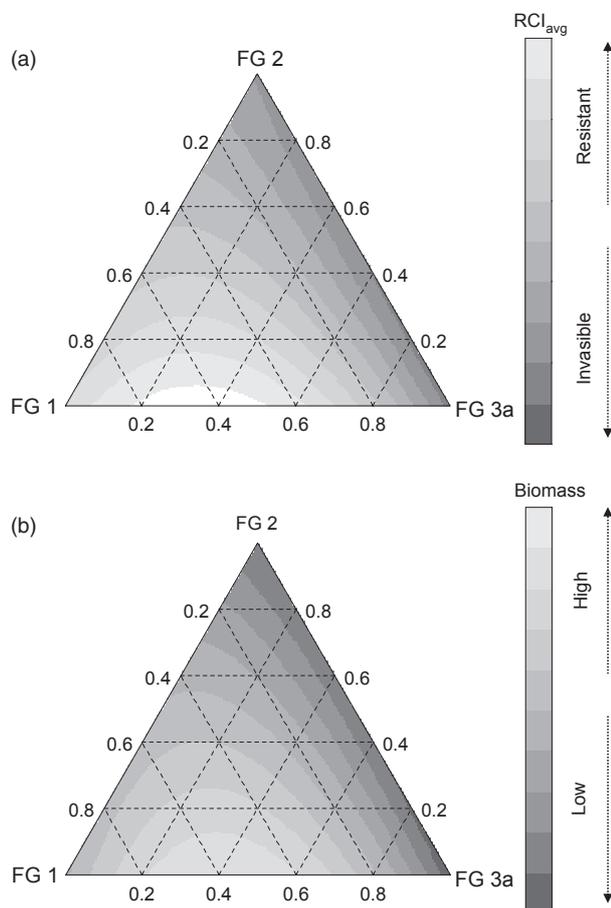


Fig. 5. Biodiversity–interaction model prediction about the effect of functional group composition on (a) RCI_{avg} : relative competition index of wetland plant(s) as indicator of biotic resistance and (b) above-ground biomass (g) of wetland plant(s) per pot, estimated from the first experiment data in 2009. Each corner of the ternary plot represents monoculture of each functional group, whereas inner area of the plot represents mixture of functional groups. For details about the model equation, see eqn 7.

species identity effect within FG 3b was due to *Leersia oryzoides*, the most resistant species in this group.

MIXTURE TREATMENTS

Mixtures of wetland plants were more resistant than monocultures, and such a diversity effect on biotic resistance came from complementarity effect and from positive interactions between FG 1 and FG 3a in the first experiment (Figs 4 and 5). RCI_{avg} was significantly greater in mixture than in monocultures ($F_{1,53} = 4.70$; $P < 0.034$; Fig. 4a). In partitioning diversity effect on RCI_{avg} in mixtures, complementarity effect rather than selection effect contributes most to the positive net diversity effect (Fig. 4b). Above-ground biomass of resident species was also significantly greater in mixture treatments than in monoculture treatments (log-transformed; $F_{1,53} = 22.72$; $P < 0.001$), and partitioning diversity effect showed similar pattern (Appendix S10).

Comparison between a pair of diversity–interaction models fitted to the first experimental data revealed distinctive species

interaction patterns by functional group contributing to biotic resistance. The functional group identity effect terms fitted as well as species identity effect terms (Model 1 vs. 2; F test; $P = 0.157$). There was strong evidence of an average interaction term effect (diversity effect) (Model 2 vs. 3; F test; $P = 0.001$). The species interaction by functional group (species interaction within and between functional group) terms fitted much better than single average interaction term (Model 3 vs. 4, F test; $P < 0.001$). However, the separate pairwise species interaction terms fitted no better than the species interaction by functional group term (Model 4 vs. 5; F test; $P = 0.425$). There was no evidence of significant species interaction within each functional group (Model 4 vs. 6, F test; $P = 0.269$). Thus, the last model (Model 6; functional group identity effect and species interaction between functional group) was chosen for the final model prediction because it fitted as well as complex models with separate pairwise species interactions.

Figure 5a shows Model 6 prediction about the effect of functional group composition in seed mixtures on biotic resistance to invasion by *P. australis*. Figure 4b shows the same model prediction when it was fitted to above-ground biomass instead of RCI_{avg} of wetland plants. In either case, we found a positive interaction between FG 1 and FG 3a in their contribution to biotic resistance. The highest RCI_{avg} and above-ground biomass were estimated when FG 1 and FG 3a were mixed in a ratio of 2 to 1, approximately. For further detail on model results and significant terms and their estimates, see Appendix S5.

Discussion

Functional group identity is a significant predictor of biotic resistance. The most consistent finding in our experiments is the strong contribution of annual plants (FG 1), even when different functional group combinations are tested. Combining functional groups in mixtures leads to a complementarity effect, resulting in higher biotic resistance than in monocultures. These findings suggest that processes such as niche pre-emption (selection effect of FG 1) and niche partitioning (complementarity–diversity effect by functional group interaction) contribute to limit seedling establishment of *P. australis*.

FUNCTIONAL GROUP AND BIOTIC RESISTANCE

Other studies relating biotic resistance to functional groups based on the various plant traits such as life longevity, growth form, root structure, plant height, or photosynthetic pathway (Tilman 1997; Prieur-Richard *et al.* 2000; Symstad 2000; Dukes 2002; Bakker & Wilson 2004; Von Holle & Simberloff 2004; Pokorny *et al.* 2005; Lulow 2006; Mwangi *et al.* 2007; Sheley & James 2010) have found a significant effect of functional group on biotic resistance, with some exceptions (Von Holle & Simberloff 2004). Which functional group resists invasion better is not always consistent among studies though. In some cases, the functional group of resident species most similar to the invader offers the most resistance (Dukes 2002; Bakker & Wilson 2004; Pokorny *et al.*

2005; Mwangi *et al.* 2007), suggesting limiting similarity, whereas in other cases, different functional groups resist better (Lulow 2006; Sheley & James 2010), suggesting fitness inequality as one of the key resistance mechanism. MacDougall, Gilbert & Levine (2009) propose that invasion success may depend on both fitness advantage and niche difference from resident species. Recently, Kunstler *et al.* (2012) showed that competitive ability related to trait hierarchy rather than functional trait similarity (Funk *et al.* 2008) drives competitive interaction in community assembly. Contradictory patterns in community assembly, including for biological invasion, highlight the need for repeated measurements with a functional approach as we did.

It is unlikely that one functional group will dominate in all contexts and at all stages of community assembly, but given the conditions of our experiments, early- and fast-growing species (FG 1) were definitely the most resistant to invasion of *P. australis*, at least in the first critical year of community assembly. The fact that some annual plants grew faster than *P. australis* in the first experiment suggests priority effect by pre-empting niche to inhibit slower growing species in community assembly (Young 2001; Fukami *et al.* 2005; Mwangi *et al.* 2007). We found that *P. australis* is also capable of early and fast growth unlike many other perennial plants, and this could provide it with some competitive advantages over other groups such as FG 2 and FG 3a. The ability to take advantage of a temporal niche early in the growing season also resulted in increased above-ground biomass and height of resident species, which are positively correlated with biotic resistance (Appendix S7). Early emergence increases components of plant fitness such as seedling growth in a controlled experiment (Verdú & Traveset 2005). Biomass of resident communities has been documented as one of the best indicators for competitive ability (Gaudet & Keddy 1988) and level of biotic resistance (Lulow 2006). High biomass of resident species could imply less resource availability for invaders, which leads to strong biotic resistance (Davis, Grime & Thompson 2000). On the other hand, legumes have been shown to facilitate invasion due to their ability to fix nitrogen (Mwangi *et al.* 2007; Frankow-Lindberg 2012). Most wetland plants that we tested, including *P. australis*, do not have nitrogen fixation ability in wetlands (Ehrenfeld 2003; TRY traits data base).

Our results provide only partial evidence to support the role of limiting similarity in biotic resistance. Although the functional group which is most similar to *P. australis* (FG 3b; tall perennial with rhizome) resists to invasion substantially, the order of functional group in level of biotic resistance (FG 1 \geq FG 3b \geq FG 2 > FG 3a; Figs 2 and 3) in the monoculture experiments was not consistent with the one expected from functional similarity with *P. australis* (FG 3b \geq FG 3a > FG 2 > FG 1; Fig. 1; Appendix S6). Interpretation from such direct comparison may be limited because functional traits of species are usually measured from mature plants and the importance of some traits will change with time for a species (Cornelissen 2003; Kattge *et al.* 2011). The effect of

functional similarity therefore may increase with time as the community matures.

Our goal was to investigate the window of invasion opportunities during community reassembly after disturbances, a condition that often favours invasive plants through seedling establishment, but the second year of the monoculture experiments (in 2010) also provides some insights into how the biotic resistance of functional group may change with time. The annuals still offered the best resistance but that effect had begun to decrease. Considering general species turnover patterns between colonizers and competitors in plant succession (Tilman 1990), perennial plants may contribute to biotic resistance as succession proceeds (Lockwood *et al.* 1997), but their effect at the time-scale of our experiments was mostly through interactions. Longer-term studies to test the effect of mixtures of functional groups on biotic resistance over time in field conditions are required to verify this assumption.

DIVERSITY EFFECT ON BIOTIC RESISTANCE

Species mixtures are more resistant than monocultures, and this result is consistent with previous community-scale experimental studies on multiple invaders (Tilman 1997; Knops *et al.* 1999; Naeem *et al.* 2000; Hector *et al.* 2001; Dukes 2002; Kennedy *et al.* 2002; Frankow-Lindberg *et al.* 2009) and specifically against *P. australis* (Peter & Burdick 2010). Field observational studies reported similar patterns at community scale (Levine 2000; Brown & Peet 2003), but opposite patterns at larger scale (Stohlgren *et al.* 1999; Levine 2000; Brown & Peet 2003; Stohlgren, Barnett & Kartesz 2003). Spatially covarying environmental factors such as resource availability or disturbance regime can affect both diversity and invasibility (Levine & D'Antonio 1999; Byers & Noonburg 2003; Davies *et al.* 2007a). Furthermore, different ecological processes such as dispersal and community recruitment can predominate at large scale (Tilman 1997; Pauchard & Shea 2006; Fridley *et al.* 2007).

More importantly, the complementarity–diversity effect in our study is best explained by positive species interactions between functional groups, implying niche partitioning among species mixtures. When selection effect is positive and strong, dominant species identity is expected to matter to invasion resistance (Emery & Gross 2007). In such case, fitness advantage of a species rather than niche complementarity among species determines biotic resistance of mixtures. The main selection effect observed in our study was a positive selection effect with FG 1 plants such as *Lolium multiflorum* and *Bidens* sp. and negative selection effect in mixture with FG 3a plants such as *Eupatorium* sp. Interestingly, our study also shows that selection effect varies with functional group composition in mixtures. In other experiments, there was a strong selection effect of *Spartina alterniflora* on *P. australis* (Peter & Burdick 2010) or *Lolium perenne* on multiple invaders (Frankow-Lindberg 2012). Both selection and complementary effect contributed to biotic resistance (Fargione & Tilman 2005), and the relative contribution of selection and comple-

mentarity effect may vary with the species and functional groups involved.

Our results in diversity–interaction models suggest species interactions between functional groups contribute to complementarity–diversity effect by increasing biomass of resident communities (Fig. 5). This result provides indirect evidence for resource partitioning between functional groups in our system. Functionally diverse resident communities can use resource more completely than simple community (Prieur-Richard *et al.* 2000; Pokorny *et al.* 2005; Davies *et al.* 2007b; Rinella, Pokorny & Rekaya 2007). Other investigations of resource uses pattern such as soil nitrogen uptake have provided more direct evidence for resource partitioning of diverse community in relation to biotic resistance (Tilman 1997; Booth, Caldwell & Stark 2003). Furthermore, functionally diverse communities with their complex canopy allow less light penetration through the canopy (Lindig-Cisneros & Zedler 2002; Frankow-Lindberg 2012).

IMPLICATION FOR MANAGEMENT

In field situations, invasion success will be determined by the interplay between environmental conditions, propagule pressure, and biotic resistance (D'Antonio 1993; Dethier & Hacker 2005; Perelman *et al.* 2007; Catford, Jansson & Nilsson 2009). Wetlands being nutrient sinks, excess nutrient supply coupled with disturbance to the vegetation cover will tend to increase vulnerability to invasion (Burke & Grime 1996; Huston 2004; Lake & Leishman 2004), especially since seedlings of introduced *P. australis* establish on bare fertile soil. Altered flood regimes, especially prolonged drawdown conditions, which may become common with climate change and increasing demand on water, will further facilitate seedling establishment of *P. australis* (Mauchamp, Blanch & Grillas 2001). Such conditions would provide the optimal window of opportunity for *P. australis*, possibly serving as invasion foci. This highlights the need, where applicable, to minimize the damage to the matrix vegetation cover and/or to facilitate the rapid establishment of a competitive cover if the goal is to restore disturbed habitats. In these cases, functional group identity and diversity of resident or restored plant communities will be the good indicators of potential biotic resistance to seed-mediated invasion by introduced *P. australis*. As for propagule pressure, most field situations are expected to show much lower seed pressure than the one tested in our experiment, but even then, complete competitive exclusion may not be reached. Follow-up monitoring and selective control of *P. australis* establishment could be necessary.

Our study indicates that guiding ecological principles to understand and/or manage, if desirable, biological invasion could emerge from advances in community theory and the use of a functional framework. Targeting widely distributed invasive plants in different contexts and scaling up to field situations will facilitate generalization. We are currently conducting such a large-scale field experiment to test whether the ecological principles uncovered in this study apply to a more complex, realistic setting.

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Supporting Information

Additional Supporting Information may be found in the online version of this article:

Appendix S1. Functional trait characteristics of each functional group.

Appendix S2. Overview of experiment.

Appendix S3. Partitioning diversity effect equation.

Appendix S4. Changes in plant cover of wetland plants and *P. australis* from 2009 to 2010.

Appendix S5. Summary of the results of the diversity interaction models.

Appendix S6. Average similarity coefficient of wetland plants to *P. australis* in each functional group.

Appendix S7. Relationship between plant traits and biotic resistance (RCI_{avg}) in the first experiment.

Appendix S8. Correlations between different response variables in the experiments.

Appendix S9. Analysing biomass of *P. australis* in monoculture experiments.

Appendix S10. Partitioning diversity effect based on the biomass of resident species in mixture experiment.